Economics in Nature

Social Dilemmas, Mate Choice and Biological Markets

Edited by Ronald Noë,
Jan A.R.A.M. van Hooff
& Peter Hammerstein

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Since the development of game theory, the analysis of animal behaviour using the theories of economics has become a growing field of biological research in which models of games and markets play an important role. Studies of sexual selection, interspecific mutualism and intraspecific cooperation show that individuals exchange commodities to their mutual benefit; the exchange values of commodities are a source of conflict, and behavioural mechanisms such as partner choice and contest between competitors determine the composition of trading pairs or groups. These 'biological markets' can be examined to gain a better understanding of the underlying principles of evolutionary ecology. In this volume scientists from different disciplines combine insights from economics, evolutionary biology and the social sciences to look at comparative aspects of economic behaviour in humans and other animals. Aimed primarily at evolutionary biologists and anthropologists, it will also appeal to psychologists and economists interested in an evolutionary approach.

RONALD NOË is Professor of Ethology at the Université Louis-Pasteur at Strasbourg, France and holds a post at the Max-Planck-Institut, Seewiesen, Germany. His main research interest is the behavioural ecology of primates and in 1991 he founded the Taï Monkey Project in the Taï National Park, Ivory Coast. He has been editor of the journal *Ethology* since 1997.

JAN A. R. A. M. VAN HOOFF is Professor of Behavioural Biology at the University of Utrecht. His research focuses on the social behaviour and organisation of primates and eusocial insects. He is a member of the Royal Netherlands Academy of Arts and Sciences and the Scientific Council of the Jean-Marie Delwart Foundation, Belgium.

PETER HAMMERSTEIN is Professor in Organismic Evolution at the Theoretical Biology Laboratory of Humboldt University, Berlin. Besides being a biologist he has a background in game theory and mathematical economics. His main research interest is in the evolutionary analysis of conflict and cooperation at the level of genes and organisms.

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Contributors

MIKE A. BALL
Department of Mathematical Sciences, University of Liverpool,
Liverpool L69 3BX, UK

LOUISE BARRETT
School of Biological Sciences, University of Liverpool, Liverpool L69
3BX, UK

REDOUAN BSHARY
Max-Planck-Institut für Verhaltensphysiologie, Seewiesen, Postfach
1564, 82305 Starnberg, Germany

ROBIN I. M. DUNBAR
ESRC Research Centre in Economic Learning and Social Evolution,
School of Biological Sciences, Nicholson Building, University of
Liverpool, Liverpool L69 3BX, UK

PETER HAMMERSTEIN
Innovationskolleg Theoretische Biologie, Humboldt-Universität zu
Berlin, Invalidenstr. 43, D-10115 Berlin, Germany

S. PETER HENZI
Behavioural Ecology Research Group, University of Natal, Durban 4041,
South Africa

JASON D. HOEKSEMA
Department of Environmental Sciences and Policy, 1 Shields Avenue,
University of California at Davis, Davis, CA 95616, USA

JAN A. R. A. M. VAN HOOFF
Ethologie en Socio-oecologie Groep, Universiteit Utrecht, Pb. 80.086, 3508 TB, Utrecht, The Netherlands

YOH IWASA
Department of Biology, Faculty of Science, Kyushu University, Fukuoka 812-8581, Japan

REBECCA J. LEWIS
Department of Biological Anthropology and Anatomy, Box 90383, Duke University, Durham, NC 27708-0383, USA

RONALD NOË
Lab. Ethologie des Primates, CEPE–CNRS 2130, 7 rue de l'Université, F-67000 Strasbourg, France and Max-Planck-Institut für Verhaltensphysiologie, Seewiesen, Starnberg, Germany

CHARLES L. NUNN
Department of Biology, 221 Gilmer Hall, University of Virginia, Charlottesville, VA 22903-2477, USA

ELINOR OSTROM
Center for the Study of Institutions, Population and Environmental Change, Indiana University, 513 North Park Bloomington, IN 47408-3895, USA

GEOFFREY A. PARKER
Population and Evolutionary Biology Research Group, School of Biological Sciences, University of Liverpool, Liverpool L69 3GS, UK

BOGUSŁAW PAWŁOWSKI
Department of Anthropology, University of Wroclaw, ul. Kuznicza 35, 50-138 Wroclaw, Poland

ANDREW POMIANKOWSKI
Department of Biology, University College London, 4 Stephenson Way, London NW1 2HE, UK

MARK W. SCHWARTZ
Department of Environmental Science and Policy, 1 Shields Avenue, University of California at Davis, Davis, CA 95616, USA

Preface

The constraints of life force every organism to behave economically. The study of economic behaviour is therefore not limited to 'economics'. Scientific disciplines that concentrate on other aspects of human behaviour, such as psychology, sociology and anthropology, have to pay close attention to the economic decisions that drive human behaviour. The same is true for biological disciplines in which strategic options of individual organisms play a central role, notably ethology, behavioural ecology and evolutionary ecology. In order to determine in how far a behavioural strategy is 'economical', it has to be compared to some ideal norm: the strategy that would yield maximum payoff. In economics this norm is set by the strategy of a hypothetical 'super-rational' individual. For most of us the term 'super-rational' has a connotation of 'very intelligent'; a strategy achieved by the use of superior cognitive capacities. Evolutionary biologists have realised, however, that even the dimmest of organisms, such as fungi and flatworms, often use 'super-rational strategies', because a process of selection running over a vast number of generations can shape the behaviour of every species to near perfection, as long as the circumstances in which it lives change slow enough compared to the rate of evolution. There lies the common ground between biology and economics: while Adam Smith's human producers and consumers are driven by the 'invisible hand' of self-interest, Charles Darwin's living organisms are driven by the selection for maximising individual fitness.

The present volume gives a number of examples of the common grounds on which economics, biology and the social sciences meet. In his introductory chapter Peter Hammerstein shows that there are striking parallels between the use of game theory in economics and evolutionary biology, although the fields were originally developed largely independently.

In Part I we see how humans as well as non-humans can be caught in ‘social dilemma’s’, situations in which the individual has to choose between a certain, but small profit extracted from a common pool, and an uncertain, but eventually larger profit reaped after an initial investment in that common pool.

In the introduction of economics textbooks one can often find a statement like: ‘Markets consist of producers and consumers of goods or services.’ The chapters in Part II show that such ‘markets’ can be found everywhere in nature. Examples range from the exchange of services among members of primate groups to interactions between different species of fish and trade between fungi and plants.

The idea to apply the principles deduced by economists for human markets to cooperative and mutualistic interactions in biology is relatively recent, but the idea of a ‘mating market’ has been around ever since Darwin identified sexual selection as a powerful motor of evolution.

Part III concentrates on the reproductive behaviour of humans and other animals. The title of the section, ‘mating markets’, seems warranted, because reproductive decisions are often governed by economic principles.

Acknowledgments

The idea to publish the present volume was born after an international seminar 'Economic aspects of behaviour in animals and man', which was held at Louvain-la-Neuve, Belgium, 18–20 October 1996. The seminar was sponsored by the Jean-Marie Delwart Foundation. A number of chapters of this book have seen the light as a contribution to that symposium. Our special thanks go, therefore, to the founder of the foundation, Mr Jean-Marie Delwart, and to its president, Professor Georges Thinès, for the opportunity they gave us to organise the seminar. The meeting could not have been such an inspiring event without the charm and organisational talent of Mrs Raphaëlle Holender. We are also very grateful for the guidance and support we received from our editor at Cambridge University Press, Tracey Sanderson.

PETER HAMMERSTEIN

1

Games and markets: economic behaviour in humans and other animals

1.1 Introduction

Economists think they know how humans ought to behave if only they were smart enough. Biologists have some knowledge of how animals actually do behave. It does not seem a feasible question to ask how animals ought to behave. Yet, there is a conceptual link between normative economic theory and its empirical biological counterpart. Darwinian evolution often creates animal traits that look to an observer as if the animal did care about the economist's advice. Therefore, economic analysis of animal behaviour has become a flourishing field of biological research in which games and markets play an important role. This chapter discusses fundamental concepts in human and animal economics. They are illustrated with examples from both disciplines. Furthermore, it is shown that the facts often do not meet theoretical expectations. Some hints are given as to why this may be so. Theory development in animal and human economics is far from being completed.

1.2 Evolutionary adaptation and bounded rationality: are animals better economists than humans?

Classical economic theory based most of its thoughts on the idea that decision makers are rational in the sense of maximising subjective expected utility. Savage (1954) axiomatised this Bayesian approach to decision making and Harsanyi & Selten (1988) explored it further in the game theoretic context of strategic interaction. However, the more the economic notion of rationality had been made precise, the less it seemed adequately to reflect properties of the real world. Rational decision makers are assumed to possess unlimited cognitive and computational power and to solve correctly every mathematical problem in zero time at no cost.

Furthermore, they are supposed to have clear, invariant preferences that can be described by a utility function. In contrast, we know from research in psychology and experimental economics that (a) human preferences are far from being stable and (b) most decisions are made without the help of sophisticated mathematics. If mathematics is used at all, it is often used incorrectly. In particular, humans in their everyday life seem to avoid dealing with probabilities and are poor statisticians from a Bayesian point of view (Kahneman *et al.* 1982).

To illustrate this, let us consider a phenomenon called 'the winner's curse' (Thaler 1988). This phenomenon was found to occur in real-life auctions of oil-fields (Capen *et al.* 1971; Levinson 1987). Businessmen who overestimated the value of an oil field most were the ones who received it in the end. As a result, many of them ended up with an unprofitable deal – the winner's curse. It is possible to design a simple experiment in which a similar phenomenon occurs even if only one bidder is involved. The experimental scenario is as follows. A dealer has a car that he wants to sell. He knows x which denotes what the car is worth to him. The car is worth 50% more to a potential buyer. However, the buyer does not know x. He only knows that x is uniformly distributed between 0 and 1. At the beginning of the experiment, a random number generator is used to determine x. The buyer has one bid y and the dealer, played by a computer, will sell if y is greater than x. Therefore, if $x<y$, the object will be traded and the buyer's net payoff is $1.5x-y$, otherwise the payoff is zero.

How much should a buyer offer in this experimental setting? When faced with the decision problem in a single-shot game without any possibility for learning, bids near 0.5 are frequently observed (Ball *et al.* 1991). At first sight this may look like a reasonable bidding decision. Bidding 0.5 seems to imply a positive expected payoff of 0.25 because the average value of the object to the buyer is 0.75. This argument, however, contains a fatal error in that it overlooks the *conditional expectation* that really matters in the scenario under discussion. One has to take into account that the trade only takes place if $x<y$. The expected value of *x given that* $x<y$ is $0.5y$ (as opposed to 0.5). Therefore, in an actual trade, the expected value of the object to the buyer is only as small as $0.75y$. His expected net payoff then is $-0.25y$. On average the buyer, therefore, makes losses if he comes up with any positive bid. This is the winner's curse and the only rational way of playing the game is to bid zero.

Why do so many humans fail to avoid the winner's curse? We have just seen that in order to foresee the winner's curse, a decision maker would have to calculate his payoff as a conditional expectation. If not trained by mathematicians, humans do not seem to have the cognitive skills to correctly deal with conditional expectations in this and many other experiments. Even if they have a chance to learn their bidding strategy in the scenario described above, they typically do not arrive at the rational solution. This was shown by Selten (1996) in a version of the bidding experiment where subjects were exposed a hundred times to the buyer's situation. Selten also offers an explanation of the phenomenon. In order to see why learning is *not* a powerful mechanism to overcome the winner's curse, consider a person who shifts the bidding tendency according to last experience. Let this person start with the bid $y = 0.5$. With probability 0.5 the person will not get the object and may simply classify the situation as 'I bid too low'. With the same probability he will get the object and reach the opposite conclusion 'I bid too high'. If learning consists of a simple shift of bidding tendencies according to this classification of situations, it will probably not take the learning individual anywhere near the rational solution. This is an example of what Selten (1996) calls 'learning direction theory' and it may to some extent explain the facts.

To summarise the experimental results, both learning and higher cognitive abilities fail to generate economic rationality in the winner's curse example. Let us now conduct the following thought experiment. Suppose that animals of a given species have to act generation after generation in a situation resembling the buyer's situation of the winner's curse problem. Suppose that the animal's payoff is an increment (or decrement in case of a negative sign) of its expected reproductive success (fitness). Assume further that the bid is coded for by genes and genetically transmitted to the next generation. New bids only arise by rare mutations and the animals do not even try to analyse the bidding situation by any cognitive means. They act instead as if they were robots controlled by an inherited computer program. How is the program going to evolve? In the long run, the evolutionary process of mutation and selection will take our genetically coded bid to zero. This means that the evolutionary process itself (not the animal!) generates a behavioural feature that would look to an observer *as if* it had been brought about by rational decision making. We often find such quasi-rationality in models of Darwinian adaptation. The bidding example is particularly interesting because it shows that evolution can 'do better' than both human learning and time-limited cognition. However, in principle it is possible for learning to also outcompete evolution. The reason is that evolution has no anticipatory power, whereas learning combined with some cognitive skills can include elements of anticipation.

1.3 Games and Nash equilibria in economics and biology

Classical game theory studies two or more individuals who interact and whose payoffs depend on how everybody in the game behaves. In such an interactive situation, the rational decision maker has to solve a particularly intricate problem, namely what to expect about other players? Are they also rational and if not what are they like? Game theory in economics has eliminated this problem by ignoring it in an elegant way. It is assumed that all players know that all know that all are rational. Needless to say that this assumption of an entirely rational world made it possible for generations of game theorists to earn their living with writing papers, but it did not bring game theory any closer to reality. The assumption of omnipresent rationality implies that the players in a game will play a so-called Nash equilibrium. To see how this is defined, consider an n-person game. For every player i choose one of his strategies and call it p_i. Looking at all players simultaneously one then obtains the strategy combination $p = (p_1, p_2, \ldots, p_i, \ldots, p_n)$. This combination p is called a Nash equilibrium if it has the following property for every player i: Player i gets maximum expected payoff by playing p_i (compared to his other strategies) given that everybody else plays his strategy of p. In other words, in a Nash equilibrium every player's strategy is a best response to the joint strategic action of all other players. If a player assumes the others to play according to a Nash equilibrium, then he has no incentive to deviate from this equilibrium himself. In this sense a Nash equilibrium is self-enforcing. However, the problem is that (a) playing a strategy of a Nash equilibrium can turn into a payoff disaster if at least one other player is not rational, and (b) there often exist several Nash equilibria.

Let us look at the example of a coordination game in which cooperative exploitation of a resource is possible but may not be achieved. Suppose that 10 persons are asked independently, in separate rooms without seeing one another, to put money in an envelope. The experimenter collects the envelopes and empties their contents into a large box. He counts the total sum collected in the box and checks whether it amounts to at least 100 monetary units. If not, he keeps the money for himself and all subjects have lost what they put into the envelope. However, if the total in the box is 100 or more, the experimenter adds 50 units to this amount and distributes the enriched contents of the box equally among the subjects, no matter what an individual's original contribution had been. Searching for symmetric Nash equilibria (where everybody gives the same amount) we find two alternative solutions: one in which everybody puts 10 units into the envelope and one in which all envelopes are empty. In the first Nash equilibrium, the subjects cooperate and exploit the experimenter. Everybody has a net gain of 5 units. In the second Nash equilibrium, no cooperation takes place and the 'resource' (i.e. the experimenter) remains unexploited. How do these solutions compare? The first one is risky in the following sense: if only one player gives a little less than 10, everybody else has a net loss of 10 units

The Nash equilibrium was originally created as a tool for analysing human behaviour. However, in theoretical evolutionary biology Nash equilibria have an even better foundation than in classical economics. At first sight this appears like a silly statement because animals are not supposed to be rational, and it would be absurd to assume that all animals know that all animals know that all of them are rational. Yet, if animals play a game generation after generation and if strategies are inherited, then natural selection will often drive these strategies towards a Nash equilibrium. Suppose that after evolving for quite some time in the same environment, a population has reached a situation in which the current strategy is maintained by the forces of natural selection. This means that no mutant strategy should be able to invade the population if it initially occurs at a low frequency. John Maynard Smith (1982) called a strategy with this uninvasibility property an evolutionarily stable strategy (ESS). If one studies ESSs in selection models with asexual reproduction, exact inheritance and encounter rates of strategies proportional to their population frequencies, then it can be shown very easily that an ESS will necessarily be a Nash equilibrium (e.g. Hammerstein & Selten 1994).

To some extent, John Nash himself had foreshadowed this result in an unpublished part of his Ph. D. thesis where he briefly talks about the 'mass action interpretation' of game-theoretic equilibrium (Nash 1950). We only know this because, decades after Nash got his Ph. D., the Nobel award made people curious to have a look at his thesis. Historically speaking, the field of evolutionary game theory was initiated by Maynard Smith & Price (1973). Much later, economists developed their own evolutionary game theory (e.g. Weibull 1995; Samuelson 1997). Hofbauer & Sigmund (1998) review evolutionary game theory from a dynamical systems point of view. Hammerstein (1996) discusses the links between population genetics and evolutionary game theory. He compares the phenotypic trajectory of an evolving population with the course of a streetcar. There are temporary stops of the streetcar in which the logic of phenotypic game theory is blurred by genetic constraints. These stops do not correspond to a Nash equilibrium. However, evolution is capable of removing genetic constraints. After successive elimination of such constraints, the streetcar will often reach a final stop that can be characterised (in the sense of a necessary condition) by a Nash equilibrium.

Consider now a fictitious biological example of an evolutionary game that resembles a little the above coordination game. Animals usually do not put money into envelopes, but imagine instead a situation where 10 genetically unrelated predators would be able to kill a large prey item by jointly injecting a large amount of toxin. Suppose that the minimum lethal dose of the toxin is 100 mg and that the energy needed to produce 1 mg of the toxin is 1 joule. Assume further that by communal consumption of the prey each predator would have an energy gain of 15 joules. Let an individual's fitness depend linearly on the difference between energy gain from prey consumption and energy loss from toxin injection (the energetic cost of producing the toxin).

The biological coordination game has two symmetric Nash equilibria. In the cooperative equilibrium everybody injects 10 mg and has a net return of 5 joules. In the non-cooperative equilibrium everybody injects a zero amount of toxin. We can easily convince ourselves that both the 10 mg strategy and the 0 mg strategy are evolutionarily stable. In a population playing the cooperative strategy, a mutant injecting less or more than 10 mg would always have less than the return of 5 joules. In contrast, the average return of cooperators would be 5 joules, at least in an infinitely large population. We conclude that it is an ESS to inject 10 mg. Similarly we can show that zero mg is also an ESS.

What do we learn about animal cooperation in this fictitious biological context? On the one hand, a population of cooperators would be maintained by natural selection. On the other hand, a population of non-cooperators would also be maintained by selection. Therefore, it is difficult to get an evolutionary transition from non-cooperation to cooperation and we may never see the latter evolve. This transition problem occurs in many other biological scenarios. For example, in the context of repeated interactions (see section 5 of this chapter), 'reciprocal altruism' or the strategy 'Tit-for-Tat' cannot easily evolve because of the transition problem.

In the above example of predators injecting a toxin, cooperation is biologically plausible if one assumes the existence of some peculiar historical path that led the population of predators towards the cooperative state with its evolutionary maintenance property. There are other games where cooperation, though highly beneficial to all cooperators, would not be maintained. Needless to say that the Prisoner's Dilemma has this property (Luce & Raiffa 1957). Most readers probably are saturated with discussions of this game which has been 'on the charts' for too long. So, let us be quick. In the Prisoner's Dilemma, there are two strategies, namely 'cooperate' and 'defect'. Both players would be very successful if they both defected. However, due to a payoff incentive for unilaterally exploiting a cooperator, defection is a strictly dominant strategy. The term dominating strategy means that by playing this strategy one always receives a higher payoff than by playing strategic alternatives, regardless of how the other player behaves. Obviously, the only Nash equilibrium, and the only ESS, is to defect.

In experiments of the Prisoner's Dilemma, humans often play the cooperative strategy instead of the Nash equilibrium. After all, our intuition is adapted to a highly social context where defection might have negative consequences outside the narrow setting of the game. However, the term 'tragedy of the commons' would not exist if humans always cooperated in games with the flavour of a Prisoner's Dilemma. Ostrom (1990, this volume) analysed how human communities found ways to resolve the tragedy of the commons. She describes various human policing strategies by which defectors are punished. However, there is a twofold tragedy which unfolds (Hammerstein 1996). Individuals often have an incentive to save the effort that would go into policing. Splitting the cost of policing is yet another tragedy of the commons.

1.4 Games in which players react to what has been done before

In most real-life games, the players act one after another. Simple game theoretical models in normal form – with conflict being represented by a payoff matrix – do not explicitly depict sequences of actions. In contrast, the theory of games in extensive form – where conflict is represented by a decision tree – was especially designed to give an adequate mathematical picture of the course of actions in a game. This makes it possible to analyse more deeply how players should react to one another.

One of the simplest games in which at least one player can react to what has been done before is the ultimatum game. Suppose that the Nobel committee has introduced a new Nobel prize in biology but cannot really afford to pay any substantial amount of money to the winners. This year, the prize goes to evolutionary biology. Let us assume there to be two fictitious winners who share the prize, say Richard and Steven. In order to deal with the shortage of money, Stockholm invents the following rule. Richard will be asked about the percentage he claims of the total award. After he has made up his mind, his decision will be communicated to Steven who may or may not accept the deal. If he rejects, both winners will only get the Nobel dinner and no cash. The total award is $1 million.

What are the Nash equilibria? One of them can be described as follows. Steven rejects unless he gets at least 50%. Richard offers 50%. Both are playing a best response to each other's strategies. Why is this so? As long as both play these strategies, Richard gets half a million. If he goes for more than 50%, his reward will be zero. If he goes for less than 50%, his reward will be less than half a million. So, we clearly understand that Richard's strategy is a best response to Steven's strategy. Conversely, if Richard asks for 50%, Steven cannot improve his payoff by shifting the acceptance threshold. If he raises this threshold, he will get nothing, if he lowers it, he will get no more than half a million. In other words, Steven is playing a best response to Richard's strategy. Now, the fact that both strategies are best responses to each other means that we are talking about a Nash equilibrium.

In real life, the equal-split solution would often occur in an ultimatum game. If the total is something like a dollar, it would be very risky to ask for more than 60%. However, what about the concept of economic rationality? The Nash equilibrium in which Richard claims 50% looks, on the one hand, quite reasonable because both players optimise against each other. However, Steven is not considered to be entirely rational if he is assumed to reject any split that treats him in an unfair way. Suppose Richard demands 80% for himself. By rejecting this, Steven is 'trashing' $200 000 that he otherwise could have brought back home. Would his wife say: 'how rational you are in playing games'? Certainly not. This is my caricature of a discovery by Selten for which he actually got the Nobel prize. He maintained that if players are considered to be rational then they have to be rational in *all situations* of the game, not only before the game starts. Selten (1975) coined the term *subgame perfection* in order to make this idea precise. He looked at substructures of a game that would also qualify as a game. These are called subgames. Obviously, strategies of the original game specify what a player would do in a subgame. Furthermore, a Nash equilibrium specifies a combination of subgame strategies so that one can ask the following question about the equilibrium's consistency with rationality assumptions: will the Nash equilibrium under consideration induce Nash equilibria for all subgames? If the answer is yes, the players remain rational while playing the game. In this case, the Nash equilibrium is called subgame perfect. Many Nash equilibria fail to have this property. For illustration, let us reconsider the fair Nash equilibrium of the 'Richard and Steven' game which is to 'claim 50% in Richard's role and accept a share of 50% or more in Steven's role'. We have already looked at a subgame with only one player, namely Steven, being informed that Richard demands 80% for himself. In the fair equilibrium, Steven rejects the remaining 20% and both players end up with zero payoff. Subgame perfection, however, requires for Steven to make an optimal decision *in this situation*. Obviously he then must accept the unfair deal.

Where does subgame perfection matter in biology? Consider the parental investment game between the sexes. A male and a female have copulated and the offspring needs some care. Who will provide the care? Suppose we are studying an animal example in which both male and female would have an advantage from leaving their partner alone with the offspring. An assumption of this kind can be justified if the time and energy gained by mate desertion has a positive effect on the deserting individual's future reproductive success. The structure of the mate desertion game can be similar to the 'Stockholm' ultimatum game. We begin to look at the interaction after a copulation has taken place. The male is in a role similar to Richard and can either decide to be unfair, by running away, or to be fair and stay in order to help. If he runs away, the female finds herself in a situation similar to that of Steven. She is associated with the fertilised eggs and may either 'trash' them or accept the unfair deal and care for them. In a subgame perfect equilibrium, depending on the parameters, she may have to accept the unfair deal very much like Steven has to accept it in the Stockholm ultimatum game. If subgame perfection really mattered in evolutionary biology, it would help us to understand why in many animal species with uniparental care it is the female and not the male who looks after the offspring.

Does subgame perfection indeed matter? Let us play devil's advocate and discuss the particular Nash equilibrium of the mate desertion game which is not subgame perfect, and in which the female is prepared to abandon the fertilised eggs if left alone by her mate. Her mate stays and cares. Is this an ESS? Note that, if the sexes behave like this, the female is never left alone with the offspring. However, in reality there are external causes of why females might be left alone with the offspring. Let us make the realistic assumption that occasionally a male is killed by a predator, or lightning, or another environmental effect. In such a case, the female will be left behind 'holding the babies'. If this happens frequently enough, compensatory care will evolve. This means, however, that she cares when he is gone. Deliberate male mate desertion will then evolve. In other words, an evolutionary transition takes place towards the subgame perfect equilibrium, imposing the burden of parental care upon the female. We conclude that the concept of subgame perfection has a strong biological appeal in the context of parental investment between the sexes.

1.5 Repeated games

Since the early days of game theory (Luce & Raiffa 1957) it is well known that in a repeated game more cooperation is typically possible than in the single-shot case where the game is played only once. A repeated game, or supergame, consists of a series of interactions between the same two players. In each interaction they play the *same* game, which is the building block of the supergame. The intuition behind cooperation in repeated games is simple. A player can act as a conditional cooperator, relating his behaviour to how 'well behaved' the other player was in previous rounds of the same game. Unlike popular belief in biology, this insight has little to do with the Prisoner's Dilemma because it holds, roughly speaking, for any game used as the building block. Mathematical results capturing the idea of cooperation in supergames are known as 'folk theorems' (e.g. Fudenberg & Tirole 1991). They are called folk theorems because 'all the folks in game theory' knew them for a long time and it would be difficult to pin down the exact origin of ideas. Axelrod (1984) did not create the classical theory of cooperation in repeated games but he succeeded extremely well in making the subject known to scientists outside the field of game theory.

Trivers (1971) was the first to realise that the theory of repeated games might be of great importance to biology. He caused many biologists to start an empirical search for 'reciprocal altruism' in animal behaviour. Axelrod & Hamilton (1981) initiated a similar search for animal strategies resembling 'Tit-for-Tat'. They also discuss some of the theoretical problems that arise in evolutionary theories of repeated games. Looking back at the three decades of research since Trivers advocated the biological supergame, we observe a considerable discrepancy between how excited behavioural biologists were about the subject, and how little evidence could be collected to support the theory under discussion. Therefore, this section aims at discussing (a) the narrow scope of the notion of a repeated game and (b) the lessons to be learned from empirical examples.

Let us start with discussing finitely repeated games in which the end is foreseeable. Suppose that a player knows on a Monday morning that from now on every night until Friday he will play the Prisoner's Dilemma with the same opponent. After Friday he will never interact with this opponent again. This is a repeated game with exactly five rounds. We have to ask what to call economically rational behaviour in the finitely repeated game. As demonstrated in the last section, subgame perfection is an important 'ingredient' of rationality. If we are to analyse the finite supergame for its subgame-perfect Nash equilibria, a method called 'backward induction' is applicable. This method is similar to dynamic programming. We start by looking at the last round, i.e. the game on Friday. Since there is neither future interaction nor a possibility to change the past, the players are essentially in a situation as if they were playing the single-shot game. Therefore, both players have to defect on Friday. And how about Thursday? Knowing already what is going to happen on Friday, they see that nothing can be lost in the future by defecting on Thursday. Thinking backwards through the entire week, they each end up with the insight that there can be only one solution to the finite supergame, namely to defect every night.

Do humans rely on backward induction? Selten & Stoecker (1986) conducted experiments in the laboratory where this game was played. In the population of subjects, pairs were formed who played a given finite number of rounds of the repeated game. After this, they played the same repeated game with other members of the population, and this procedure went on for so long that subjects had, in principle, a fair chance of learning how to play the repeated game. To sketch the results, after some initial confusion, the players developed a cooperative attitude, but they also discovered the 'end effect', namely that it pays to defect in the last round. Subsequently, the onset of defection shifted a little towards earlier rounds of the repeated game but did not move all the way down to zero. Even after quite a lot of experience with playing the game, defection still began near the end of the supergame and the frequency of defection increased over the last periods. Selten and Stoecker argue that the population distribution of defection could result from routine learning in the population context. They give the following picture of learning. After some initial cognitive processes have taken place, the subject is prepared to initiate defection in round *i*. If an opponent defects earlier, this increases the subject's tendency of initiating defection earlier in the next repeated game with a new opponent. Conversely if the present opponent is still cooperating in period *i*, this enhances the subject's tendency of initiating defection later. Simulations show that this learning process will not lead a population to the same state as backward induction.

What is the take-home message? A repeated game has an incredibly large set of potential strategies, and it is difficult to even think of what they all are. Games in real life are even more complicated. Suppose, for the sake of questioning rationality, that the human mind was designed to routinely analyse games in the light of full economic rationality. Humans then would have to deal with the nightmare of strategic complexity. Their mental capacity would already be absorbed by thinking about a small subset of all the relevant problems in everyday life. Humans with such an attitude would die from starvation before they even reached a conclusion of how to act. From this point of view it does not seem very rational to be rational in the sense economists use this term! The empirical results on finite supergames demonstrate how humans seem to be guided by decision rules that are orders of magnitude simpler than those of an educated economist. Obviously, one cannot expect simple heuristics to always reach the conclusions of comprehensive analysis. Therefore, the predictive power of classical game theory is bound to be limited for a very fundamental reason.

How does evolution adjust behaviour to repeated games? In a finitely repeated game with a fixed number of rounds, evolution would probably 'work its way through the steps of backward induction' and generate the game theoretic solution, namely to always defect. In order to show this we would need a model in which strategies can mutate and selective forces are defined by the supergame. Furthermore, we would have to assume that animals have a 'trembling hand'. The term 'trembling hand' refers to small mistakes made in the execution of a strategy. The animal prepared to do A does B instead with a small error probability. Without such a tremble, many situations in the game would never be reached. With the tremble, they will be reached. Thus the tremble enables evolution to 'test' and improve the adaptedness of behaviour in these situations, eventually leading to subgame perfection, at least in a highly idealised world.

If the number of repeats of a repeated game is large and variable, it is mathematically convenient to model them as a potentially infinite sequence of interactions, and to assume that after each round the game continues with a probability q and stops with probability 1–q. To understand this modelling approach, imagine three shipwrecked persons sitting on a small island of the Caribbean. One of them is rich and was able to save his money from the sinking boat. The two others are poor. The rich entertains the poor by letting them play every night one round of the Prisoner's Dilemma game for some of his money. Between any two such games there is a small chance that a big ship will come by and pick them up. At the moment of being rescued, the rich will be separated from the poor and travel first class.

Given these circumstances, the two poor individuals can be conceived as playing an infinitely repeated supergame. The probability of continuation between two rounds is given by how likely it is that no ship will discover and rescue the shipwrecked the next day. How long the game continues is not the choice of the players but depends on properties of the environment, namely on the frequency at which ships arrive.

Let us look at two biological examples, one that resembles an infinite supergame and one that does not. We start with the latter. Consider a fish called the black hamlet, *Hypoplectrus nigricans*, which is a simultaneous hermaphrodite. According to Fischer (1980, 1981), the black hamlet has so many sperm in comparison with the number of eggs that mating involves the following conflict. It would often be beneficial for a hamlet to fertilise all its mate's eggs but keep its own eggs unfertilised in order to trade them in with other partners for fertilisation of their eggs. Fischer observed that mating consists typically of a number of spawning acts where one fish releases eggs and the other sperm. The eggs are 'parcelled' so that no individual can fertilise all the eggs of his mate at once.

At first sight this may look like a repeated game. However, unlike our Caribbean game, the hamlet game will often not be brought to its end by an external event. One of the potential ways of exploiting the partner is to let him give some eggs first, fertilise them and swim away in order to start another trade with another fish. In this case, the cheater will end the game. In order to understand the evolutionary stability of the hamlet's mating procedure, one has to look at the prospects of cheating and examine the local population of potential mates. As soon as one studies the problem this way, a local mating market and not a repeated game is the subject of investigation. Friedman & Hammerstein (1991) studied this market and used Fischer's data in their analysis. They reached the conclusion that hamlets do not seem to have a payoff incentive to do this kind of cheating. Furthermore, as will be explained in the next section, there does not seem to be a need for internal bookkeeping of how well the other animal behaved in the past. Now, if partner control is irrelevant, the hamlet example cannot be taken as an example for anything like Tit-for-Tat or reciprocal altruism. Thus, the popular supergame approach to thinking about black hamlets is highly debatable.

Now we turn to a more favourable example. Wilkinson (1984) studied female vampire bats. They roost in groups and every day the females fly out in search of blood. Not to obtain a blood meal for more than two days in succession takes an individual close to its starvation point. Therefore, if females return from an unsuccessful foraging excursion, they solicit a blood donation from other females. In an experiment, Wilkinson asked the question of who will serve a female if she is in need of help. Some of the potential donors had already received blood from the begging female and others not. The former turned out to be the ones who were more likely to actually donate.

Outside the primate world, this is perhaps the best example in biology where reciprocal altruism seems to be at work. However, despite Wilkinson's fascinating study, some questions still remain open, mainly because the bats could not be exposed to the crucial contingency test. What would happen if a female did not donate in a situation where a donation is expected? Would she later 'pay for this misbehaviour' by someone else letting her down? We do not really know this because the bat data allow for a number of different interpretations. One such interpretation could be as follows. If the bats tend to 'like' some females more than others, for example on the basis of smell, one could get Wilkinson's results without any bookkeeping on the side of the bats. In this case, the logic of cooperation in repeated games would not apply. Given that communally roosting females are kin groups – though they were not in the experiment – the explanation of why blood is donated may ultimately lie in their genetic relatedness.

The primate world looks more promising with regard to the existence of reciprocal altruism but it is particularly difficult to provide any compelling evidence. Seyfarth and Cheney (1984) studied vervet monkeys and conducted the following field experiment. After a female A had been groomed by a female B and after B was no longer within A's sight, a help call from B was played back from a tape. The question was: how would A respond to the help call in relation to time elapsing after the last grooming act? The later the call, the fewer cooperative reactions were observed. Unfortunately, however, cooperation could only be measured by whether or not female A was staring at the speaker. Would she have helped? We do not really know.

There are other very impressive studies of cooperation in situations with some 'flavour' of the supergame. However, it would be difficult to briefly summarise the take-home messages of these examples because of their biological complexity. Milinski (1987) was the first to devise an ingenious experiment with the contingency test in mind. He manipulated 'predator inspection trips' of sticklebacks in which normally pairs or groups of sticklebacks approach their potential killer. With the help of a mirror-image, Milinski created a 'virtual' stickleback whose cooperation could be controlled during the inspection trip. If only these trips were easier to understand in terms of their biology!

1.6 Markets

Most human markets share the following properties: there is an unequal distribution of tradable resources and thus a potential for transactions; information is gathered in order to decide with whom to have a transaction; and, finally, trading partners have to take measures to avoid being cheated when the transaction actually takes place.

To illustrate this, imagine first a minimal market consisting of only two traders, A and B. Individual A has an apple-tree in his garden and B grows tomatoes. Both would benefit from a balanced diet consisting of apples and tomatoes. As simple as the two-person case may be, we might readily observe the effect of supply and demand in this market. Think of a situation where A has many apples, B very few tomatoes, and both have a strong inclination to eat the latter. Given the great demand for tomatoes and their short supply, these vegetables will be expensive in the sense that A will have to trade in many apples for a tomato. However, with only two individuals in the market, little more can be said. As soon as there are two individuals with an apple-tree, say A and A', individual B can make an attempt to play them off against each other and to get an even better deal for his tomatoes. Noë (1990, see also his chapter in this volume) recognised the importance of this phenomenon in biology. A necessary condition is that B has a chance to actually compare the deals offered and thus gain information about the other side of this two-sided market. It may be impossible or too costly to get this information. Finally, at the moment when the apples are exchanged against tomatoes, B has to make sure that A does not cheat and run away with both apples and tomatoes.

Let us consider the moment of transaction in more detail and have a look at the illegal drug market. Consider the situation of two dealers who are about to trade among themselves a large amount of heroin for a large amount of money. How is it possible to ensure that the one who offers the heroin does not turn around with the million dollars in his hands before handing out the heroin? One way is to parcel both money and heroin and exchange small portions. If one dealer does not get his portion, he will stop trading and this is why the other has to continue being fair.

It looks a bit as if the black hamlet, discussed in the last section, knew about drug dealing. This fish parcels its eggs and two individuals alternate in releasing eggs for fertilisation. However, there is a major difference between mating in this hermaphrodite and the heroin market. Money and heroin can be kept for quite some time without getting stale. They remain trading commodities. Eggs in the hamlet are probably different and cannot be kept for very long. Mating takes place shortly before dusk and ends abruptly when it is getting dark. Although eggs are a precious good, there is a high incentive to 'sell them before dusk'. This has an interesting implication. Suppose that a hamlet releases eggs so slowly that in relation to the local mating population – where everybody is releasing eggs – it remains a valuable trading partner. Its mate then has no incentive to swim away because it pays to exploit the current mate as an egg resource. Sooner or later the mate will also have to release eggs because it would not be beneficial to carry them through the night and the subsequent day. Under these conditions a fish can 'trust' its mate to offer eggs. If, on the other hand, it released too many eggs too quickly, its own value would decline so quickly that its mate would desert and start a new deal. Friedman & Hammerstein (1991) analysed the hamlet along these lines and, in addition, examined the scope for specialisation on male function. All this is market analysis and has little to do with the theory of repeated games discussed in the last section. Bookkeeping is not essential. However, one question remains. If it is not reciprocal altruism, why do the hamlets alternate between releasing eggs and fertilising eggs? In my view, the answer is very simple: it is important for hamlets to avoid self-fertilisation!

We now switch to more general mating markets. When eggs are in shorter supply than sperm, females are in a strong strategic position. They can in some sense play off males against one another, forcing them to provide a nuptial gift or to demonstrate their quality in costly displays. If anything explains the prevalence of female choice in the animal kingdom it is certainly the asymmetric mating market. Had biologists not perceived the structure of this market, they would not know why the peacock has its impressive tail. The analysis of mating markets is technically complicated. The reason is that, by definition, female choice implies assortative mating. Therefore, genetic linkage plays a particular role in female choice theory. Furthermore, the process of sexual selection may not come to a halt so that female preferences are never truly stable. Pomiankowski & Iwasa (this volume) give an excellent survey of how the evolution of female choice can be conceived.

Are there other markets with a similar asymmetry allowing for unilateral choice? We know from the human labour market that companies hiring employees have to adjust salaries to the number of job-seeking individuals. If many search for a job they will get a bad deal and will have to adjust strongly to the demands of the company. What would be the analogy of job seeking in animals? In various species, subordinate males try to be allowed to become 'assistants' of a dominant male. If more than one potential assistant lines up to help the dominant, the latter has the choice. In evolution, this choice could, in principle, lead to morphological changes in subordinate males. For example, if dominants prefer young-looking assistants, this could have the evolutionary effect of delayed plumage maturation in birds so that sexually mature individuals still look like juveniles for some fraction of their adult lives (Noë & Hammerstein 1994). If this is true, delayed plumage maturation could not be understood without reference to the asymmetric market.

The story of the biological labour market does not end here. Once an 'assistant' is chosen by a dominant male, the latter has a certain interest in keeping the assistant. If he treats him too badly, the assistant will quit and search for another 'employer'. Vehrencamp (1983) was the first to realise problems of this kind in biology. Using the term 'reproductive skew' she argued that dominant members of social groups may have to split resources with subordinates in such a way that it is just worthwhile for them to stay. When is it worthwhile to stay? This depends on the market!

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Part I

Economic behaviour in social networks

Living in a group is a cooperative strategy. Animals live in groups only if groups yield a net advantage compared to living solitarily. Group living inherently implies competition, however: one's worst rivals in the competition over food or mates are the conspecifics with the same needs and desires. The same is true for human social networks: common interests often go hand in hand with conflicts over the partitioning of utilities or duties. Thus both humans and non-humans are frequently caught in '*social dilemmas*' and face similar problems: to find the optimal balance between contribution and exploitation and to keep cheaters and free-riders in check. Animals use strategies shaped by selection in the course of evolution when they deal with these challenges. Humans have the alternative option of using their cognitive capacities to plan their strategies rationally.

In the first chapter of Part I Elinor Ostrom, who has her roots in the social sciences, reviews the vast body of empirical as well as theoretical knowledge on the behaviour of humans caught in social dilemmas. She finds that humans tend to behave more cooperatively in social dilemmas than theory would predict. Charles Nunn and Rebecca Lewis look at social dilemmas with the eyes of evolutionary biologists. In this field the emphasis has traditionally been on dyadic interactions. Nunn and Lewis therefore first show how dyadic game theoretical models can be developed into the *n*-player models that are more meaningful to the study of social dilemmas. Both chapters point out the essential difference between 'common pool resources', which can be exploited at a cost to others, and 'public goods' that cannot be exhausted by a few, but have to be maintained by the community.

Both common interest as well as tension due to competition force members of social units to maintain good relationships. Jan van Hooff points out that the mode of competition over resources, by 'contest' or through 'scramble', largely determines the quality of the relationships between members of a group. Frequent contest may lead to strategies that help to resolve conflicts, such as the formation of dominance relationships, but also to strategies that help to mitigate the disruption caused by conflicts, such as the use of ‘reconciliation’. Contest competition also sets the scene for the formation of alliances, which again calls for the maintenance of good relationships. Van Hooff ends with a discussion of the ‘mental bookkeeping’ by which each animal checks for deviations from the ideal state of a relationship. He suggests that feelings of sympathy and antipathy have evolved to provide a running tally of the payoffs gained in each relationship.

ELINOR OSTROM

2

Social dilemmas and human behaviour

2.1 Introduction

Social dilemmas and the resulting problems of collective action are at the core of the study of how humans behave in interdependent situations. After an era of gloomy predictions based on the initial study of Prisoner's Dilemma (PD) games and the theory of collective '*in*action' (Olson 1965), recent theoretical work has made important breakthroughs for understanding human behaviour with guardedly more optimistic predictions. It is now theoretically well established that when individuals, modelled as fully rational actors, interact in an indefinitely repeated social dilemma situation, a PD game for example, it is *possible* for them to achieve optimal or near optimal outcomes and avoid the dominant strategies of one-shot and finitely repeated games that yield non-optimal outcomes (Aumann 1981; Fudenberg & Maskin 1986). Recent work in evolutionary game theory (Güth & Kliemt 1995; Sethi & Somanathan 1996) also identifies conditions under which cooperative behaviour backed by norms can be stable against invasion by narrow, self-interested strategies. It is also possible for individuals in social dilemma situations to do as badly round after round as is predicted for a one-shot or a finitely repeated series of situations. All potential outcomes between that produced by the dominant strategy and strategies leading to optimality are also possible equilibria. Empirical studies conducted in experimental laboratories (Ledyard 1995) and field settings (Bromley *et al.* 1992; Ostrom *et al.* 1994) provide evidence that more cooperation is achieved in social dilemma situations than the predicted zero level in one-shot or finitely repeated settings. Empirical studies of animal communities show both that the collective action problem exists in these settings and that multiple strategies are frequently found in these settings including full cooperators, conditional cooperators, full free-riders and conditional free-riders (see Nunn & Lewis this volume; and Nunn 2000).

The image of individuals stuck inexorably within social traps has been replaced by a recognition that individuals in many social dilemmas face the *possibility* of achieving results that avoid the most deficient equilibria. The grim, clear and unambiguous prediction of earlier theories has been displaced by a broad range of predictions including some that are far more optimistic. The theoretical enterprise has, however, become more opaque and confused. The heady days of assuming that a general and parsimonious theory of collective action was close at hand are past. Large theoretical and empirical literatures point to many variables that are posited to affect whether individuals will successfully overcome social dilemmas. Important studies are now being undertaken in ecology, economics, evolutionary game theory, evolutionary psychology, game theory, history, law, political science, sociology and social psychology. The literature is becoming so vast and specialised by discipline that it is no longer possible to refer to a single theory of human (or animal) behaviour in social dilemmas.

What I plan to do in this chapter is a partial attack on this problem. In section 2.2, I will define what is meant by a social dilemma. In section 2.3, I will discuss some variables posited to affect the likelihood of individuals cooperating in diverse types of one-shot social dilemmas. I will then provide an overview of recent findings from empirical research in laboratory experiments with human decision makers (section 2.4). In the last section of the chapter, I will draw some initial conclusions.

2.2 Social dilemmas

The term 'social dilemma' refers to an extremely large number of settings in which individual humans make independent choices in an interdependent situation. If each individual in these situations selects strategies based on individual rational calculation, all individuals are predicted to receive an equilibrium outcome that has less value (however this is measured) than one or more alternative outcomes that the individuals could obtain by cooperating (Dawes 1980). In other words, a set of individuals is involved in a game where the Nash equilibrium for a single iteration of the game yields less than an optimal outcome for all involved. The optimal outcome could be achieved if those involved 'cooperated' by selecting strategies other than those prescribed by a Nash solution to a non-cooperative game. Since the less-valued outcome is an equilibrium, no one is motivated independently to change, given the choices of all other participants. The reason such situations are dilemmas is that there is at least one outcome yielding higher returns for *all* participants, but rational participants making independent choices are not predicted to achieve this outcome. Thus, a conflict exists between individual rationality and optimal outcomes for a group.

Many ways of formalising social dilemmas exist in the literature (see Schelling 1978 and Lichbach 1996). Besides the assumption regarding the structure of payoffs and the presence of a deficient equilibrium, other assumptions made in almost all formal models of social dilemmas include:

1 All participants have common knowledge of the exogenously fixed structure of the situation and of the payoffs to be received by all individuals under all combinations of strategies.
2 Decisions about strategies are made independently, often simultaneously.
3 No external actor (or central authority) is present to enforce agreements among participants about their choices.

If such a game is finitely repeated, and everyone shares complete information about the structure of the situation, the predicted outcome for each iteration is the Nash equilibria for the constituent game. If uncertainty exists about the time or the number of rounds involved, or if the repetition is infinite, possible equilibria explode in number (Abreau 1988). Among the predicted equilibria are strategies yielding the deficient Nash equilibria, optimal outcomes and everything in between. Those who find ways to coordinate strategies in some fashion receive the 'cooperators' dividend' equal to the difference between the Nash equilibria and the outcome achieved.

Social dilemmas abound in human affairs. A group of individuals who could jointly provide a public good – a benefit, such as national defence, that is automatically received by all individuals living within a country whether or not they contribute – is one example. Appropriators using an open-access common-pool resource (CPR), such as the ocean fisheries, could jointly harvest at a rate that maximises economic returns to the group (or the sustainability of the resource), but the incentives facing each appropriator lead to an equilibrium of substantial overharvesting. Cartel formation is also a social dilemma for the members of the cartel, but one that, if solved, generates externalities for others. The most famous social dilemma is the Prisoner's Dilemma (PD) in which each prisoner separated from the other is motivated to defect (tell the prosecutor about the other prisoner's involvement in a crime), while, if both prisoners had remained silent, the penalty for both would have been less. Traffic jams, residential flights, runs on scarce goods, extending and keeping trust in long-term economic relations, organising labour unions, work-teams, demonstrations or any group seeking common interests, all tend to be social dilemmas. Sociologists have also long been interested in generalised social exchange, whereby individuals contributed resources to others and over the long-run received benefits from others (Emerson 1972a,b; Ekeh 1974), and stressed the importance of trust in building and sustaining such forms of reciprocity. Yamagishi and Cook (1993) point out the structural similarity of generalised social exchanges with that of social dilemmas. Finding ways to overcome the strong incentive not to cooperate in settings that generate well-being for participants without negative externalities for others is a major contribution to social welfare.

Social dilemmas have also been of considerable interest for biologists (see, e.g. Nowak *et al.* 1995; Nunn & Lewis this volume). The pressure of natural selection is predicted to favour free-riding phenotypes and select against cooperating types. But yet, research on many types of animal communities reveals an amazing array of cooperation including warning of danger, helping in fights, and joint hunting. Kin selection and reciprocal altruism are two of the leading explanations for such behaviour. The overlap of interest among biologists and social scientists in this topic is substantial.

2.3 Variables predicted to affect the likelihood and level of the cooperators' dividend

A rich array of theoretical speculations, formal game-theoretic models and computer models of evolutionary processes have generated a large number of variables postulated to affect the likelihood of participants achieving outcomes greater than the deficient Nash equilibrium – or the cooperators' dividend. In one-shot dilemmas, theorists identify the number of participants, their heterogeneity, the shape of the production function, and security and payback mechanisms as variables likely to affect the likelihood and size of a cooperators' dividend.

The number of participants

In his influential *The Logic of Collective Action*, Mancur Olson (1965) argued that, as the size of a group increased, the probability of a group achieving a public good decreased and the extent of non-optimality increased (see also Buchanan and Tullock 1962). Olson supported this hypothesis with two arguments. First, as group size increases, the noticeability of any single input to the provision of a public good declines and it is easier for the individual to think that their own free-riding will not be noticed and thus will not affect the likelihood that the good will be provided. Second, larger groups potentially involve higher transaction costs in order for individuals to come to an internal agreement about coordinated strategies. Theorists who are primarily interested in the evolution of norms of behaviour, such as Werner Güth and his colleagues (Güth & Kliemt 1995; Bester & Güth 1994), stress the importance of participants learning the characteristics (types) of the individuals with whom they are interacting. Group size affects the likelihood that individuals can learn substantial information about one another. Interactions within a family, within a neighbourhood or within any long-lasting small group are more likely to enable individuals to know the relevant characteristics of the others with whom they are dealing. Thus, the most frequent theoretical hypothesis has been that increases in the number of participants will likely reduce the probability of achieving collective action or at least diminish the amount of the cooperators' dividend that could be achieved.

The impact of group size has been subject to considerable theoretical debate. Some theories have generated the opposite prediction from those based on the work of Olson. In an effort to understand the phenomena of age-grade organisations that were so frequently used in most of Africa as a means of providing public goods – particularly defence – Bates and Shepsle (1995) developed a formal model of a three-period, overlapping generations, public-good providing game. One of the corollaries of this model generates a prediction that the provision of public goods is *positively* correlated with group size.

Chamberlin (1974) pointed out that changes in group size involved changes in other key variables including the marginal impact of an individual's contribution of a fixed amount (see also Frohlich & Oppenheimer 1970; McGuire 1974; Hardin 1982). Thus, how size might affect the likelihood of cooperation depends on how other variables are affected by the changes in the size of a group. Weissing and Ostrom (1991) present an extensive analysis of the impact of the number of individuals involved in a social dilemma game where each player has an opportunity to take a legal amount of water from an irrigation system or steal water, and between monitoring or not monitoring the behaviour of others in the system. When all other variables are analytically held constant, an increase in the number of players increases the rate of stealing at equilibrium. Many variables are affected by an increase in the number of participants. Unless other factors lead to counteracting tendencies, water is likely to become more scarce as the number of participants increases. The value of water at the margin for irrigators is likely to increase (thus making stealing more attractive). The impact of one person's stealing may be spread out over more individuals and thus the loss to any one farmer of someone else stealing water may be less severe at the margin (thus making monitoring less attractive). An increase in the number of participants may also mean a larger system where more water is available and the consequences listed above would then not follow. Thus, whether size has any impact, a positive impact, or a negative impact is dependent upon how other variables are affected by a change in the number of participants (see Ahn 1998).

The impact of the number of participants is also related to particular types of social dilemmas. In Olson's original analysis, he included all social dilemmas where it was difficult to exclude potential beneficiaries from the outcomes whether or not they had contributed to the provision of a benefit. Unfortunately, Olson's analysis confounded situations where the consumption of benefits by one individual subtracted benefits from others (such as harvesting from a CPR) with situations where consumption was non-subtractive in nature (such as a public good, like knowledge). Goods that are subtractable in nature are better defined as CPRs. Social dilemmas related to CPRs share with public goods provision the problems of free-riding, but they also include the problems of overharvesting and crowding (Gardner *et al.* 1990). In a CPR environment, an increase in the number of participants, holding other variables constant, is negatively related to achieving social benefits (e.g. Weissing & Ostrom 1991). In a public goods environment, however, increasing the number of participants frequently brings additional resources that could be drawn on to provide a benefit that will be jointly enjoyed by all. It is because of the additional resources available in a larger group and the non-subtractability characteristic of public goods, that Marwell and Oliver (1993: 45) conclude that when 'a good has pure jointness of supply, group size has a *positive* effect on the probability that it will be provided'.

The heterogeneity of participants

Participants can be heterogeneous in many ways. Olson (1965) argued that, if there were one or a few individuals who had much stronger interests in achieving a public good (in other words, they faced different payoff functions), the probability of a group achieving a public good increased even though it was likely to be underprovided. Privileged groups may be found among animal communities as well, since highly ranked individuals have the most to protect against invasion by other threatening individuals (see Nunn 2000). Closely related to the concept of a privileged group is the theory of hegemonic stability in international relations (Kindelberger 1973; Keohane 1984). Hegemonic stability theory sees heterogeneity as promoting cooperation because larger actors are endowed with more resources and are better able to produce a public good such as international peace, whose benefits are provided to all whether they contribute or not. The theory predicts that, when there are a limited number of larger states dominating international relations, the collective good of peace is more likely to be provided than when international relations involve many more homogeneous actors.

Others have speculated that heterogeneity in assets, information and payoffs is negatively related to gaining the cooperators' dividend, due principally to the potential conflict that would exist over the distribution of benefits and costs to be borne. In fact, the literature contains many arguments that point to heterogeneity as a serious deterrent to cooperation (Johnson & Libecap 1982; Hackett 1992; Bardhan 1993). Like the size of group, the impact of heterogeneity on levels of collective action achieved frequently interacts with other variables (Marwell & Oliver 1993; Heckathorn 1991).

The shape of the production function and the criticalness of individual inputs

All social dilemmas involve individuals who could take actions that produce benefits for others (and themselves) at a cost to themselves. The production function that relates individual actions to group outcomes may take any of a wide diversity of forms (see Fig. 2.1). One possible form is a step function ((b) in Fig. 2.1), in which actions by up to k participants make no difference in the benefit function, but actions by k or more participants discontinuously shift the benefit functions upward. Russell Hardin (1976) was among the first to argue that, when the shape of the production function for a public good was a step function, solving social dilemmas would be facilitated since no good would be provided if participants did not gain sufficient inputs to equal or exceed the provision point (k). Until the benefit is actually produced, it is not possible to 'free-ride' on

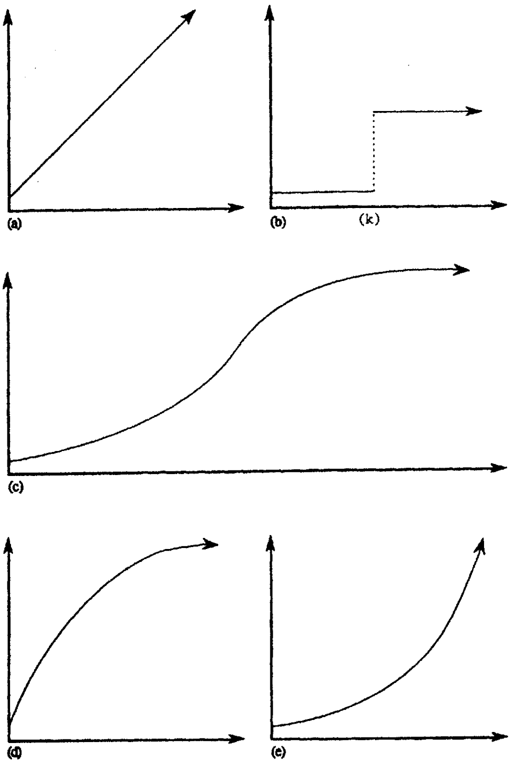

Fig. 2.1 General types of production functions: (a) Linear; (b) discontinuous, or step; (c) general third order; (d) decelerating; (e) accelerating. k = number of participants whose participation is necessary to provide the good (Marwell & Oliver 1993: 59).

the contribution of others. In these settings, individuals may assume that their participation is critical to the provision of the good. This type of production function may create an 'assurance problem' rather than a strict social dilemma. For those who perceive their contribution as critical, not contributing is no longer the unique Nash equilibrium. Participants are motivated to contribute so long as they are assured (have an expectation) that other critical participants will contribute. In these settings, the question is what mechanisms can be devised to provide the required assurance. Step functions characterise facilities such as bridges, tunnels and roads that have little value if not completed.

Closely related to this attribute of the production function itself, are sharing formulas that may be developed by participants to make each person of the entire group, or a designated minimal contributing group, feel that their contribution is critical (van de Kragt *et al.* 1983). By agreeing that each person will contribute a set proportion of what is believed to be the total cost of obtaining a good, the individuals in such a minimal contributing set face a choice between not contributing and receiving nothing or contributing and receiving the benefit (assuming others in the minimal contributing set also contribute).

While some scholars have argued that most public goods are characterised by provision points (Taylor 1987; Hampton 1987; Taylor & Ward 1982), many public goods are represented by the other production functions in Fig. 2.1. Marwell and Oliver (1993) conduct an extensive analysis of monotonically increasing, linear and nonlinear production functions relating individual contributions and the total benefits produced. Linear production functions are used extensively in *n*-person PD and public goods games where the prediction is that a homogeneous group will contribute zero resources. Marwell and Oliver focus on non-linear functions, and distinguish between third-order production functions that are decelerating and those that are accelerating. In the decelerating case ((d) in Fig. 2.1), while every contribution increases the total benefits that a group receives, marginal returns decrease as more and more individuals contribute. When contributions are made sequentially, the initial contributions have far more impact than later contributions. The example they use to illustrate such a production function is calling about a pothole in a neighbourhood where a city administration is sensitive to citizen support (ibid.: 62). The first call brings the pothole to the attention of city officials and puts it on the list of things to be repaired (raising the probability of repair from zero to perhaps 0.4 or higher). The second call increases the probability of repair still further, but not as much as the first call. Later calls continue to increase the probability but with a smaller and smaller increment.

With an accelerating production function ((e) in Fig. 2.1), initial contributions make small increments and later contributions yield progressively greater benefits. 'Accelerating production functions are characterised by *positive interdependence*: each contribution makes the next one more worthwhile and, thus, more likely' (ibid.: 63). Settings where mass actions are needed in order to gain a positive response involve accelerating functions.

The theoretical predictions depend sensitively on the particular shape of the production function, on whether all participants are symmetric or have different levels of assets, on the sequence in which individuals contribute, and on the information generated by each action. For homogeneous groups facing decelerating curves, which Marwell and Oliver assert characterise many field situations involving large numbers of potential beneficiaries, getting over the initial period where the returns to participants are negative defeats collective action before it can generate sufficient inputs to gain net benefits. Thus, collective goods that have a decelerating production function are unlikely to be provided by large groups of relatively homogeneous individuals acting independently, or, if provided, they will be provided as Olson predicted at a suboptimal level. The prediction for homogeneous groups and accelerative functions is also gloomy. The key is whether the initial contributions are made, and this is somewhat less likely with a homogeneous group than with a heterogeneous group who may have some members with high levels of interest and who would be more interested in contributing the initial inputs.

To explore the interactions among diverse levels of heterogeneity of interest in the benefits to be produced and the shape of the production function, Marwell and Oliver analysed a series of Monte Carlo simulations. If some individuals value the group benefits produced by collective action more than others, the likelihood of achieving positive returns with decelerative functions is relatively high. There may be significant order effects, whereby the maximum contributions are achieved when those with the lowest interest in the group benefit contribute first and it is possible for groups to achieve a surplus of contributions. This preferred order is, however, unlikely to occur in an unorganised group. In organised fund-raising efforts, highly interested donors can overcome this ordering phenomenon by promising to match smaller contributions and thereby encouraging those with lower interests in the benefits to contribute first.

Heterogeneous groups facing accelerative production functions may need substantial organisation to overcome the initial start-up costs. Whether these benefits are produced at all depends on the presence of a *critical mass* of individuals (a subgroup of individuals who have a sufficient large interest in the benefits received and sufficient resources needed to cover the initial start-up costs). In other words, some degree of heterogeneity of the valuation of joint outcomes, and in many cases of the resources needed to generate those outcomes, is necessary to achieve the cooperators' dividend. If interest in joint outcomes and availability of resources are positively correlated, the likelihood of a critical mass is higher (ibid.: 87). Once the initial contributions are made, a bandwagon effect may occur where those with a lower valuation of the outcome can contribute and see a substantial return on their contribution. Marwell and Oliver repeatedly discuss the importance of participants communicating with one another to cope with the diverse problems associated with heterogeneity of interest combined with the shape of the production function, but communication is not included in their formal analysis.

Security and payback mechanisms

It is argued that one of the major reasons that individuals do not cooperate in a social dilemma situation is that they do not want to be 'suckered' by contributing when others do not contribute. Thus, diverse mechanisms to prevent free-riding, and to give contributors a sense of security that they will not contribute while many others free-ride, have been of theoretical interest. In a model of simultaneous, voluntary contributions to the production of a discrete public good, Bagnoli and Lipman (1989) posit a guarantee that contributions will be returned if insufficient contributions are made to provide the good. In this secure situation, Bagnoli and Lipman predict that participants face sufficient incentives to achieve Pareto-efficient outcomes. Admanti and Perry (1991) examine similar mechanisms to increase security. They develop alternative models of sequential contributions to a public good in which two symmetric players alternate in deciding whether to contribute to a public good. In a 'subscription game', the players actually pay the cost of their pledge if, and only if, the total contributions are equal to the cost of providing the good. In this setting, they predict an efficient equilibrium outcome. In a 'contribution game', payment is made at the time of contributing and cannot be returned. Even in a setting where players alternate, the contribution game does not lead to an efficient outcome unless the cost function is linear and the benefit is greater than the cost for one player (in other words, a privileged group).

2.4 An overview of recent experimental research on one-shot social dilemmas

Experiments involving human subjects placed in one-shot social dilemma situations have been conducted by economists, political scientists, social psychologists and sociologists. In fact, immense numbers of experiments have been conducted without an effort to synthesise the findings across disciplines. In this chapter, I can only offer an initial effort to summarise results related to one-shot social dilemma experiments. A complement to this effort focusing on repeated situations is presented in Ostrom (1998) and in other works in progress. Many experiments have been conducted of 2-person PD games (see Rapoport 1966; Rapoport &

Chammah 1965). Since the more difficult theoretical problems exist in situations with $n > 2$, this review will focus on settings involving three or more individuals.

The number of participants

Some of the early survey articles on social dilemmas presumed that cooperation levels would decrease with increasing numbers of participants (Dawes 1980; Messick & Brewer 1983). Stroebe and Frey (1982) even conclude that: 'All in all the studies using *N*-Person Prisoner's Dilemma or related *n*-person games provide strong evidence for the free rider hypothesis and for the group size effect on free riding.' Several other variables also changed in the early experiments, however, so the impact of group size is hard to assess. When experiments have carefully controlled for the impact of size on other variables, group size does not appear to make an independent difference in the level of cooperation. Dawes, McTavish and Shaklee (1977) were originally interested in testing the effects of communication, but show-up rates for their baseline experiments varied from 5 to 8 participants. Both the incentive to defect and the impact of a defection on payoffs remained constant across size of group. For the baseline experiments in which decisions were made in private without prior communication, Dawes and his colleagues report no impact of group size on a cooperation rate of just under 30%. Franzen (1990, summarised in Franzen 1994) told his subjects that they were in groups that ranged from 2 players to 101 players and held constant the temptation to defect and total group gain. Nominal group size made no difference in the percentage of contributions. Kerr (1989) varied group size from 9 and 54 to 324 in a provision point, public goods experiment in which payoffs were assigned to a random sample of all players. Kerr reported no effects of group size on levels of contributions, even though subjects reported an increased sense of efficacy in smaller groups.

The heterogeneity of participants

One of the earliest public goods experiments with groups larger than two was conducted by Marwell and Ames (1979) who drew a sample of 256 high-school students living in the Madison, Wisconsin, area. Each student was allocated 225 tokens in groups with equal resources; 405 tokens to one player and 165 to the others in groups assigned unequal resources. Subjects could invest their tokens in a private exchange or a group exchange (the public good) that generated more total revenue than the opportunity cost of the tokens invested after reaching a provision point. Marwell and Ames found that the contribution level for all subjects was relatively high – an average of 127.6 tokens or 57% of all resources were invested in the group exchange. Only 13% of the participants contributed the predicted zero tokens. One out of five subjects contributed *all* of their tokens and two-thirds contributed more than half of their tokens. Few groups reached an optimal level of contribution.

Groups where one member had a substantially greater payoff function (e.g. privileged groups in the sense of Olson 1965) did achieve significantly greater returns. Unequal resource endowments did not make a statistically significant difference in outcomes. It was the extremely high levels of cooperation found by Marwell and Ames in this early one-shot experiment that sparked considerable interest among social scientists in general and experimental economists in particular to pursue these questions further. The initial experiments provided relatively strong support for Olson's hypothesis related to privileged groups.

The shape of the production function and the criticalness of individual inputs

In a series of public goods experiments, Robin Dawes, John Orbell and colleagues used various institutional arrangements to create a discrete provision point or a step-level function. All of these experiments had seven participants who were given a promissory note for $5.00 at the beginning of the experiment. Subjects were told that if a minimal contributing set (MCS) – either 3 or 5 – contributed their promissory note, all subjects would receive $10.00, including those who had not contributed. With less than the required number of contributions, no good would be provided. In a series of baseline experiments, subjects were not allowed to communicate and were told only the size of the MCS needed to obtain the public good. In one of these baseline experiments, subjects were asked to estimate three probabilities prior to their own and others' decisions: (1) the probability of their action being futile if they were to contribute, (2) the probability of their action being critical to the achievement of the public good, and (3) the probability of their action being superfluous. The level of cooperation in these one-shot games without communication is quite high. The public good is provided in 7 out of 10 of the experiments where the minimal contributing set equalled 3 (50% of the individuals contributed) and in 4 out of 10 of the experiments with a MCS of 5 (64% of the individuals contributed). On the other hand, in the experiments where subjects were asked to estimate the probabilities of their own contribution being futile, critical or superfluous, none of the five experiments achieved the MCS that had been set at 5 (23% contributed).

Security and payback mechanisms

Dawes, Orbell and colleagues were particularly interested in examining the efficacy of two conditions when compared to their baseline experiments. The first condition was to give subjects a 'money-back guarantee' that anyone who contributed in an experiment where the public good was not provided would have their promissory note returned. This condition was intended to test whether subjects hesitated to contribute because of their 'fear' of being a sucker as predicted by Brubaker (1975; see also Bagnoli and Lipman 1989). The second condition involved an enforcement of equal contributions from all subjects if the MCS was met (or, imposing a 'fair share'). Their findings clearly supported the efficacy of the solution that required all subjects to contribute their fair share of the public good. 'In all three replications it was superior to the standard dilemma at a high level of statistical significance. In two of three, it was significantly superior to the money-back guarantee and was marginally better in the third' (Dawes *et al.* 1986: 1,183).

Face-to-face communication

In non-cooperative game-theoretical models of social dilemmas, it does not make any difference whether the participants can communicate via face-to-face negotiations or use any other mode of signalling intentions. Communication without an external enforcer of promises is considered only 'cheap talk' and has no impact on the predicted outcomes. In cooperative games, it is assumed that players can communicate freely and make *enforceable* agreements. On the other hand, in non-cooperative game theory, players are assumed to be unable to make enforceable agreements and whether they can communicate is considered irrelevant (Harsanyi & Selten 1988: 3). When placed in a laboratory setting, the assumption is that verbal commitments do not change the formal game structure and no strategic content is assigned simply to the capacity to communicate on a face-to-face basis.

In the experimental lab, however, communication has repeatedly been shown to affect results (see citations in Ostrom & Walker 1991). An early communication experiment was conducted by van de Kragt, Orbell and Dawes (1983) in a one-shot provision-point public goods game. In all 12 communication experiments, subjects used the opportunity for discussion to decide exactly who would or would not be expected to contribute to the public good (ibid.). They used lotteries, overt volunteering, and, in one case, the need of several subjects for the additional $5.00 associated with non-contribution. In 10 of these 12 experiments, the discussion led to a decision designating the optimal number of participants. In all 10 cases, those designated did contribute even though their decision was independently and privately made. In the other two experiments, the discussion led to the identification of a group of contributors larger than necessary. The authors attribute the high level of success in these communication experiments to the sense of criticalness that participants gained when a minimal contributing set was actually designated through their discussion period.

In addition to enhancing the sense of being necessary, other explanations offered by those doing experimental research for why communication facilitates cooperation include: (1) transferring information from those who can figure out an optimal strategy to those who do not fully understand which joint strategy would be optimal, (2) exchanging promises, (3) affecting subjects' expectations of each others' behaviour, (4) adding new values to the payoff structure, (5) reinforcement of prior normative values and (6) developing a group identity (Ostrom & Walker 1997). All of these may be involved and they appear to reinforce one another interactively. Orbell, van de Kragt and Dawes (1988) summarise the findings from 10 years of research on one-shot public goods experiments by stressing how many processes seem to be evoked when communication is allowed (see also Banks & Calvert 1992a,b for a discussion of communication in incomplete information games).

Communication is also efficacious in repeated situations where subjects are able to communicate between each decision round (see Ostrom & Walker 1997; Ostrom 1998). Subjects are also willing to put in time and other resources to reach agreements that change the structure of the game. Evidence from field studies is consistent with the experimental evidence (see Ostrom *et al.* 1994).

2.5 Initial conclusions

Evidence from laboratory experiments provides consistent and anomalous evidence that individuals are not always trapped inside one-shot social dilemmas as predicted by non-cooperative game theory. The capacity of participants to communicate and the heterogeneity of their assets affects cooperation levels even in one-shot settings. These variables are not predicted to improve the likelihood of participants cooperating. Whether a social dilemma is a public good or a CPR, also affects behaviour directly and interacts with other variables, such as the size of the group, to affect behaviour indirectly. Not all behaviour is inconsistent with theory. Changing payoff functions affects behaviour in a manner consistent with theory. In step-level production problems, for example, individuals are more likely to cooperate than when production functions are continuous.

While the experimental evidence presents a less grim picture of the individual capacity to cope with social dilemmas, it does not eliminate the importance of social dilemmas for understanding human behaviour. The temptation to 'defect' is always there in any dilemma situation. From an evolutionary perspective, individuals who are cooperative and face defectors receive lower payoffs and are less likely to carry their genes into the next generation. On the other hand, when individuals can use reliable signals to let others know that they wish to cooperate, if given some assurance that others will cooperate as well, conditional cooperators improve their joint payoffs substantially. Thus, when individuals have a choice regarding with whom they interact and can signal their intentions relatively accurately, conditional cooperators have an advantage both in the short run as well as the long run. Humans use communication for this purpose. Animals use other forms of signalling. Since empirical evidence is mounting to show that cooperation in human and animal communities is more frequently achieved than currently posited in our respective theories, there is a lot of theoretical work to be done to catch up to empirical knowledge.

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CHARLES L. NUNN AND REBECCA J. LEWIS

3

Cooperation and collective action in animal behaviour

Introduction

Models of cooperation in animal behaviour frequently address issues of cheating (also called defecting; reviewed in Dugatkin 1997). In the simplest case, cheaters gain more than cooperators because they obtain the benefits of another's action without paying the costs. Cooperation has been modelled extensively using two-player game theory models (especially the Prisoner's Dilemma; Axelrod 1984). However, these two-player models fail to capture the dynamics of cooperation in larger, polyadic social settings, which often require more complicated mathematical representations (*n*-player games; e.g. Joshi 1987; Boyd & Richerson 1988; Dugatkin 1990).

An empirical study by Heinsohn and Packer (1995) illustrates the difficulties of modelling cooperation in large social groups. These authors provide experimental evidence for cheating in lions by simulating territorial intrusions using playbacks. In their study, the perceived benefits of territorial defence were altered by playing back different numbers of roaring neighbours. The patterns of response suggest that female lions use one of four strategies: some females always participate (unconditional cooperators), others participate when they are most needed but not at other times (conditional cooperators), and some females never participate (unconditional laggards), or actually participate less when they are most needed (conditional laggards). Heinsohn and Packer (1995) examined whether some cooperative strategies commonly used in game theory might apply to lion cooperative territoriality (i.e. Tit-for-Tat and Pavlov; Axelrod & Hamilton 1981; Nowak & Sigmund 1993). However, these attempts were unsuccessful, probably because more complicated models are needed to represent the complex behavioural interactions expected with four strategies in a polyadic setting (Heinsohn & Packer 1995). Thus, one conclusion from their research is that existing models are insufficient for capturing the dynamics of cooperation in actual animal social groups (see also Noë 1990).

In this chapter, we explore an approach related to traditional game theory approaches in animal behaviour, but which potentially offers new insights into animal cooperation. This complementary approach is based on economic models of *collective action* designed for human societies (e.g. Olson 1965; Hardin 1968; Taylor 1987; Ostrom 1990, this volume; Hawkes 1992; Sandler 1992). These models examine cooperation in the context of *collective benefits*: when one individual in the group obtains a benefit, usually at some cost, other individuals in the group also benefit (terminology summarised in Box 3.1). In this case, one or more *free-riders* may withhold contributions to the good while benefiting from the production of others. These same principles should also apply to situations involving collective benefits in animal behaviour (Nunn 2000). For example, collective territorial benefits likely exist among lions, in that individuals that fail to participate in territorial encounters (laggards) still gain from the efforts of participants (cooperators).

We first review economic principles of collective action. Then, we examine game theoretic models of collective action. We start with simple game theory models, and then we investigate more complex models. Many of these same game theoretic approaches have been used to address related and unrelated problems in biology. Next, we examine mechanisms that overcome free-riding within the general framework of these game theory models. These mechanisms are especially important in human societies, and the same is likely to be true in non-human societies. In the Discussion, we compare how cooperation is studied in economics and biology, and we consider how the collective action approach expands on existing models of cooperation in biology.

Collective action and animal behaviour

General principles

In economics, the *collective action problem* (CAP) arises when benefits accrue to individuals who do not contribute toward obtaining some good. In this case, free-riders may withhold contributions to the good, while benefiting from the production of others. Two types of free-riders exist: *strong free-riders* provide none of the collective good, while *weak free-riders* contribute

Box 3.1 The terminology of collective action

Coercion: use of force to compel contributions to a collective good. Coercion is equivalent to punishment (Clutton-Brock & Parker 1995) and retribution (Boyd & Richerson 1992), as coercion refers to active, aggressive retaliation (or the threat of such retaliation) for failing to cooperate, rather than simple non-cooperation in future interactions.

Collective action problem (CAP): suboptimal level of a collective good is provided due to free-riding by one or more group members.

Collective benefit: a benefit that accrues to all group members so that when one individual (or a coalition of individuals) obtains the benefit, other individuals in the group also benefit (also called collective good or public good).

Common pool resource (CPR): a good for which exclusion is possible, but at some cost (similar to club good; Sandler 1992).

Free-rider: an individual that benefits from the production of others by contributing less than his or her true value of the collective good. The term free-rider has also been used in market models to refer to cheating among members of the same trading 'class' (Noë & Hammerstein 1994). We follow this terminology here because it corresponds to the general use of free-rider in economics, where individuals of the same class are contributing (although perhaps to varying degrees) towards a single collective good.

Private incentives: monopolisable benefits provided to encourage individual contributions to a collective good.

Privileged group: one individual (or a coalition of individuals) benefits to the extent that this party provides the good, despite the existence of free-riders; involves situations of asymmetrical benefits, where the net benefits of some collective good vary among the beneficiaries of the good.

Synergies (economies of scale): decreasing per capita costs associated with greater participation in providing the good.

to the collective good, but they contribute less than the benefit that they receive (Marwell & Ames 1981; Isaac *et al.* 1984; Sandler 1992). CAPs may therefore result in a departure from Pareto optimality, which describes a situation in which no individual can be made better off without making another individual worse off (see Sandler 1992). In other words, CAPs often result in suboptimal behaviour because members of the group would be better off if individual participation increased.

CAPs can only arise in conjunction with *collective goods* (also called *public goods*). As mentioned above, collective goods are characterised by non-excludable benefits, so that an individual cannot be denied benefits when the good is obtained by others (Samuelson 1954). Many examples of collective goods are found in human societies (see Olson 1965; Ostrom 1990; Sandler 1992). For example, public radio in the US is supported largely through charitable contributions; however, anyone with a radio can listen to the broadcasts without making a donation. In animal societies, collective goods also exist, including the benefits of territorial defence, predator mobbing and building of protective structures, such as burrows. We should note, however, that these and other animal examples probably involve the confounding effect of kin selection, and so existing economic models may need to be elaborated to take kinship into account.

Collective goods vary in their *rivalry* (also called congestion or crowding; Sandler 1992). In rival goods, use by one individual reduces the amount available to others. For example, roads are provided at a collective level but become congested as more people drive. Similarly, in animal societies, individuals may be crowded out of rival collective goods, such as food patches obtained through territorial expansion. In non-rival collective goods, the utility derived from the good is not dependent on the number of users. Thus, public radio is a non-rival good in human societies: an individual benefits regardless of how many others listen. An example of a non-rival good in animal societies might include predator warnings, since all who hear the warning can benefit. When a collective good is entirely non-excludable and non-rival, the good is termed *purely collective*. A related concept involves *common pool resources* (CPR; Ostrom 1990), which we define as a rival good for which exclusion is possible but costly (see also *club good* in Sandler 1992). Exclusion from collective benefits may also exist in animal societies (e.g. eviction of free-riders from the social group or exclusion of free-riders from food patches). For most of this chapter, however, we simplify matters by focusing on purely collective goods.

An important component of this economic framework involves the mechanisms that humans use to overcome CAPs (Ostrom 1990, this volume). We return to these issues later, as the factors involved are probably highly relevant to non-human behaviour.

Evidence for CAPs in animal behaviour

A number of studies indicate the existence of cheating (or 'scrounging') in a variety of behavioural acts (e.g. Barnard & Sibly 1981; Scheel & Packer 1991; Heinsohn & Packer 1995). However, only a few studies of animal behaviour have taken an approach explicitly based on theories of collective action. In primates, van Schaik (1996) argued that CAPs apply to patterns of male territorial behaviour: using intraspecific variation in the number of males (or variation among closely related taxa), van Schaik (1996) showed that male langurs (*Presbytis* spp.) and sifakas (*Propithecus* spp.) participate less in intergroup encounters when they share the benefits of this defence with other males (i.e. in multimale groups). Home range overlap is also greater in multimale situations, further suggesting that territorial boundaries are less well defended. In this interpretation, the benefits of group defence are more collective in multimale groups.

Nunn (2000) expanded on van Schaik's (1996) analysis of male intergroup conflict by examining patterns across a wider array of species. Nunn (2000) showed that proxies for male intergroup encounters, especially the presence of loud calls, are correlated with proxies for the collectiveness of male benefits. For example, loud calls tend to be absent in multimale taxa when there is more scramble competition within groups, as measured using relative testes size and breeding seasonality. Thus, within-group shareability of benefits (scramble competition for fertilisation opportunities) may affect behaviours involving extragroup defence (loud calls).

The limited evidence currently available therefore suggests that CAPs exist in animal societies. As in humans, however, experimental approaches are needed to more directly test these models in animal behaviour (e.g. Heinsohn & Packer 1995).

Game theory, cooperation and collective action

Two-player game theoretic models of collective action

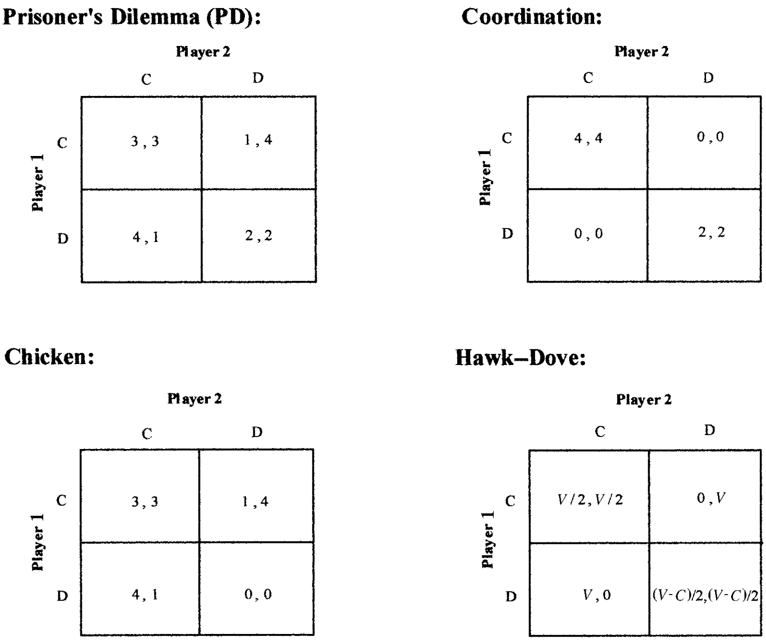
Various models of collective action have been proposed since Olson's (1965) initial formulation of the idea. Because collective action involves interdependent decisions among multiple actors, game theory has played a prominent role in these models. Social scientists have used several different game structures to represent the CAP in human systems (e.g. Taylor & Ward 1982; Taylor 1987; Bates 1988; Sandler 1992). Which game is used depends on how the costs and benefits of the good are distributed among the players.

We begin this section with relatively simple two-player games that are played simultaneously and only one time. Then we expand the analysis to include the effects of repeated interactions, dynamic interactions (i.e. sequential moves), incomplete information and multiple players. Some of these same two-player game structures have also been used to study cheating in animal behaviour (e.g. Axelrod & Hamilton 1981; Parker & Hammerstein 1985; Dugatkin 1997). A secondary (but important) aim of this chapter is to review alternatives to the standard Prisoner's Dilemma game.

Two-player models would at first seem to have little relevance to the CAP, which is usually envisioned as occurring in larger groups; thus, *n*-player games might seem more relevant than two-player games. However, the two-player model serves its purpose by representing, at the most basic level, the temptation to free-ride under varying payoff structures and assumptions, such as the order of play and the amount of information available to each player.

Nash equilibrium (NE) is the solution concept used to identify outcomes in non-cooperative games, such as most of those discussed here. In NE, each player uses the strategy that is the best response to every other players' strategies, so that no player has an incentive to change strategies. NE may involve pure or mixed strategies (i.e. individuals randomise their strategies). For reasons of space, however, we focus on pure strategies. The concept of an evolutionarily stable strategy (ESS) is related to NE, but involves this distinction: a strategy is an ESS if, when adopted by the majority of the population, it cannot be invaded by a rare alternative strategy (Maynard Smith & Price 1973; Maynard Smith 1982). All ESSs are NE, but not all NEs are evolutionarily stable (see Parker & Hammerstein 1985).

Economists make assumptions regarding the rationality of human players in their game theory analyses (Myerson 1991). While in humans rationality often implies cognitive awareness of alternative strategies and their corresponding utility functions, the assumption of rationality implies no such awareness by non-human actors. Instead, biologists expect natural selection to identify behaviours that maximise individual reproductive success (see Parker and Hammerstein 1985). The same is true in our



Prisoner's Dilemma (PD):

		Player 2	
		C	D
Player 1	C	3 , 3	1 , 4
	D	4 , 1	2 , 2

Coordination:

		Player 2	
		C	D
Player 1	C	4 , 4	0 , 0
	D	0 , 0	2 , 2

Chicken:

		Player 2	
		C	D
Player 1	C	3 , 3	1 , 4
	D	4 , 1	0 , 0

Hawk–Dove:

		Player 2	
		C	D
Player 1	C	$V/2, V/2$	$0, V$
	D	$V, 0$	$(V-C)/2, (V-C)/2$

Fig. 3.1 Four game theoretic models used to study collective action. Each player has the choice of two strategies: cooperate (C) and defect (D). In each cell, the first value corresponds to Player 1's payoff, while the second value corresponds to Player 2's payoff. Higher values represent higher utility and so are preferred. These games are simultaneous, symmetric and played only once.

study of animal CAPs: we do not require that individuals are cognitively aware that the benefits accrue to all, or that they view non-participants in normative terms (as might be implied by terms like free-rider, collective action 'problem', and cheater). However, we might expect the evolution of high-level cognitive awareness and behavioural norms in some species when these factors help solve CAPs. Although we do not imply perfect equality with human behaviour, we retain the game theory terminology for consistency and to facilitate cross-disciplinary communication.

Prisoner's Dilemma

Much of the economic literature uses the Prisoner's Dilemma (PD) to examine problems concerning the acquisition of collective goods (Fig. 3.1). Player 1 receives the highest payoff by defecting (D) when Player 2 cooperates (C). But this outcome is the worst possible payoff for Player 2, who would prefer that the roles were reversed. If both players defect, their payoffs are lower than if they had both cooperated. Thus, the NE is for both players to defect (D,D), but the socially (Pareto) optimal solution is for both to cooperate.

Such models have relevance to collective goods in situations when one player suffers great costs in providing the good for free-riders (i.e. the individual cost of provision exceeds the individual benefit). For example, in renewable CPRs, such as fisheries, overexploitation by one player may result in huge gains for this player but huge losses for the 'cooperator'. In this situation, mutual overexploitation (i.e. mutual defection) is likely to be the NE (e.g. Taylor & Ward 1982; Ostrom 1990; Sandler 1992). The PD has been used to represent observed patterns of animal cooperation (Packer 1988; Fischer 1988). However, the applicability of the standard PD to specific instances of animal cooperation is controversial (Noë 1990; Brembs 1996). As in economics, the appropriate model to use depends on the circumstances (Taylor & Ward 1982).

Coordination

In the game of Coordination (Fig. 3.1), the worst possible outcome occurs when individuals play different strategies. Hence, the NE are (C,C) and (D,D). While cooperation is clearly preferred, if play starts at mutual defection, escaping this equilibrium is difficult in the absence of communication.

An example of Coordination in human collective goods may involve political revolutions (Bates 1988; see also Sandler 1992). In these situations, individuals are better off if everyone plays the same strategy, as the existence of traitors may make life worse for all (e.g. through government 'crackdowns'). If all individuals join the revolution, however, the dictator is easily overthrown, and everyone benefits. Hence, the problem involves getting individuals to coordinate their efforts, which under other assumptions could involve communication (e.g. underground printing presses).

Because of its application to revolutions, the Coordination game might seem relevant to dominance hierarchies in animal societies (cf. Matsumura & Kobayashi 1998, who used the game of Hawk–Dove to analyse dominance interactions). In this context, however, overthrowing the highest-ranking individual does not necessarily result in a collective benefit for all subordinates. Coordination may also apply to some cases of cooperative territoriality in which a mismatched strategy on the part of the defenders leads to a more costly outcome for each. For example, when a lone individual faces extreme risks in defending the territory (e.g. death), and the other individual also experiences a cost in the process (e.g. loss of a coalitionary partner), then a Coordination game might apply.

Chicken

In some cases, the collective good may be so important that one player provides the good regardless of whether the other player cooperates. A game that captures this situation is Chicken (Fig. 3.1), which is based on the following situation. Two cars race towards one another, and the car that holds its course longest wins (i.e. the other 'chickens out'); however, if both individuals continue on course for too long, the cars collide, and the worst possible outcome is obtained (i.e. D,D). Chicken is similar to the PD in that each player would prefer to defect while the other cooperates. Unlike PD, however, the worst scenario for both players is that none of the collective good is provided (i.e. the cars collide); thus, cooperation in the presence of a free-rider is less costly to each individual than is mutual defection. Chicken may therefore apply when each player would prefer to free-ride, but being the sole provider of the good is preferred to not having the good provided at all. Two pure strategy NEs exist for the game of Chicken: (C,D) and (D,C).

An example of a collective good in the form of Chicken might be preventative steps taken to avert a national disaster: no action has significant costs for all should a disaster occur, and so being the sole provider may be preferred to not having the good provided at all (Sandler 1992). Given the importance of many collective goods to survival and reproduction in nature, this situation is also probably highly relevant to animal behaviour. For example, being the sole individual to provide territorial defence may be preferred to not having a defended home range.

It is necessary to clarify the difference between Chicken and the game called Hawk–Dove (Fig. 3.1). In Hawk–Dove the payoffs are represented as formulas relating the fitness gains of winning (V) to the costs of injury (C; Maynard Smith 1982). Each player has a choice between two strategies: Hawks (corresponding to defection) escalate the contest until injured or until the other player retreats; Doves (cooperators) display and retreat as soon as the other player escalates. Thus, under different ratios of V to C, this situation represents either PD or Chicken: when $V>C$, the NE is (H,H), representing a PD; but when $V<C$, the NE are (H,D) and (D,H), which correspond to the equilibria in Chicken (if $V=C$, then H,H is weakly dominant and still a PD). Thus, the game switches as the costs change relative to the benefits.

Hawk–Dove therefore illustrates the point that PD, Coordination and Chicken are simply names for particular payoff structures. Other game structures are discussed elsewhere (e.g. Taylor & Ward 1982; Bates 1988; Hawkes 1992; Sandler 1992). We next turn to elaborations on these basic games.

Beyond the two-player simultaneous game

The simple games reviewed so far capture the essence of collective action. Such games therefore serve as a first step in modeling CAPs. However, these 'cookie-cutter' models are often gross oversimplifications of the real world and their assumptions can often affect the predicted outcome. In this section, we examine these assumptions and how they change the expected results of game theoretic analyses of collective action.

Repeated games

Thus far we have examined situations where individuals play each other once (also called one-shot games). Another component that can be added to the model is repeated interactions, where the same individuals play one another repeatedly with some probability of continued play. Thus, repeated games allow for non-cooperation in the future, based on patterns of behaviour in the past (i.e. history). For example, over a large number of repetitions, strategies such as Tit-for-Tat signal a willingness to cooperate as long as the cooperation is mutual (Axelrod & Hamilton 1981).

Repeated interactions are typically assumed in the 'tragedy of the commons' (Hardin 1968) or CPR problems (Ostrom 1990). One common proposal is that repeated interactions facilitate cooperation (Axelrod & Hamilton 1981; Dugatkin 1997). However, even in long-lasting human CPRs, free-riding is observed (Ostrom 1990). Game theorists have shown that cooperation need not always be the NE when repeated interactions occur (the so-called 'folk theorem'; for further discussion see Myerson 1991 and Binmore 1998), and other strategies may invade even Tit-for-Tat (Boyd & Lorberbaum 1987). Thus, private incentives or coercion may be needed to shift the payoff structure to overcome CAPs in iterated games (see below).

In stable social groups, individuals presumably experience iterated games. Heinsohn and Packer (1995) showed that female lions were aware of one another's past strategies; thus, individual history appears to be a factor, consistent with iterated models. Interestingly, however, retaliatory noncooperation was not observed among lions.

Dynamic games

Thus far we have examined simultaneous games. However, games can also be dynamic, where players move sequentially (also called extensive form games). In a sense, a repeated simultaneous game among two individuals could be considered dynamic, in that the interaction is iterated sequentially. By dynamic games, however, we are referring to situations where one player moves after the other.

Animals often move sequentially, for example in allogrooming among impala (Hart & Hart 1992). Dynamic games may therefore be important for understanding collective action in animal societies (cf. Fischer 1988). Economists have not commonly modelled dynamic interactions outside of what are more accurately called repeated games (e.g. Hardin 1982; Sandler 1992), although biologists have addressed issues related to sequential play (Enquist & Leimar 1993; Frean 1994; Roberts & Sherratt 1998). These analyses show that sequential play may have important impacts on the outcome, depending on the game structure and whether it is iterated. Box 3.2 provides an example of Chicken as a dynamic game, with special emphasis on sequential moves that might exist in territorial defence.

Incomplete information

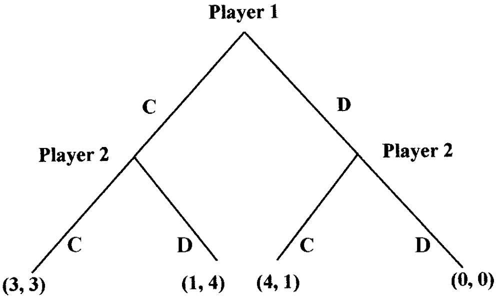
Another assumption involves complete information. In games with complete information, each player knows with certainty the other player's payoffs for every action. Economic models of collective action have also considered situations where players are uncertain of the utility obtained by other beneficiaries of the good (see Fudenberg & Tirole 1991). Returning to lions, one female may not be certain of the value that another pride member places on the particular section of territory that is being challenged. These models may therefore be useful in animal behaviour. Box 3.3 provides a general example of a game with incomplete information.

N-player games

Finally, models can include polyadic interactions, where multiple individuals play against one another. This scenario calls for *n*-player games, which can produce outcomes that differ from two-player games (e.g. Joshi 1987; Boyd & Richerson 1988; Dugatkin 1990). Here, we are referring to a specific type of *n*-player game: models of collective action are correctly modelled as all individuals in a group benefiting when at least one of the

Box 3.2 Dynamic games

Dynamic games use a game tree instead of a matrix:



In the game shown here, players have identical strategies (C or D). Player 1 makes the first move. After Player 1 moves, Player 2 chooses whether to cooperate or defect. Backward induction predicts that Player 1 will defect and Player 2 will cooperate (D, C). The sequential game of Chicken, therefore, differs from the simultaneous game of Chicken in that Player 1 will never cooperate when she moves first; hence, there is only one equilibrium (two NE exist, but only one is subgame perfect; see Fudenberg & Tirole 1991).

The question therefore becomes: which individual gets to move first? A number of factors probably determine which individual has priority. In a territorial encounter, one individual may simply be closer to the territorial boundary, and thus more in the 'line of fire' of an intruder. This individual may be forced to move because her risks are higher. Other factors, such as age or reproductive condition, may change individual costs and benefits, and therefore lead to one individual acting first. Finally, some individuals may force the order of play: more dominant individuals may have the power to manipulate who participates.

This distinction between simultaneous and dynamic games may be critical for understanding cooperation in animal behaviour. In the case of lions, and, if the game is dynamic, the cooperator (referred to by Heinsohn & Packer 1995 as the 'leader') is actually Player 2 and is leading only because she is forced to do so by Player 1's failure to act. The dynamic game predicts that, if Player 2 could move first, she would switch her strategy.

Box 3.3 Incomplete information

Players in games of cooperation may not be fully informed about their opponents' costs and benefits. In such cases, players may instead use a probabilistic model to determine which strategy to play. An example of a collective good game with incomplete information is provided in Fundenberg and Tirole (1991). The following is a simplified version of that game.

The incomplete information in this game is related to the costs. Each player knows his own cost of cooperating (c_i), but not the other player's (c_j), and Player i believes that c_j ranges between 0 and 1. Such a situation might arise with cooperative territoriality, where the players do not have complete information regarding their groupmates' costs in intergroup defence (which might vary according to individual fighting ability, reproductive state, or health).

		Player j	
		C	**D**
Player i	**C**	$1-c_i, 1-c_j$	$1-c_i, 1$
	D	$1, 1-c_j$	$0, 0$

Optimal behaviour depends upon the costs of cooperating for Player i. The optimal strategy (for each player) is to fix some benchmark level c_i^*, such that Player i will cooperate when $c_i < c_i^*$ and defect when $c_i \geq c_i^*$.

The probability that Player j will cooperate in any given situation is P. This number is fixed for any one game. The optimal strategy is to cooperate when $c_i < 1 - P$ and to defect when $c_i \geq 1 - P$. The strategy 'cooperate when $c_i < 1 - P$' is the benchmark value c_i^* for Player i. Given c_j^*, the probability that Player j will contribute is

$$\text{Prob}\,(c_j \leq c_j^*) = c_j^*$$

Therefore, there exists some benchmark $c_i^* = 1 - c_j^*$. As long as $c_i^* + c_j^* = 1$, a Bayesian equilibrium exists. The symmetrical equilibrium is $c_i^* = c_j^* = 1/2$.

		Player 2	
		C	**D**
Player 1	**C**	$b_1-(1/2)c_1$, $b_2-(1/2)c_2$	b_1-c_1 , b_2
	D	b_1 , b_2-c_2	0 , 0

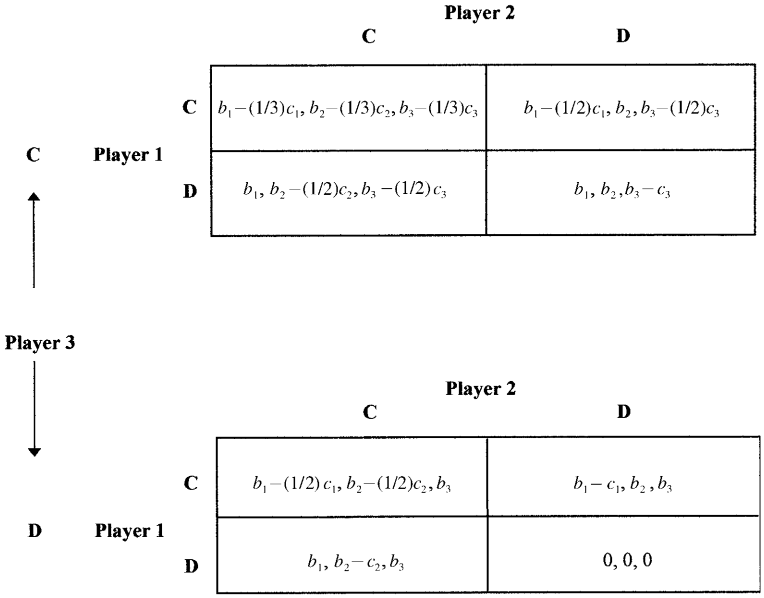
Fig. 3.2 Generic two-player game of Chicken. Notation and assumptions as in Fig. 3.1. Costs (c) and benefits (b) are represented as variables.

players contributes (not simply that two of *n* players engage in a dyadic exchange, as in some models; Enquist & Leimar 1993). Among these *n*-player models, Boyd & Richerson (1988) showed that reciprocal cooperation is more difficult when the Prisoner's Dilemma game is played among *n* players, although the generality of this conclusion is known to depend on other variables (see Ostrom, this volume). Furthermore, multiple equilibria commonly exist in *n*-player games (e.g. Boyd & Richerson 1992; Sandler 1992).

N-player games are more difficult to represent and often involve more complicated mathematics (see Sandler 1992). These models become even more complicated when multiple strategies exist, as suggested in the case of lions (Heinsohn & Packer 1995). Therefore, rather than continuing with this example, we take a simpler example that demonstrates the effect of adding a player by comparing the results of a two-player simultaneous game of Chicken to a three-player game of the same general type.

We begin with a generic two-player game of Chicken (Fig. 3.2). In this game, *c* and *b* represent the costs and benefits of providing the collective good; subscripts indicate the costs and benefits to each of the two players. We assume that both players experience identical costs and benefits ($b_1 = b_2$ and $c_1 = c_2$). To meet the assumptions of Chicken, $b > c > 0$. As in Fig. 3.1, the NE are (C, D) and (D, C).

This generic two-player game can then be expanded to a three-player game (Fig. 3.3). When the same conditions are met, three pure strategy Nash equilibria exist: (C,D,D), (D,C,D) and (D,D,C). An important conclusion from this analysis is that the good is still provided by only one player, with the number of free-riders increasing from one to two. This finding is consistent with previous *n*-player analyses of Chicken (Bornstein *et al.* 1997).



Player 3

C

Player 2

Player 1	C	D
C	$b_1-(1/3)c_1, b_2-(1/3)c_2, b_3-(1/3)c_3$	$b_1-(1/2)c_1, b_2, b_3-(1/2)c_3$
D	$b_1, b_2-(1/2)c_2, b_3-(1/2)c_3$	b_1, b_2, b_3-c_3

D

Player 2

Player 1	C	D
C	$b_1-(1/2)c_1, b_2-(1/2)c_2, b_3$	b_1-c_1, b_2, b_3
D	b_1, b_2-c_2, b_3	0, 0, 0

Fig. 3.3 Three-player game of Chicken. The two-player game in Fig. 3.2 expanded to three players. Net benefits in each cell correspond to Player 1, Player 2 and Player 3, respectively.

Overcoming collective action problems in animal behaviour

In human societies, collective goods are commonly obtained despite the temptation to free-ride (e.g. Ostrom 1990). As noted above, collective goods are also obtained in animal societies, including territorial defence of a shared range, cooperative hunting and shared vigilance. Collective goods are not limited to the social vertebrates; among invertebrates, examples may include web-building and prey digestion in social spiders (Ward & Enders 1986) and interspecific mutualisms, such as the relationship between lycaenid butterfly larvae and ants (Axén & Pierce 1998).

Economists have identified a number of ways in which free-riding is overcome in human societies, and much of the economic literature focuses on policy issues and institutional structures that facilitate collective outcomes (e.g. Olson 1965; Ostrom 1990). We hypothesise that when cooperation is advantageous, natural selection will use some of these same mechanisms to overcome free-riding in animal societies. General indicators of selection for overcoming CAPs in non-human societies might include elaborate signals for communicating intent over some cooperative act (e.g. Noë *et al.* 1991), or intelligence to more easily (and accurately) monitor free-riding by group members (e.g. Machiavellian intelligence: Byrne & Whiten 1988). Documentation of these and other mechanisms would therefore be consistent with the selective force of free-riding.

Here we review some of the major factors thought to facilitate the acquisition of collective goods in human societies, and we examine how these factors relate to animal cooperation. We also consider more general features that help overcome CAPs. When possible, we place these mechanisms in the context of the games presented above. It is important to note, however, that these factors may interact with other variables to produce non-intuitive results. Ostrom (this volume) provides a review of these issues in human collective goods.

Asymmetric benefits

In animal societies, individuals often differ in how the benefits of some good are shared. For example, in between-group territorial conflict, dominant individuals within the group may consistently obtain greater benefits from the defended territory. These dominant individuals are therefore more likely to participate in territorial defence. Similar effects have been investigated for cooperative hunting (Packer 1988). The general principle behind asymmetric benefits therefore has clear applications to animal societies, where dominance hierarchies and reproductive skew could be used to assess asymmetries and thus to predict levels of individual involvement (see also Nunn 2000).

If individuals participate according to their benefits, then a CAP does not technically exist: individuals are ‘getting out of it’ what they are ‘putting in’. However, economists have shown that, in cases of asymmetric benefits, ‘privileged’ individuals (or coalitions of individuals) may end up contributing a disproportionate share of the costs, leading to what Olson (1965) called ‘a systematic tendency for “exploitation” of the great by the small’ (p. 29). In these *privileged groups*, collective action is achieved because the benefit for one individual (or coalition) exceeds the costs of providing the collective good. This individual (or coalition) is therefore willing to provide the good, while other individuals free-ride (see also Packer 1988). If privileged groups exist in animal societies, one implication would be that along with the benefits of high rank come a number of costs in terms of providing collective goods.

Asymmetries can be modelled by changing the assumption of symmetry in the generic game of Chicken. Thus, the values of b and c can be varied to create asymmetry in Figs. 3.2 and 3.3. For example, Player 1 may be the dominant male in a polygynandrous primate social group, and the collective benefit among males is successful defence of females in the group. While subordinate males may also reap some of the collective benefit, their opportunities to mate with the females will be more limited; thus, $b_1 > b_2 > b_3$.

Coercion and private incentives

An intuitively obvious way to achieve a collective outcome is to coerce free-riders into participation through punishment, where punishment refers to aggressive retaliation for failure to cooperate rather than simple non-cooperation (Boyd & Richerson 1992; Clutton-Brock & Parker 1995). Expulsion from the group may also qualify as coercion, especially when it serves to threaten remaining group members into greater participation. Economic concepts of coercion are therefore closely related to 'policing' in biology, where policing usually refers to behaviours that reduce competition and selfish behaviour within the group so that a collective outcome is obtained (Frank 1995; Ruxton & van der Meer 1997).

A related factor involves private incentives that are provided to those that contribute (related to bribery in animal behaviour; Clutton-Brock & Parker 1995). Private benefits, in contrast to collective ones, are monopolisable. Hence, these benefits can be shared among participants but excluded from free-riders (unlike collective goods). In human societies, for example, magazine subscriptions commonly accompany membership in special-interest groups (e.g. academic or environmental groups). Private incentives in animal behaviour may include grooming (Seyfarth & Cheney 1984) or access to food resources (de Waal 1989), as these benefits can be shared or given to participants but excluded from non-participants. If private incentives are exchanged for cooperative acts in nonhumans, this interaction would technically involve 'interchange' (Hemelrijk & Ek 1991) between private and collective goods.

Private incentives and coercion can be analysed by including their effects in a game theory payoff matrix. In theory, private incentives and coercion are identical through their effects on the net benefits; in practice, however, some differences may exist in how each affects the net benefits. For example, coercion may have a larger negative effect on the net benefits, especially when the coercion results in serious fitness consequences, such as expulsion from the group (e.g. ringtailed lemurs: Vick & Pereira 1989).

Coercion and private incentives at first appear to be relatively straightforward. However, several additional factors should be considered. First is incomplete information and 'noise' in the form of errors: depending upon the game structure, too many enforcement errors can lead to collective failure, as through mutual defection (D,D) in Tit-for-Tat (e.g. Ostrom 1990). Second, costs of enforcement need to be factored into the payoffs. Finally, and related to the previous point, this simplistic depiction of coercion and private incentives conceals a deeper, more complicated issue: punishment and bribery are themselves collective goods (Bates 1988; Boone 1992; Boyd & Richerson 1992). In this 'second-order' CAP, individuals may avoid providing the private incentives or punishment needed to achieve a collective outcome because other group members will also benefit (the 'policing problem'; Hammerstein 1995). However, we believe asymmetric benefits make this less of a problem in animal behaviour, as individuals that benefit most should be more willing to both monitor and enforce participation, and their threat of coercion should therefore be more credible (Ostrom 1990; see also Clutton-Brock & Parker 1995; Frank 1996).

One final aspect of variable participation is worthy of mention: participants may obtain additional benefits if their costly actions serve as an honest signal to other group members (Zahavi 1977, 1990). This information could be used by these group members when they choose a future mating or coalition partner (Noë & Hammerstein 1994; Roberts 1998), or as a factor in deciding to cooperate or defect with a particular partner in the future (i.e. reputation; Pollock & Dugatkin 1992). Individual participation could also serve as an honest signal of competitive ability, which could be important for within-group dominance struggles (e.g. ringtailed lemurs: Nakamichi & Koyama 1997). Because participation is costly yet provides a benefit, individual participation could be an especially effective means to signal individual quality (see also Roberts 1998).

Kinship and mutualism

Cooperative behaviour should increase as the relatedness of the interacting individuals increases (e.g. Hamilton 1963). Thus, free-riding might be expected to decline with increasing relatedness (e.g. Hawkes, 1992; van Schaik 1996). However, punishment of free-riders poses a problem in kin groups: when a cooperator is faced with free-riding kin, the cooperator may actually decrease its inclusive fitness if it punishes too severely (e.g. through expulsion). Thus, in general, current thinking suggests that CAPs will be reduced in kin groups, but additional mechanisms may still be needed, especially as relatedness declines (Frank 1995).

		Player 2	
		C	D
Player 1	C	4 , 4	1 , 3
	D	3 , 1	0 , 0

Fig. 3.4 Effect of economies of scale. In this case, both players benefit most from mutual cooperation, and so cooperation is expected (see also Dugatkin 1997).

Another factor involves what economists call economies of scale or synergies (Fig. 3.4). This factor has similarities to byproduct mutualism (or no-cost cooperation) in animal behaviour (Dugatkin 1997). In such cases, the sum of two or more individuals is worth more than their parts, so that individuals do worse if they fail to cooperate (e.g. chimpanzee cooperative hunting: Boesch 1994). However, an important point is commonly overlooked in larger groups: diminishing returns to cooperation can lead to a low level of free-riding when groups become large. For example, two individuals in a social group may be able to defend the territory more effectively than a single individual (synergistic mutualism); however, equivalent gains may not be achieved by adding more participants (diminishing returns). Mutualistic benefits may therefore 'overcome' free-riding most effectively in small groups, with the level of free-riding increasing in large groups (see also Nunn 2000).

Ostrom's (1990) design principles

We conclude this section by considering other features that may overcome free-riding in human collective goods and may therefore also apply to non-human behavior. Important factors that facilitate collective action in humans include low monitoring costs, escalating penalties for continued non-participation, private benefits that accrue to enforcers, conflict resolution mechanisms (reconciliation) and clearly defined boundaries and rules governing who gets what, with the ability to enforce these rules (e.g. dominance hierarchies). Ostrom (1990) also notes that harsh environments are correlated with successful CPRs in human societies (which could also be evaluated by changing the payoffs in a game theoretic model). This correlation predicts that, in interspecific comparisons, species that inhabit particularly harsh environments should exhibit behavioural mechanisms to achieve collective outcomes. Ostrom (1990) makes another point that should be kept in mind when applying these principles to animal behaviour: multiple solutions often exist for achieving a collective outcome. Studies of animal cooperation may therefore reveal similar variability. However, some of these principles require the existence of individual recognition and memory of past interactions; thus, we should not expect to observe all of these factors in all animal societies.

Discussion and conclusions

Economic models of collective action and existing models of cooperation in biology address common themes (e.g. the effect of group size on cheating; Olson 1965; Boyd & Richerson 1988; Sandler 1992). However, these models have important differences, primarily because they focus on different systems and because they often have different goals (e.g. description of ultimate factors in biology versus policy recommendations in economics). Thus, economic models focus inquiry in biology by framing issues of cooperation in different ways. These economic concepts may therefore shed new light on the factors underlying animal cooperation.

With the goal of elucidating these similarities and differences, we briefly compare economic approaches based on collective action with more traditional approaches to cooperation in animal societies. As an example of how the approaches are similar, both economists and biologists examine decisions to cooperate or defect at the individual level (e.g. through game theory; Sandler 1992; Dugatkin 1997). However, collective action models explicitly frame individual motivations in the context of collective gains, where one individual cannot easily be denied the benefits obtained by others. The economic framework therefore focuses attention on how the benefits of different goods are shared.

Similarly, both animal behaviour and economic approaches to cooperation consider mechanisms that overcome cheating (e.g. punishment and coercion; Olson 1965; Boyd & Richerson 1992). However, economists have generally considered a wider range of solutions than have biologists. Most of these features, like asymmetric benefits, have clear applications to animal behaviour. Economists have also established the varied conditions under which these mechanisms operate, which provides a conceptual framework and a set of predictions for empirical studies of cooperation in animal behaviour.

In general, economic theories of collective action have the potential to provide an improved conceptual framework for investigating animal cooperation in large, complex social groups. Although both approaches tend to use a common set of theoretical tools (i.e. game theory), the general principles derived from these models likely differ. However, collective action models do not overcome the problems of quantifying interactions in actual social groups: behaviour among many interdependent actors will never be simple to model, whether the focus is on human or nonhuman societies.

Models of collective action in animal behaviour will also be complicated by factors beyond those discussed here. For example, Niou and Tan (1997) suggest that the ability of individuals to free-ride in one group may depend upon the number of free-riders in a competing group. Thus, in cases of territoriality, individuals play off one another not only within the group, but also against their ‘enemies’ in the other group (cf. trench warfare in humans; Axelrod 1984). Several other factors should be taken into account, including histories of individual participation (i.e. repeated games and potential reciprocity; Axelrod & Hamilton 1981). In addition, individual patterns of participation in collective activities (e.g. group hunting or vigilance) may offset lagging in another collective good (e.g. territorially; cf. ‘service economies’: de Waal 1997). Hence, no easy solution is apparent for perfectly modelling collective behaviour in any society, be it human or nonhuman.

Simultaneous, one-shot games with two players, such as those in Fig. 3.1, have been used to model interdependent outcomes in both economics and biology. By first examining CAPs within dyads, these models illuminate individual decisions regarding cooperation and the temptation to defect. These models also highlight important aspects of cooperation by forcing biologists to evaluate the assumptions of their models, which can then be elaborated to fit more complex realities. One point we wish to emphasise is that the PD is not the only game available for analysing cooperation in animal societies; in fact, it may often be inappropriate (e.g. Taylor & Ward 1982; Noë 1990; Hawkes 1992).

Future directions

Some comparative evidence suggests that economic models of collective action apply to non-human societies (van Schaik 1996; Nunn 2000). However, these comparative studies fail to demonstrate the causality implied by this theoretical framework. In addition, we need information on how CAPs are overcome in animal societies.

Probably the most direct test for the existence of CAPs would involve experimental manipulations of the conditions predicted to lead to free-riding. Primate field studies show that involvement in intergroup encounters is sufficiently flexible (e.g. van Schaik 1996) to allow for tests of these hypotheses using an experimental approach. Thus, informed observations and experiments are an important next step in testing the applicability of this general framework. Such research has been conducted with the semi-free-ranging ringtailed lemurs at the Duke University Primate Center, where one of the authors (C. L. Nunn, in collaboration with R. Deaner) has studied free-riding in the context of territorial behaviour (unpublished data). We have been able to show that, in this system, the basic conditions for applying the framework of collective action are met: territorial defence is costly for individuals to provide, and the benefits of range defence provided by one individual 'spill over' to other individual females in the group. Consistent with these conditions, individuals vary in their participation in intergroup encounters, with at least one individual free-riding entirely (i.e. no participation in intergroup encounters; $n = 14$ individuals in two social groups over two years of study). Presently, we are investigating the factors that lead to individual participation in territorial defence, including any factors that might overcome the temptation to free-ride. This chapter will hopefully stimulate similar research in other taxa, which will likely reveal great diversity in patterns of free-riding and in the mechanisms that overcome this free-riding.

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JAN A.R.A.M. VAN HOOFF

4

Conflict, reconciliation and negotiation in non-human primates: the value of long-term relationships

The despotic society model

In 1932 an English zoologist, the later Sir Solly Zuckerman, published a book entitled *The Social Life of Monkeys and Apes*. It was based to a large extent on his studies of the social behaviour and relationships in a colony of hamadryas baboons (*Papio hamadryas*) in the London Zoo. This book would influence the scientific view on animal societies for a long time to come. Zuckerman painted a rather grim picture of this baboon society. He emphasised its despotic character. Despotic dominance relationships were maintained by severe, sometimes lethal, aggression and bullying, and were expressed in sexual violence and raping. Sexual drive was supposed to form the main cohesion factor. Sexual presenting, typically a female solicitation behaviour, but also used by subordinate males, was supposed to function as a submissive means to avert violence and the tensions of conflict. We now recognise this picture as a caricature. The situation was caused by the unnatural, and – one might say – even pathological condition of this colony. The hamadryas baboons had been collected from the wild and had been put together in the zoo, without due regard for the natural growth and for the history and maturation of their social relationships.

The complexity of natural social organisation

The hamadryas baboon has a rather peculiar social organisation, unlike that of many other primates (Kummer 1957, 1968). In the wild these baboons live in large groups with a multilayered structure. The basic units are formed by harems, in which, as a rule, a single adult male herds a few females and their offspring. In the barren desert environment in which this species lives, these harems are the basic foraging units. These comparatively small social units obviously are a compromise: the units are probably sufficiently large to defy predators but not so large as to induce prohibitive competition within the unit for the small-sized resources that are available in their arid environment. At night the harems of a troop congregate on one of the few sleeping cliffs that are available in the desert in which this species lives, but during the day they split up to travel and to forage independently, widely separated from one another. A few of such harems remain in closer association with each other than with others. The harem leaders may coordinate their behaviours and they may, for instance, congregate during resting pauses. Together these harems form a clan, led by males who are usually closely related. These males, remarkably, show great 'respect' for the male–female bonds in the other harems that belong to their own clan. This is expressed in a restraint to interfere in the male–female bond. Such restraint does not exist with regard to the sexual bonds of non-clan males (Kummer *et al.* 1974; Götz *et al.* 1978). The males express their affiliation by ritualised sexual presentations and mountings that serve as 'greetings'. The clans, in turn, may operate in bands, which, in turn again, form the total troop.

A young adult male starts to form his own harem usually by 'stealing' juvenile females from an existing harem. He can abduct these juveniles, because the 'harem lord' has little interest in his own juvenile daughters. The new male adopts the role of a 'surrogate mother' for the young female, carrying her on his back, but also punishing her with a ritualised neck bite whenever she wanders away from him too far. At the same time, however, he offers her comfort when she returns to him, the only source of reassurance which she has got, now that she is no longer in the harem of her mother.

I have given a detailed account of these aspects of hamadryas social organisation, because it reveals the complexity of a historically developed system of relationships, many elements of which are lost or messed up when you put a number of individuals together haphazardly. But that is precisely what happened in the London Zoo. And what one saw were the frustrated, deregulated attempts of the individuals to restructure their relationships, making use of elements of behaviour that function in an adaptive, well-integrated fashion in their natural context, in accordance with the norms stemming from these animals' natural heritage. As Hinde (1979) has emphasised: social structure is a set of patterned relationships between individuals, emerging from interactions which are determined both by experiences from the past and expectations about the future, which, in turn, evolve in dialectic interaction with the evolutionary, genetic endowments of the species.

Aggression and social harmony, a contradiction?

The picture of animals, forced to live together by ecological pressures (as in nature) or by human-imposed constraints (as in the zoo) and coping with the grim aspects of competition and aggression in a strongly hierarchical social world, was not in discord with the prevailing view on the nature of evolution, namely of 'nature red in tooth and claw', as a result of 'the struggle for life and the survival of the fittest'. In keeping with this one-sided view on the process of evolution, aggression was seen as the instrument of competition and rather as a socially disruptive force. If social cohesion was maintained, it was in spite of the dissociating force of aggression. This view of aggression was certainly reinforced by the type of laboratory research, 'en vogue' up to the 1970s, in which aggressive behaviour was studied in isolation from its natural functional embedding (de Waal 1996b). It only slowly gave way to a view in which aggression, in resulting in stable dominance orders, was seen as not only an egotistic, but also a stabilising factor in social relationships (see, for instance, Jolly 1972).

It was especially Konrad Lorenz (1966) who, in his classical work on the biology of aggression, emphasised that aggressive competition between conspecifics is often of a subdued kind, expressed in the form of ritualised displays. He pointed out that aggression must be conceived as an adaptive process regulating the relationships between conspecifics in such a manner that the aggressor can achieve vital objectives. Although this is achieved at the cost of other animals, it would occur as a rule without unduly damaging the survival chances of the loser, and would still give the loser a fair chance to adjust or to withdraw and try his luck elsewhere. The evolution of ritualised fighting and displaying thus provided the restraint necessary to prevent – as Lorenz put it – the survival of the species being endangered. In the first point Lorenz has proved to be right. However, in invoking the survival of the species (or of the group, for that matter) as the restraining factor he was at odds with the insight, developing at the time, that natural selection cannot take the interest of the species into account, because it selects on the basis of the inclusive reproductive success of *individuals*.

In the late 1960s and the 1970s models were developed to explain altruistic behaviour and the restraint of selfish impulses. They were based on the recognition that evolution proceeds as a result of selection at the level of individuals. The models were those of 'kin selection and inclusive fitness maximisation' of Hamilton (1964) and of the 'reciprocal altruism' of Trivers (1971).

In these models behaviours came to be seen as strategies, based on decisions, choices, trade-offs. These are basically economic evaluations. Animals are supposed to follow rules which take into account the costs and benefits relating to the inclusive fitness consequences for the individual involved.

Thus formulated, the neo-Darwinian paradigm of evolution has proved enormously powerful in generating testable deductions. It has succeeded in providing elegant explanations for a great variety of biological phenomena as adaptive structures and processes. This includes the organisation and strategies of behaviour. We understand how these emergent properties are shaped economically so as to contribute to the fitness of their bearers in the optimal balance of effectiveness and efficiency. The principles involved have been elaborated first and most extensively in optimal foraging theory (e.g. see Krebs & Kacelnik 1991). The present symposium offers many examples that are well documented empirically.

Social organisation: the outcome of compromising

Social behaviour and social organisation are important phenomena to look at from this perspective. In many cases they can also be understood as trade-offs reflecting such economic principles.

Animals organise themselves in patterns of relationships that show great variation between species. In the past two decades socio-ecological theorising and the consequent empirical testing have come to provide explanatory models for these variations. They have come to show that the social pattern is the result of a number of evolutionary ‘choices’.

First there is the choice between a more solitary or a more social life style. Studies especially concerning the social organisation of primates have revealed the nature of this choice. For primates there has been growing consensus that the major benefit of social life is the increased safety against predators; this benefits females and their vulnerable offspring in particular (van Schaik 1983; van Schaik & van Hooff 1983; Dunbar 1988). Other benefits that may have contributed to the evolution of social cohesive systems are within-group collaboration, especially in between-group competition (Wrangham 1979, 1980). Recently the defence against infanticide by males has been invoked as another major factor facilitating social bonding (van Schaik & Dunbar 1990; van Schaik 1996; van Schaik & Kappeler 1997). It might either stimulate cohesion between primate females of some species. Or it might, alternatively, induce primate females to join under the protection of a male who is strong enough, for the time being, to offer safety against attacks by contesting males on infants born under the protection of the selected male (Sterck *et al.* 1997). From the point of view of the male, it might convince him to give up a possible 'roving-male' strategy, and to opt for a protective bond instead (see Dunbar this volume). The development of the monogamous bonding found in gibbons and siamangs has been explained in this way (van Schaik & Dunbar 1990).

Competition, the unavoidable consequence of social association

Whatever the major reasons may have been for any particular species to live together, such association is bound to entail increased competition between the associating members. There is evidence for a growing number of species that the individuals of a group have to invest more energy and to take higher risks to reach the same level of resource exploitation when they are in the presence of others than when they are on their own. For example, free-living long-tailed macaques living in larger groups were found to travel further and longer during their daily foraging trips, and to spend less time on the anabolically important behaviour of resting. Similarly, these monkeys reached a higher level of fruit-picking when they foraged in small sub-parties instead of in the main party of their group (van Schaik & van Noordwijk 1986). This measure showed also an interesting effect of rank in addition to that of party size: higher-ranking animals had higher fruit-picking rates, whether they were in a large or in a small party. We detect here two components of competition, namely *contest* or *exclusion competition* and *scramble competition* (van Schaik and van Noordwijk 1988) (see Box 4.1).

These are instances of the many studies which show that competition is part and parcel of social life, whatever form it takes. When such competition takes the form of contest or exclusion competition, it leads to more-or-less frequent aggressive conflicts, and to resulting dominance hierarchies. This is the aspect that has commanded most attention for as long as the social life of animals has been studied.

Competition and the value of long-term relationships

Of course, aggression and contest in competition are behavioural mechanisms which an animal uses to safeguard certain of its interests. Recently, however, it has become realised explicitly that these mechanisms should be embedded in long-term social strategies so as not to jeopardise the

Box 4.1 Contest and scramble competition: the influence of the type of competition on social relationships

It is important to distinguish two components of competition, namely *contest* or *exclusion competition* and *scramble competition* (van Schaik & van Noordwijk 1988; Milinski & Parker 1991). Which of these components prevails in the patterns of competition that members of a particular species experience has great influence on their social relationships.

Contest competition is manifest when there is an unequal distribution of resources between animals of different social rank. It occurs when one animal can effectively exclude another from access to a resource. This is possible only when the distribution of the items of that resource or the size of its items are such that monopolisation is possible and economically feasible. Then the more powerful animals (or the more powerful coalitions) can monopolise access to resources until they have satisfied themselves; only thereafter can lower-ranking animals take their turn. As a result there will be a clear rank effect in exploitation success.

When, on the other hand, the size and/or dispersion of the resource items is such that attempts to monopolise these make no sense, then the group members will, irrespective of their rank, race to scramble for their share of the cake. If a stronger animal goes for a piece here, the less strong animal will go for a piece there. Consequently exploitation success will, in the ideal case, hardly be skewed in relation to social rank. In most practical cases though, both the components of contest and scramble competition will be present. We do recognise the scramble component of competition when there is an effect of group size: when more individuals compete for a share of the same cake and each, therefore, gets an equal but smaller part.

Van Schaik and van Noordwijk (1988) have pointed out how important this distinction between ‘contest’ and ‘scramble’ competition is for the social relationships. Competition for food affects females in the first place, because their fitness depends on a long life in good condition. This is the crucial condition allowing them to successfully raise many offspring in succession. When contest competition is possible, then, as a consequence, natural selection can be expected to stimulate the physical and motivational dispositions required to obtain dominance and power. Consequently also, societies are to be expected in which the females develop strong nepotistic bonds and comparatively despotic, family–clan rank systems. If, on the other hand, competition tends towards the scramble type, the adaptive advantage of investments in the maintenance of status hierarchies will be lower, and more egalitarian and symmetrical relationships will develop (Vehrencamp 1983; Hand 1986; van Schaik 1989).

Similarly, the relationships between males will be determined mainly by the competition for those resources that primarily determine their fitness, namely for fertilisations (van Hooff & van Schaik 1992, 1994). Again, the degree to which the access to fertilisable females can be monopolised depends on the degree to which females, for reasons of their own concern, form temporally and spatially cohesive groups. If groups of females can be monopolised, there is a selective advantage for males to be larger and stronger and contest-motivated. Sexual dimorphism is undoubtedly the result of such a selection regime (Alexander *et al.* 1979). If, on the other hand, fertile females distribute themselves in a dispersed manner, or if they come into oestrus at about the same time, then it may simply be impossible for a male to monopolise access to all these females. Consequently there are two possibilities. Either a system of scramble competition in the form of frequent matings and sperm competition may ensue; the fact that males living in promiscuous multimale groups have comparatively large testes and invest in frequent matings has been regarded as support for this deduction (Harcourt *et al.* 1981; Møller 1988; Kappeler 1997). Or, alternatively, a male may choose to concentrate its investments on one female and form a monogamous bond (of course only if his help or protection make a difference for the survival of his offspring with that female; his contribution should offset the competition disadvantage for that female and offspring because of his presence).

beneficial consequences of the association with conspecifics on which the animal depends for its own survival and inclusive fitness. An individual which suffers from the disadvantages of competition within her/his group has to decide whether the advantages of staying in that group outweigh these disadvantages.

When there is 'only' scramble competition, ideally only group size in relation to local resource abundance is the factor to be considered. If the group grows too large, its members may decide to leave the group or expel certain others (of course such costs as those of giving up a familiar association and settling in an unfamiliar environment, and the risks of moving elsewhere have to be included in the 'calculations').

When competition is of the contest type, an individual's relative dominance position is a factor as well, if not the crucial factor. Subordinates always bear the brunt of contest. A subordinate is the first to be confronted with the dilemma: 'Are my benefits of being associated with these conspecifics worth the misery which I suffer because of the contest competition with them?' Clearly then, the scales are tipped in favour of quitting from the association earlier for subordinate than for dominant animals.

But, if this is the case, then there is also a reason for concern for the dominant. He simply cannot exploit his superiority in power to secure advantages at the cost of his partner.

First there is, of course, the obvious risk that the subordinate may be tried too far and go for a confrontation. There is always a cost for both contestants because of the energy required, because a fight disrupts other maintenance functions, because it distracts from keeping an eye open for dangers and – last but not least – because it entails the risk of getting hurt. This aspect of risk has been recognised for a long time and is an essential element in the first game-theoretical models that considered the evolution of strategies of confrontation (Maynard Smith & Price 1973).

But equally, if not more importantly, there may be a long-term effect. If the mere presence of a conspecific or, perhaps, an active investment on his part yields a benefit to the dominant, then the dominant should take care to maintain a positive balance for the subordinate in his association with him: the association should remain sufficiently attractive for the subordinate to maintain his investment into it. Deductive reasoning predicts that the interest which different parties have in their long-term relationships must exert a corresponding moderation on the selfish exploitation of that relationship.

Reconciliation: reducing post-conflict stress

To what extent are these growing theoretical insights corroborated by empirical data. Recent findings concerning the existence of processes of reconciliation are of especial interest in this respect.

In 1979 de Waal and van Roosmalen found that conflicts between chimpanzees, living in the Arnhem Zoo chimpanzee colony, were often followed by an affiliative or 'friendly' contact. The former contestants would approach, touch, embrace and 'kiss' each other. Systematic studies on a number of species have shown since then that the likelihood of such a friendly contact between contestants was much higher in the first minutes after the conflict than between these same two animals in a matching control period in which there had been no preceding conflict (rhesus macaques: de Waal & Yoshihara 1983; long-tailed macaques: Aureli *et al.* 1989). For details of the method see Box 4.2.

It appeared to be justified to call these affiliative contacts 'reconciliations', because their occurrence indeed lowered the likelihood of a new conflict. Their occurrence also reduced expressions of tension and nervousness that had increased strongly after the conflict. The behaviours obviously reduce the tension by restoring a disturbed relationship and by maintaining a certain social homeostasis.

A beautiful experimental demonstration of the reconciliatory effect has been given by Cords (1992). Pairs of *Macaca fascicularis* had to compete for access to a water supply. When, before the drinking test, a conflict between the pair members had not been reconciled, then mutual tolerance was lower during drinking competition. However, when the conflict had been reconciled, the tolerance was restored to baseline levels (Fig. 4.1).

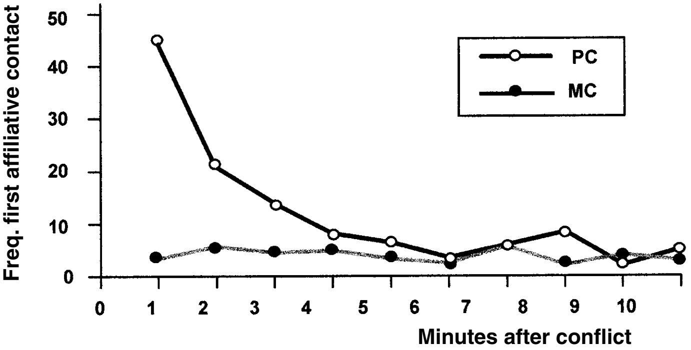
The term reconciliation, therefore, is not a vague anthropomorphic concept, but is a precise and proper functional label for such a Post-Conflict Affiliative Contact (PCAC).

The occurrence of reconciliation behaviour and a number of its characteristics have by now been demonstrated, using the same or similar methods, for quite a few other primate species (e.g.: *Macaca arctoides*, de Waal & Ren 1988; *M. fascicularis,* Cords 1988; *M. nemestrina,* Judge 1991; *M. fuscata, M. sylvanus,* Aureli *et al.* 1993, 1994; *Erythrocebus patas,* York & Rowell 1988; *Rhinopithecus roxellanae,* Ren *et al.* 1991; *Cercopithecus aethiops,* Cheney & Seyfarth 1986; *Pan paniscus,* de Waal 1987; for review see de Waal & Aureli 1997).

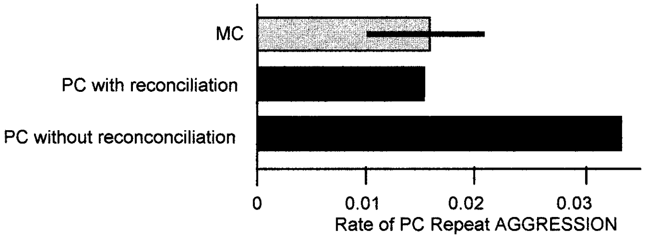
Box 4.2 How to measure reconciliation?

When there is an aggressive conflict between two animals, the behaviour of these two interactants is followed for a given length of time after the conflict, and their interactions with one another and with other group members are recorded. What they do and when in this 'post conflict' period (PC) is then compared with the same behaviours of the same interactants in a so-called 'matched control' (MC) period, i.e. at the same time on a subsequent day when there had been no preceding conflict.

Fig. 4.1 shows the distribution of affiliative contacts in PCs and the corresponding MCs, as measured in a group of long-tailed macaques (*Macaca fascicularis*). It shows that the frequency of the affiliative contacts is markedly higher during the first three minutes than in the MCs. By the fourth minute the level in the PC period has returned to the base-line level of the MC (Aureli *et al.* 1989).

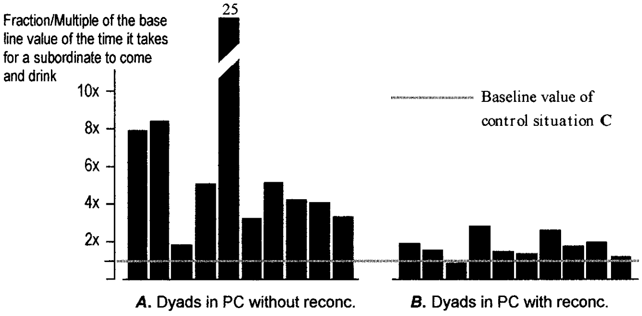


These 'post-conflict affiliative contacts' (PCAC) were termed 'reconciliations'. This is a functional term. Its use is justified only if it can be shown that these PCACs indeed decrease the likelihood of renewed aggression (i.e. if the frequency of subsequent aggressive acts in reconciled PCs is lower than in unreconciled PCs). In unreconciled conflicts new acts of aggression against the victim, not only from the aggressor but also from other group members, were more likely than in matched control situations (Aureli & van Schaik, 1991b). However, the likelihood of a new fight or a resumption of the conflict appeared to be lowered if there had been a PCAC (long-tailed macaques: Aureli & van Schaik 1991b; Aureli 1992) (see Fig. 4.2).



Similar results have been obtained for other species: chimpanzees, de Waal (1992); other species: Kappeler and van Schaik (1992); de Waal (1993); de Waal and Aureli (1997).

Box 4.3 Reconciliation after a conflict restores the relationship between former contestants in a subsequent situation where competition is invoked



In a series of drinking competition tests 10 pairs of two *Macaca fascicularis* monkeys were tested: they were given access to a water source after having been in 1 of 3 conditions: (*A*) after having been provoked into a conflict which was not followed by reconciliation; (***B***) after having been provoked into a conflict which was followed by a reconciliation and (**C**) after having been in a non-conflict situation, the control situation. The modal latency, that is the time it took before the subordinate of each of the 10 pairs could come to drink in conditions (*A*) and (***B***) is expressed as a fraction of the latency in condition (**C**), the baseline value (after Cords 1992).

Reduction of stress or restoration of a damaged relationship

There could be different functional motives for reconciliation. After a fight a victim might be uncertain whether the conflict has indeed been ended to the satisfaction of the winner. Sure enough, conflicts often do flare up again. But the many experiments described above indicate that reconciliation indeed lowers the probability of a renewed attack. So the PCAC could be motivated by the desire to avoid repetitions of the thrashing. However, there clearly is more to it than the fear of getting a new beating.

This is indicated by the fact that not all conflicts are followed by such a reconciliatory affiliative contact. In the macaques studied by Aureli *et al.* (1989), roughly only one-fifth of all the conflicts occurring between group members were followed by a reconciliation. The authors wondered whether this could be explained by assuming that only intense conflicts were reconciled, with an emotional intensity above a certain threshold level. They could show, however, that reconciliation was not related simply to the level of stressful arousal generated by the conflict. Might it be, then, that characteristics of the relationship between the respective contestants have an influence on the likelihood of reconciliation; in other words, does it make a difference who was in conflict with whom?

There is indeed evidence that the nature of the relationship between aggressor and victim plays a role. Two aspects (which probably interact strongly) appeared to be of influence: one is genealogical relatedness or consanguinity between contestants. The other is the 'quality' of their relationship. First, close relatives appeared to be more likely to be involved in conflicts (Aureli *et al.* 1989, 1997). This is not as astonishing as it appears at first sight, because relatives tend to live in closer association with one another; obviously their closeness also creates more opportunities for friction. However, it is remarkable that a higher percentage of their conflicts were reconciled than of those between non-relatives or distant relatives. Secondly: irrespective of their relatedness, individuals who had an otherwise good relationship, as manifest from their frequencies of being in close proximity and of mutual grooming, were more likely to reconcile than others (Fig. 4.1). This was true particularly between non-related contestants. In other words, a disturbance in a close or good relationship creates emotional concern. This, then, means that the value of a relationship is a factor of importance, and that these primates have developed a sensitivity for the long-term interest of their relationships.

There is another indication that reconciliation is not caused simply and solely by the fear of being beaten up once more. If this were the only motive, then we would expect the victim to be the individual who intitiates reconciliation. However, after the conflict, the winner also shows behavioural signs of stress and worry, such as increased levels of scratching and increased levels of 'uneasy' locomotory unrest (e.g. Aureli & van Schaik 1991b; Das *et al.* 1998; Castles & Whiten in press; Aureli 1997), and also the winner may approach the loser for a friendly contact (Das *et al.* 1997). Therefore, for him also there is a discomforting aspect of having been involved in a conflict. In contrast to the loser, the winner is in no particular danger because after a conflict he was not attacked more than in matched control situations. Still, it was specifically the friendly contact with the loser which reduced stress scratching in the winner, whereas friendly contacts after the conflict with other animals, even with family of the victim, did not (Das & van Hooff in press)! We must conclude, therefore, that the aggressor is stressed by the disturbed relationship with the victim. Obviously the behaviour is motivated by a 'concern' about the consequences of the conflict for the relationships with the opponent. This means that this concern stretches wider than the immediate context of the conflict; it reflects a sensitivity for the long-term aspects of social relationships.

Involvement of third parties

It is not only the contestants who are likely to have an interest in the quality of long-term relationships. From a theoretical perspective, outsiders also may be expected to have such an interest, namely in as far as the relationships between group members affect the benefits and costs of their own participation in the group. For example, tensions flaring up between others may create an unrest that has detrimental effects for them also. This could be, first, because the unrest emotionally distracts and disturbs their involvement in other, vital occupations. For instance, they may be disturbed in their foraging behaviour or in their vigilance against predators. Secondly, the others may themselves become involved, namely as victims of redirected or escalated aggression. Thirdly, positive relationships between certain group members might be damaged; this might have consequences for these others because it decreases the prospects for future communal strategies. Thus one can expect that outsiders might interfere in the interaction between contestants in such a way as to steer their relationship in a direction that is beneficial for the social fabric on which these outsiders also depend. Such triadic interferences can take various forms.

The first forms of triadic interference to attract ethological attention were those in which outsiders participated in conflicts by agonistically supporting one of the contestants. It is not difficult to see why such kinds of interference may, if only temporarily, lead to aggravation of the conflict. A coalition may release counter-coalitions and thus lead to an escalation.

A third individual might also show friendly behaviour to one of the contestants. The first explanation which comes to mind is that such friendly behaviour may function as a restoration of confidence or as a consolation of that contestant. One would then expect that such comforting behaviour was directed to the most aroused animals, in particular to the victim. If a third party has an interest in a good relationship between the contestants, one might expect also processes of pacifying mediation (de Waal 1982). Indications for a variety of such functions have been found in a community of chimpanzees (de Waal & van Roosmalen 1979; de Waal & van Hooff 1981). Remarkably, these have not been found in macaques (Aureli & van Schaik, 1991a; Judge 1991; Das & van Hooff in press), except for the Tonkean macaque (Petit & Thierry 1994). In summary: there is the strong suggestion that the long-term trade-offs of the costs and benefits involved in particular relationships influence the evaluations animals perform with respect to short-term interactions and oscillations in the relationship. This is social economics.

Social negotiation and biological markets

It is no longer a question whether animals behave ‘economically’. A number of studies, reported also in this volume, show that animals exert choices and make investments, and that they do so following rules which lead to near optimal benefit : cost ratios. Thus, in experimental studies on conditioning, animals appeared able to tune their performance of operant behaviour to the expectations of rewards and punishments, their values and balances. That animals do behave according to such rules in natural daily life has been demonstrated especially in studies on optimal foraging behaviour (Stephens & Krebs 1986). They appear to be able to monitor the developments in various areas of their foraging range and relate these to the costs and profits of the different options for foraging. These options are complicated by the fact that an individual rarely forages on its own. Sophisticated economic modelling is being developed that can explain the decisions of foragers operating in populations where other animals are exploiting the same patches concurrently (Giraldeau & Livoreil 1998).

It is no great surpise, therefore, that animals also behave economically in their social interaction, and that they weigh expected benefits and costs of diverse cooperative and competitive options, while taking into account the history of the relationship with their partners. Still, I consider it a remarkable suggestion of the studies on reconciliation that animals such as primates possess some kind of sensitivity by which they take into account not only immediate but also remote benefits and costs and their ratios. They seem able to organise their behaviour by comparing these ratios and deriving from the comparisons relative urgencies of action or the inhibition of action. Also there is a changing emphasis in research on human negotiation and conflict settlement. Rubin (1991) has emphasised that research on conflict settlement and negotiation has traditionally concentrated on the immediate economic results that participants draw from their interactions. He notes, though, that a richer perspective should be employed, namely that which takes into account long-term relational considerations.

The importance of long-term relationships is also indicated by studies on the exchange of services and favours between animals. This can even involve 'altruistic' behaviour varying from voluntary tolerance in competition to active investments which are to the profit of a conspecific. Such 'altruistic' services and favours can be explained if they are founded in a mutual exchange which yields surplus value to those contributing (Noë *et al.* 1991). This principle of reciprocal altruism was first formulated by Trivers (1971): 'One good turn deserves another.' In other words, the altruism can create or maintain good relationships which are to the benefit of the altruist in the future.

Various game theoretical models and market models have been proposed to describe the strategies of animals confronted with conflicts of competition and compliance (e.g. Dugatkin 1998; Riechert 1998). An example is the well-known tit-for-tat principle (e.g. Axelrod & Hamilton 1981). It is a very simple rule. It tells players in a competition–cooperation dilemma to start an interaction with a cooperative move, and then to respond to a cooperative or defective move of the partner in a likewise fashion. In computer simulations the tit-for-tat rule competed successfully with more complex rules (Axelrod 1984). Animals acting on the basis of such a simple rule or modifications of it (Nowak & Sigmund 1993) could maintain a stable relationship of mutually beneficial reciprocal altruism. This is certainly an important theoretical conclusion. Another question is whether such models are a sufficient explanation for the processes actually encountered. In reality these processes and their context seem to be much too complicated to be accomodated in these models (e.g. Noë and Hammerstein 1994). Noë arrived at this conclusion on the basis of his studies of coalition behaviour in wild baboons (e.g. Noë 1986, 1990; Noë and Sluijter 1995). Animals may not respond immediately as described by the tit-for-tat rule. They may also exchange services or favours of a very different nature, for instance, tolerance in feeding competition or in competition for sexual and social partners, support as coalition partners in conflicts, grooming and care, etc. (Noë *et al.* 1991). They may also react with punishing revenge (de Waal 1996b). So they may reciprocate with qualitatively and quantitatively different responses. Also, more than two players may be involved. Market models which allow for multiple players provide better explanations than traditional two-player games (Noë *et al.* 1991; Noë 1992).

The mechanisms of socio-economics: calculations or emotional rules of thumb?

Modelling studies can tell us which rules are the winning and stable ones. They can, however, tell us neither which rules animals actually follow in reality nor what mechanisms are involved in the mental bookkeeping. We noticed that different services may be exchanged and that more than two players may be involved simultaneously. The question, then, is how these variables are translated in a single currency and how the actual accounting is being done. This is an empirical issue which is far from resolved. In addition there is still much discussion about both the methodology of measuring the transactional processes and the interpretation of results (see, e.g. the discussions by de Waal 1996b, and Hemelrijk 1996, 1997).

Especially recent research on chimpanzees carries the strong suggestion that these animals engage in negotiation and have an awareness of the ‘economics’ of their behaviour (e.g. de Waal 1996b). This raises the questions: if the interaction resembles a process of negotiation, how are these negotiations executed? What are the mental mechanisms involved? Again in chimpanzees recent studies have revealed advanced cognitive competencies, such as numerical and attributive competencies, that would come in useful in evaluations of the kind supposed (e.g. Matsuzawa 1985, 1996; Savage-Rumbaugh 1986; Povinelli *et al.* 1990; Boysen & Capaldi 1993; Savage-Rumbaugh *et al.* 1993; Povinelli & Eddy 1996). Must we then see the participating individuals as players calculating the different positive and negative risks? Or is the negotiation-like pattern a side effect of local interactions on the basis of very general rules of thumb (Hemelrijk 1997)?

Introspection on how we proceed ourselves on many occasions suggests that the mental bookkeeping involved could be done at a level of emotional evaluation. The common currency into which the benefits and costs of social acts are translated is feelings of relative sym- or anti-pathy: you like better or worse those who treat you better or worse, and you are emotionally inclined to treat them accordingly. In man the emotional attitude of trust in the relationship appears to be a condition for keeping the cooperative exchange going. It is based both on confirmed positive expectations (i.e. predictability and consistency in the pattern of cooperative exchange) and on the expectation that the interactions are open-ended and, therefore, suppose a continuous good relationship (Boon & Holmes 1991; Good 1991).

Good relationships and the roots of morality

We have seen growing evidence that primates, in the context of competition and cooperation, have some kind of feeling for the long-term value of relationships (van Hooff & Aureli 1994; de Waal & Aureli 1997). This does concern not only their own relationships with others but also those between others. The maintenance of relationships of mutual benefit should be weighed off against the benefits of short-time competitive advantages. It involves, first, the moderation of momentary impulses directed at immediate selfish gratification and giving room to others. Secondly, it can even involve active investments which are to the profit of a conspecific in order to create or maintain good relationships. We have noted already that such 'altruistic' behaviours can be explained if they are founded on the principle of reciprocity (Noë *et al.* 1991), which was first formulated by Trivers (1971).

These findings have assumed particular interest in connection with our thinking about the biological precursors of moral systems. It has long been broadly accepted that moral systems and the underlying psychological mechanism of a moral conscience were a specifically human achievement. Even if some metaphysical origin of categorical imperatives in the sense of Kant (1893) finds few protagonists these days, the opinion that it is a unique cultural attribute, developed as a consequence of, and – in turn – favouring the growing collaborative complexity and attributive humaneness of society, is widely held. Yet the quest for a biological and evolutionary explanation of morality has a long history (see discussions in: Wickler 1971; Stent 1978; Alexander 1984; Ruse 1986; Thinès 1993).

The essence of morality is the partial subordination of selfish impulses and behaviours by complying with a system of norms and rules to optimise human welfare (e.g. Stent 1978). It does so by safeguarding the interests of others and by maintaining a social and societal fabric on which the welfare of its members depends. The idea that the behavioural dynamics involved and the underlying dispositions can be understood in evolutionary terms has gained considerably in strength ever since Trivers (1971) formulated the model of reciprocal altruism. It necessarily rests on the assumption that animals have some kind of ability to monitor the exchange of favours and that they can adjust their social investments accordingly, taking into account the costs and profits in a long-term perspective (e.g. de Waal 1989a). Observations show that animals do invest in the relationships with conspecifics to create a situation in which they harvest benefits later on. Such investments can be maintained only if the system guarantees that obligations are met, and that free-riders and cheaters are discriminated against. In as far as individuals profit from the social fabric to which they belong, they must also be held to cooperate in maintaining the social fabric which is beneficial for all, in order to avoid a 'tragedy of the commons'. Recent research, especially on non-human primates, suggests that we deal with processes here that may also be at the roots of our moral systems. The suggestion that this can clarify the development of systems of moral rules and norms and the origin of morality has been proposed eloquently by de Waal (1989b, 1996a).

Conclusion

In primates, and probably also in some other animal species, conflicts between individuals may be followed, with a higher than random likelihood, by affiliative contacts between the opponents. These post-conflict affiliative contacts (PCACs) can be regarded as reconciliations since they reduce signs of post-conflict stress in the opponents and reduce the likelihood of renewed aggression. The existence of such PCACs is significant in that it reveals the value which primates attach to long-term relationships. For the victim, such a 'reconciliation' can have an immediate benefit in that it diminishes the likelihood of resumed aggression and thus restores the relationship. But also the winner of a conflict shows signs of uneasiness, which are diminished by a PCAC. This and the tendency of third parties to engage in PCACs require another explanation (Das *et al.* 1997, 1998). An indication is that the occurrence of a reconciliation after a conflict is determined by the overall nature of the relationship between the victim and its opponent. Reconciliations were more likely, independent of the intensity of the preceding conflict, if this relationship in general was important (e.g. kinship relationships) or if it was 'good' (i.e. of an affiliative and tolerant character throughout). Both relatives, who as a rule have comparatively strong affiliative and supportive relationships, and non-relatives with a close bond, reconciled after a larger proportion of conflicts than animals lacking this bonding (*e.g.* de Waal & Yoshihara 1983; Aureli *et al.* 1989). In other words, there is strong evidence that the long-term trade-offs determining relationships influence short-term perturbing oscillations in the relationship.

The same is indicated by recent investigations on the exchange of services and favours between individuals. Simple reciprocity models, such as the tit-for-tat paradigm obviously do not suffice to explain some of the more complex patterns of involvement, as, for instance, in multi-player interactions. Observations show that animals do invest in the relationships with conspecifics to create a situation in which they harvest benefits later on. Such investments can be maintained only if the system guarantees that obligations are met, that free-riders and cheaters are discriminated against. In so far as individuals profit from the social fabric to which they belong, they must also be held to cooperate in maintaining the social fabric which is beneficial for all, in order to avoid a 'tragedy of the commons'. Recent research, especially on non-human primates (e.g. de Waal 1996a), suggests that we are dealing here with processes that are also at the roots of our moral systems.

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Part II

Biological markets

Various models have been proposed to explain how patterns of cooperative (between conspecifics) and mutualistic (between different species) interaction can arise and can be maintained. Game theoretical approaches, which began with the application of the Prisoners' Dilemma paradigm, proved very stimulating, but it has become clear that they fall short in accommodating the complexities of the majority of real-life interactions. Various assumptions and implications of these models are not realistic. Thus cooperative and mutualistic interactions do not often occur in dyadic isolation, but mostly take place in a setting where there are many potential players. This implies that partner choice should be an essential element in models of cooperation. Moreover, the ratio of supply and demand for the commodities that the different parties seek to acquire may vary. Depending on this ratio, there may be competition between potential 'buyers' and 'sellers'. Last but not least, there can be communication between the parties, leading to a process of bartering. These are characteristics which we normally associate with a 'market'.

Ronald Noë was one of the first to realise the limitations of the game theoretic models which were current when he conducted his studies on coalition formation in savannah baboons. In the first chapter of Part II he reviews the different models which have been proposed and argues that a market approach offers a most appropriate perspective for understanding systems of cooperative and mutualistic interaction.

In the following chapters both theoretical considerations and supportive empirical evidence are presented to show that a market model offers the appropriate framework for studying such exchange systems.

Thus Louise Barrett and Peter Henzi show that in baboon groups grooming can be given in different functional contexts to obtain different commodities. Grooming may be given in exchange for being groomed. This exchange is highly reciprocal and of an 'egalitarian' character. It may, however, also be given to be permitted access to different commodities, or to 'buy' tolerance from coercive competitors. The authors show that the respective patterns of interchange can be understood best by considering the influence of the different factors in a market approach.

The risky relationship between cleaner fish and their clients has been a proverbial example of mutualism. Clients vary from harmless herbivores to dangerous piscivores, and from resident 'dependable' customers to clients that can choose between different stations. In addition, cleaner fish may render their cleaning services, but can also be seduced to try parasistic bites in which they damage their client. Redouan Bshary is the first to present a detailed analysis of the way the different factors involved operate on this multi-player market, for example the risk factors, the supply-and-demand factors and the choices open to cleaners and clients. His analysis demonstrates, on the one hand, how market factors influence the decisions of the parties, and on the other hand, how difficult it can be to separate these influences from those that are based on punishment and blackmail.

Jason Hoeksema and Mark Schwartz address another aspect of the exchange in mutualistic relationships between species, namely specialisation in the production of certain commodities to be traded. This has long been known in economic theory as Ricardo's law of comparative advantage. Hoeksema and Schwartz demonstrate that the trade between members of different species resembles the trade between nations: there can be an economic incentive to abandon the production of certain commodities if these can be obtained from the other party.

RONALD NOË

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Biological markets: partner choice as the driving force behind the evolution of mutualisms

Choice as a selective force

Selection, the driving force of evolution, is the process by which varieties that are better adapted to their environment increase in frequency relative to less well-adapted forms over the generations. The ‘environment’ is often perceived as a relatively passive mould into which the organism fits more or less well. Often enough, however, organisms literally select among other organisms and by their choice alter the relative fitness of the individuals among which they choose. Cheetahs, for example, may select the weakest individual in a group of Thomson gazelles (Caro 1986) and peahens may prefer peacocks with large, elaborate trains (Petrie *et al.* 1991).

Systems such as the peacock’s mating system, in which the members of one class of organisms benefit from being chosen by members of another class, have properties similar to human markets on which goods or services are exchanged. These properties are:

- Commodities are exchanged between individuals that differ in the degree of control over these commodities.
- Trading partners are chosen from a number of potential partners. On average the interaction with a chosen partner yields a higher ‘profit’ than an interaction with a random partner, i.e. a fitness gain in evolutionary terms.
- There is competition among the members of the chosen class to be the most attractive partner. This competition by ‘outbidding’ causes an increase in the value of the commodity offered and hence its production costs. In evolutionary terms: stronger competition forces organisms to accept less favourable fitness effects from interactions.

- Supply and demand determine the bartering value of commodities exchanged.
- Commodities on offer can be advertised. As in commercial advertisements there is a potential for false information.

There are two major classes of biological interaction which have the properties of biological markets: mating systems and mutualistic interactions between members of different species. Market effects may further play a role in cooperation among unrelated conspecifics (Noë *et al.* 1991; Noë 1992) and in interactions among kin, such as between parents and offspring or among cooperative breeders. In this chapter I concentrate on the remarkable analogies between evolution through sexual selection and the evolution of mutualisms. I would like to argue that, when it is productive to demarcate sexual selection as a distinct mode of (natural) selection, it may make sense to identify 'market selection' as a special mode of selection in the context of the evolution of mutualisms.

Sexual selection, interspecific mutualism and the evolution of cooperation: historical developments in separate fields

Peter Hammerstein and I (Noë & Hammerstein 1994, 1995) have advocated the view that mating systems, intraspecific cooperation and interspecific mutualism have enough common denominators to make it worthwhile to carry empirical results and theoretical advances from one field to the next. Theoretical biologists have mainly concentrated on sexual selection and the evolution of cooperation. Models and ideas of both fields can be useful for the study of mutualisms, and attempts can be made to construct universal models (cf. Noë & Hammerstein 1994)

I say nothing new when I talk about 'mating markets' in the context of sexual selection. The issues of partner choice, competition over access to partners, sampling costs etc. have always been central in this field. There is an extensive literature on the economic decisions that rule in human mating markets (see Grossbard-Shechtman 1993 for a review). The use of dowry in many societies make human mating markets easier to quantify than most non-human mating markets. The transfer of ideas will therefore be largely a one-way street running from economic and sexual selection theory towards cooperation theory. However, sexual selection theory has something to gain by incorporating ideas from cooperation theory about partner verification and 'cheating' (see also Bshary this volume).

The puzzle of the evolution of cooperation started with a single question: 'How can altruistic behaviour evolve?' In the sixties several evolutionary biologists realised that the occurrence of altruism could not be explained with a concept popular at those times: group selection. Group selectionists hypothesised that altruistic behaviour could evolve, because the members of a group of altruists would have higher fitness than the members of a group of non-altruists. Selection was thus supposed to act at the level of groups of organisms. The flaw in this view was exposed especially by Williams (1966) in a critique of a book written by Wynne-Edwards (1962). Poor Wynne-Edwards had to take the blows as a figurehead for a whole generation of biologists. The amazing fact is that Darwin had it right from the beginning on. In *On the Origin of Species* (1st edn 1859, ch. 3) he clearly indicated selection at the level of individuals as the most powerful force driving evolution. The generally accepted view these days is that group selection is a rather weak mode of selection, but that it can play a significant role in specific cases (see Dugatkin 1997 for a review).

Instead of the easy answer 'group selection takes care of it', theorists had to think hard about the evolutionary mechanisms that made the selection of such a behaviour possible. How can selection favour a behavioural strategy that lowers the fitness of its performer? It was soon realised that two classes of interaction had to be considered separately: cooperation among relatives and cooperation among unrelated individuals. Hamilton (1964a,b) and Maynard-Smith (1964) were the first to put forward the idea of 'kin selection'. Kin selection stands for the nowadays generally accepted idea that selection favours the support of relatives by relatives, because this behaviour promotes the chances that copies of the genes of the altruist that are identical by descent with those of the recipient penetrate in future generations.

With his verbal model of 'reciprocal altruism', Trivers (1971) kicked off a discussion on the mechanisms that could explain altruism among unrelated organisms. This ongoing discussion applies to interactions between unrelated members of the same species as well as to members of different species. In both cases the 'genes' of the interacting parties that govern their cooperative behaviour are assumed not to be identical by descent (but see Rothstein 1980). Inspired by Hamilton (personal communication in Trivers 1971), Trivers decided to use the 'Prisoner's Dilemma' (PD) as a paradigm, because he realised that the potential of 'cheating' makes reciprocal altruism unstable. Why would a participant in a reciprocal exchange not refuse to be altruistic after having benefited from an altruistic act? In

Box 5.1 Terminology

The terminology used in the literature is confusing. I therefore list a number of terms and the sense in which they are used in this chapter.

altruistic interaction	Interaction between two individuals in which the fitness of the 'altruist' is lowered, while the fitness of the 'beneficiary' is increased. The altruist is not forced to act by aggression or threat.
reciprocal altruism	A series of altruistic interactions between two individuals in which both alternately take the role of 'altruist' and 'beneficiary'.
cooperation	Interaction between two individuals as a result of which both increase their fitness. The term 'cooperation' is especially used for interactions between conspecifics.
reciprocity	Often used to refer to reciprocal altruism and (serial) cooperation taken together. (*Not used in this chapter*).
mutualism	Reciprocity between individuals belonging to different species.
symbiosis	Long-lasting, continuous interaction between individuals belonging to different species, rather than a relationship with short, discrete interactions.

economic theory the Prisoner's Dilemma was long established as THE paradigm for the problem of cheating between cooperative partners. The 'Repeated Prisoner's Dilemma' (RPD; also called 'Iterated PD') still is the dominating paradigm in the study of the evolution of cooperation (e.g. contributions in Dugatkin & Reeve eds. 1998). Because the two players have to choose simultaneously between the options 'cooperate' and 'defect', strictly speaking the RPD cannot be a paradigm for reciprocal altruism, because reciprocal altruism assumes alternating choices (Noë 1990), but varieties on the RPD theme suited to describe alternating moves have been presented (Boyd 1988; Nowak & Sigmund 1994; Leimar 1997). Thus, the two-player RPD is an ideal paradigm for the study of the cheating problem stripped from all complications. However, this myopic point of view misses most of the richness of reciprocal interactions.

The effect of partner choice: an example from baboons

At least two closely related issues are not considered in models based on the Repeated Prisoner's Dilemma: (1) How do two individuals split the spoils in a reciprocal relationship? (2) What happens if one or both individuals have alternative partners (Noë *et al.* 1991; Noë & Hammerstein 1994, 1995)?

It became clear to me that partner choice can have a strong effect during my study of coalition formation in male savannah baboons (Noë 1990, 1992). These coalitions, formed in conflicts over the access to receptive females, had been presented as the first example of reciprocal altruism (Packer 1977) and have been a textbook example ever since. Observations of Bercovitch (1988) and myself (Noë 1990) have cast severe doubts on the validity of the example, however (see Alcock 1993: 523–4): the pattern of taking turns in receiving access to receptive females expected between reciprocal altruists has never been shown in baboon alliances, neither in the original study by Packer (1977), nor in later studies. On the contrary, several examples have been given in which this was obviously *not* the case (Collins 1981; Bercovitch 1988; Noë 1990).

The example I described was an extreme case in which a male could play off his two potential partners against each other in such a way that he could reap almost all benefits, in this case the exclusive access to receptive females (Fig. 5.1). A paradigm for such a case is the 'veto game' (Kahan & Rapoport 1984). The classical example of a veto game is as follows: two dealers each possess a left shoe, one dealer has a right shoe. Only pairs of shoes can be sold. Clearly the owner of the right shoe can play off the owners of left shoes in such a way that they will receive the lowest possible share when the proceeds are split. In the baboons I studied, one male, the 'veto player', had to be a member of the coalition to make it successful. Although the 'veto' constellation I witnessed may have been a unique case, skewed divisions of benefits are not uncommon among coalition partners in baboons (Collins 1981; Bercovitch 1988).

In single-round veto games among human players bargaining can lead to an agreement to split the spoils in an extremely asymmetrical way. The agreement can only be effectuated, however, if both players stick to it. The conclusion of such 'binding agreements' is hard to imagine for

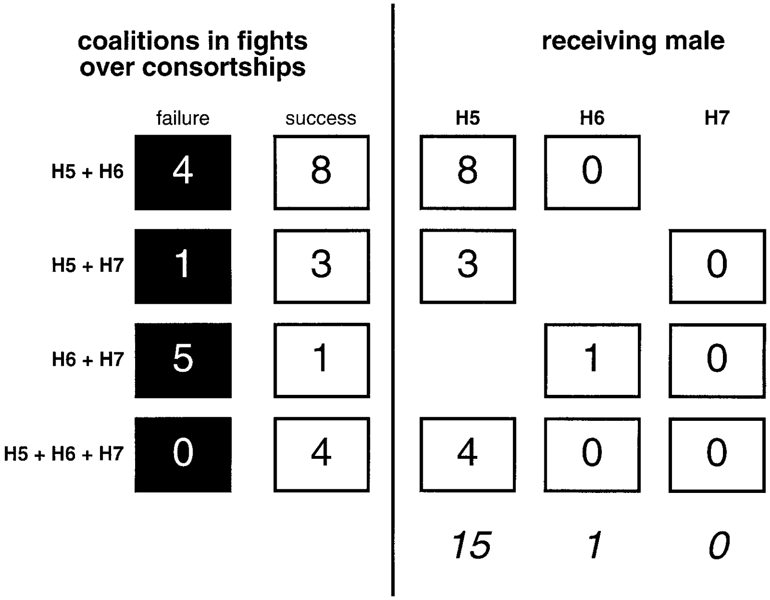


Fig. 5.1 The outcome of coalitions among three adult male savannah baboons. The coalitions were formed by the three males, H5, H6 and H7, against higher-ranking males in order to obtain access to oestrous females. Left-hand panel: outcome of the conflict with the higher-ranking male. Right-hand panel: number of times each of the coalition partners was able to form a consortship with the female. Note that H5 had to be a member of the coalition to make it successful and that this male received all of the benefits. These males were under observation during about one quarter of the time in the study period. According to observations made by colleagues, during the same period males H6 and H7 gained access to females through coalitions with H5 a few times (based on Noë 1990).

non-human players. A physically strong baboon, for example, could use his dominance to overrule any form of outcome based on game-theoretical logic. A baboon in the position of a veto player can only reap high payoffs when the game runs over multiple rounds. A switch of partners between rounds by the veto player will hurt the partner that is left out, but not the veto player. The veto player can therefore take the lion's share without being punished for it; his partners only have the choice between little and nothing. A dominant could also take the lion's share in a single coalition, but he does not have the leverage to assure the participation of a partner in a string of coalitions – unless the partner completely depends on him. The price to be paid for partner fidelity depends on the strategic options of the players, not on their dominance relationship.

The baboon example shows that the possibility to choose partners can make all the difference. Why is that? In a two-player Prisoner's Dilemma a player has two major strategic options only: to cooperate or to defect. In a number of PD-based models there is a further option of varying the investment in each round (see e.g. Connor 1992, 1995a,b; Roberts & Sherratt 1998). With more than two players several strategic options enter the game that are missing in the two-player Repeated Prisoner's Dilemma paradigm: playing off partners, outbidding competitors, and in some cases bargaining.

An example of a biological market: the ant–lycaenid mutualism

The mutualistic interaction between ants and the larvae of lycaenid butterflies has the essential elements of a biological market. Around 2000 species of lycaenid butterflies interact with ants (Fiedler 1991; Weith 1998), showing a wide variety of dynamic interactions. The mutualistic interactions of a number of species have been described in detail (Pierce 1987; Pierce *et al.* 1991; Fiedler 1991). The ants protect the butterfly larvae against predators and parasites (Fiedler & Maschwitz 1988, 1989). The larvae, in turn, offer the ants a sugar-rich solution, called 'nectar', which is produced by a gland, the 'nectar organ'. The only function of the nectar is to attract ants. Lycaenid nectar can form a substantial part of the ants' diet (Fiedler & Saam 1995). The tentacle organs of the larvae, which release a pheromone, play an important role as signals that attract ants (see section on 'Signals' below)

Work by Axén and colleagues (Axén *et al.* 1996) and Weith (1998) has shown that in some facultative ant–lycaenid mutualisms, such as between the larvae of *Polyommatus icarus* and *Lasius* ants, the amount of nectar the larvae produce depends on the number of attending ants: the amount a single larva produces increases with the number of ants attending as long as few ants are present, but is reduced again when larger numbers of ants attend (see Fig. 3 in Axén *et al.* 1996). One can interpret this result in the following way: the nectar is produced at a cost. Even if the number of ants increases linearly with the amount of nectar produced, the value of the protection does not – the principle of diminishing returns. As long as there are few ants, the larvae compete among each other to attract ants. When there are enough ants on the market, the larvae can reduce their bids.

Other lycaenids show a drop-off of nectar production under different circumstances. Axén & Pierce (1998) describe an obligate mutualistic lycaenid species in which the larvae cluster together. Here the members of a cluster can reduce their nectar output compared to that of a solitary individual, because they collectively produce enough nectar to attract enough ants to provide adequate protection. The larvae collectively attract a communal protection force, rather than competing with each other over ants, as solitary larvae would do. Note that the ultimate causes for the ability to regulate the nectar amount, as well as the stimulus that triggers a reduction of the production, could be the same for both solitary and clustering species.

The behaviour of larvae in a cluster brings us to a discussion of two notorious problems in cooperation: cheating and free-riding.

Cheating and free-riding

The term *'cheating'* is used when cooperative partners deceive each other, for example by not delivering a commodity according to the 'expectations' of the partner. These 'expectations' can be based either on individual experience built up in interactions with specific partners or trade-classes, or on 'rules of thumb' shaped over evolutionary time in interactions between two classes of traders. For example, a plant can advertise the presence of nectar with a colourful flower, although a visiting insect might find little or none (see Box 5.2). *'Free-riding'* can occur when multiple individuals simultaneously offer the same commodity in order to get some collective benefit. The cluster of lycaenid larvae protected by a security service of ants mentioned above is an example. The problem here is that single individuals could benefit from the protection without offering any nectar themselves. Such free-riders would have higher fitness and thus a distinct selective advantage. This problem is long known as the 'tragedy-of-the-commons' (Hardin 1968) or the 'collective action problem' (see Ostrom; Nunn & Lewis this volume). A paradigm often used to model this situation is the *N*-players Prisoner's Dilemma (*N*PD), a game in which defecting is the only stable strategy.

A collective action problem can be solved when free-riders are punished. It is unlikely, however, that this is done by the members of the collectively acting group themselves. This is because no one would be willing to do the job on behalf of all. The would-be punishers are caught in a second collective action problem, the so-called 'policing problem' (Ostrom 1990, this volume).

Another solution would be that the trading partners 'punish' the members of the other trading class that do not pull their weight.

Box 5.2 A pollination market

The purpose of the model described here is to illustrate some aspects of biological markets on the basis of an imaginary system that is close enough to reality to appeal to a biologist's intuitions. The two types of actors in the market are Flowers and Pollinators. I focus on the strategy of the Flowers under different supply : demand ratios in order to show the effect of the choice by one class (the Pollinators) on the strategic behaviour of the other class (the Flowers).

This is neither a formal game theoretical model nor a description of any existing pollination interaction. In real life, each class of traders on a pollination market consists of players belonging to multiple species and both classes have a much larger set of strategic options. My goal is thus very different from that of Bell (1986), who used a game–theoretical approach that assumes unlimited numbers of players ('playing-the-field'; Maynard Smith 1982) to explain the occurrence of flowers with little or no nectar (see also Gilbert *et al.* 1991).

Natural History

The Flowers

- A growth season is followed by a short flowering season in which each plant produces a single flower. The plants survive till the next season as seeds.
- Only male reproduction is considered, i.e. the strategy of the plant to attract pollinators to receive pollen is not considered.
- At the end of the growth season each Flower has a fixed amount of energy that can be allocated to three functions:

  1. **pollen**: pollen is glued to the exterior of the body of the Pollinators; pollen itself has no reward value for the Pollinators;
  2. **nectar**: the reward for the Pollinators; nectar is of uniform quality;
  3. **petals**: the petal disk forms the billboard by which the Flowers advertise the presence of a reward.

Box 5.2 (*cont.*)

- Investment strategies (i.e. the allocation of energy over the three functions) are inherited and 'breed true'.
- A Flower's fitness is directly related to the amount of pollen transported.

The Pollinators

- Free-flying, nectar-feeding insects with good vision.
- Each Pollinator visit is an independent event, i.e. there is no recruitment of other pollinators, no memory between foraging flights, no competition between Pollinators.
- Pollinators discriminate between Flowers on the basis of the size of the petal disk.

The interaction

- The interaction is mutualistic and exclusive; Flowers and Pollinators fit together as key and lock.
- Pollinators cannot find Flowers without petal disks; thus the Flowers have at least to put some energy in petals.
- Flowers grow in clusters of unrelated individuals; a foraging Pollinator can compare the size of the petal disks of the whole cluster at no cost.
- Pollinators cannot reach the nectar without taking on pollen.
- The amount of pollen that can be transported is not limited by the size of the Pollinator.
- After a visit by a Pollinator, a Flower leaves the market by closing its petal disk.
- A Pollinator leaves the market after filling its stomach with nectar.
- 'Choosiness' is maintained in the population of Pollinators due to the effect of environmental variation on the Flowers which causes the total amount of energy available at the end of the growth season to vary somewhat from Flower to Flower.

The petal disk as a handicap signal

The question is: which investment strategy do the Flowers use, when they have to choose between investment in gametes versus investment in a reward for their Pollinators and the advertisement for that reward? I do not consider the question of the 'honesty' of the reward, i.e. whether the size of the petal billboard is indeed coupled to the amount of nectar the Flower offers. The honesty of the signal is assumed on the basis of the following rationale: (1) In a population at ESS (Evolutionarily Stable Strategy; Maynard Smith 1982) all Flowers will play a strategy that optimises investment in pollen and petals, such that the Flower is both likely to be visited by a Pollinator and a maximum amount of pollen is produced and transferred to the Pollinator. (2) Pollinators will use the size of the petal disk as a clue for the presence of nectar only if, as a rule, the size of the disk correlates with the amount of nectar available. The ratio of petal disk surface to pollen amount can differ in populations with different investment strategies, but in a population at equilibrium a bigger disk should signal more nectar. (3) Only Flowers that grow under favourable circumstances will be able to invest more in their petals and their pollinator reward without reducing their pollen production. Thus, the size of the petal disk shows the characteristics of a 'handicap' signal (see main text for explanation). For the sake of simplicity, I assume here that, after many generations of stable interaction, the correlation between petal disk size and nectar amount became genetically linked.

A simple pollination game

For the present purpose it suffices to consider only two discrete strategies for only one trader class, the Flowers:

POLLEN	grow a petal disk just large enough to be seen by the pollinators and an amount of nectar just large enough to ensure the transfer of pollen to the pollinator's body and invest all further energy in pollen.
ADVERTISE	shift the investment, compared to the POLLEN-strategy, in favour of the production of a larger petal disk coupled with more nectar.

I give a numerical example based on the following assumptions:

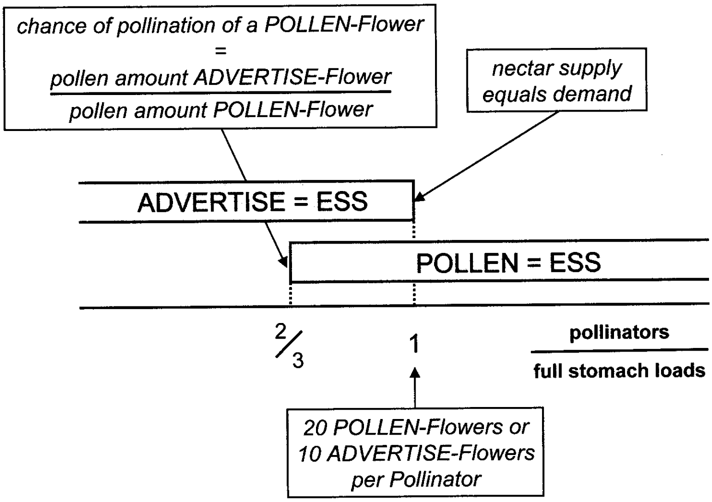
- The nectar produced by 10 Flowers playing ADVERTISE, and 20 Flowers playing INVEST, respectively, fills the stomach of a single Pollinator.

Box 5.2 (*cont.*)

- An ADVERTISE-Flower produces two-thirds the amount of pollen produced by a POLLEN-Flower

Flip-overs and switch-points

When there are so many Flowers that the Pollinators are satiated long before all Flowers have been visited, single Flowers playing POLLEN in a population of Flowers playing ADVERTISE will never be visited. Under which circumstances could POLLEN invade a population playing ADVERTISE? This is at the point that all Flowers will be visited with certainty, i.e. the amount of nectar on the market just suffices to fill all Pollinator stomachs. In a population in which all Flowers play ADVERTISE this is the case when there are 10 Flowers for each Pollinator (see Fig. 5.2). At that point the first POLLEN-strategist can invade successfully. This, in turn, reduces the amount of nectar on the market, because POLLEN-Flowers produce less than ADVERTISE-Flowers, skewing the market further in favour of the Flowers. Once this flip-over point has been passed, the replacement of ADVERTISE-players with POLLEN-players reduces the supply of nectar further, making it even easier for the POLLEN-strategy to invade.



When the Pollinator/Flower ratio is high enough, all flowers will certainly be visited and the ESS is to play POLLEN. Starting from that situation, one can now ask under which circumstances ADVERTISE could invade. Imagine that one adds one more Flower at the point at which there are just enough Flowers to satiate all Pollinators. This is the case when there are 20 POLLEN-Flowers for each Pollinator. An additional ADVERTISE-Flower would be chosen with certainty, but its fitness would be lower than the *average* fitness of the POLLEN-Flowers. This is while the slight chance of not being visited is offset by the higher fitness of those that receive a visit of a Pollinator. The flip-over point in this situation is reached when the fitness of an invading ADVERTISE-individual equals the average fitness of the POLLEN-Flowers. This is the case when there are 30 POLLEN-Flowers for each Pollinator, while at that point the chance of a POLLEN-individual being visited is as low as 2/3 and equals the ratio between pollen produced by an ADVERTISE-Flower and pollen produced by a POLLEN-Flower. Again we see that, once the flip-over point has been passed, the market forces accelerate the process: the replacement of POLLEN-strategists with ADVERTISE-strategists increases the amount of nectar on the market.

In the case of complete mutual dependency and no external influences the market would gear towards a balance between supply and demand, i.e. towards the point at which just enough nectar is produced to satiate all Pollinators. At that point the POLLEN-ESS is more stable, while the ADVERTISE-ESS is close to a switch point. External factors that affect the two trader-classes differently, such as severe winters, can drive the system over one of the points at which the dominating strategy in the Flower population switches. One could imagine that a ‘conditional’ strategy evolves among flowers if shifts in ratios are predictable. They could, for example, be programmed to play POLLEN after a mild winter and ADVERTISE after a severe winter, when their pollinators are sensitive to cold weather.

Punishing as a revenge for past behaviour without future fitness advantages cannot be ‘evolutionarily stable’. ‘Punishment’ can only work in long-lasting relationships in which the aggression of the punisher moulds the behaviour of the punished individual in a manner beneficial to the punisher (Clutton-Brock & Parker 1995a). The punishment games proposed by Clutton-Brock & Parker (1995b) resemble reciprocal altruism and have the restrictions typical for two-player paradigms. When partner choice is possible, for example female choice for males that punish least, punishment may prove to be an unstable strategy. Nevertheless behaviour that has the effect of selective 'punishment' can be a solution for cheating and free-riding in biological markets. I illustrate this with another type of mutualism in which ants provide protection and with an obligatory plant–pollinator mutualism.

Apart from lycaenid larvae, ants also protect homopterans (aphids, plant-lice etc.) in return for a sugar-rich solution, in this case called honeydew (see reviews in Cushman & Whitham 1989, 1991; Hölldobler & Wilson 1990). Homopterans usually occur in clusters, often of closely related individuals or even clones resulting from parthenogenetic reproduction. According to empirical observations lycaenid larvae (Fiedler & Maschwitz 1989) or homoptera (Way 1954) that do not produce a sugar-rich solution are eaten by the ants. Thus, the ants make an economical decision and the elimination of cheaters is a by-product: a failing producer is eaten when its body has more value than the sugar it can be expected to produce in the future. Dairy-farmers make a similar decision at the end of the productive life of a milk-cow. Thus, the possibility of discriminating between cooperative partners, the choice element that is a crucial element of a market, results in the elimination of 'cheaters' and thus also reduces the opportunities for 'free-riding'. 'Punishment' is a misleading label in this case, however.

Another empirical example of the elimination of cheaters by their trading partners is found in the mutualistic interaction between yuccas and yucca-moths. Several species of yucca-tree are exclusively pollinated by the yucca-moth, which lays its eggs in the ovaries of the plant (review see Powell 1992). The larvae feed on the ovaries. A moth can 'cheat' by putting too many eggs in an ovary. James *et al.* (1994) and Pellmyr and Huth (1994) describe how the yucca-plant aborts ovaries with a larger than average number of eggs. Again this is an economic decision, rather than a form of 'punishment', which strongly selects against cheating by the moths. A recently described interaction between a senita cactus and a moth (Fleming & Holland 1998) may show the same choice mechanism as described for the yucca–yucca-moth interaction. The same mechanism was postulated earlier by Bull and Rice (1991) for a comparable mutualism between figs and fig-wasps. To date, no empirical study has corroborated this, however, and most fig species have other ways to control overexploitation by their pollinators, such as the production of non-functional figs and flowers that are out of the reach of the ovipositors of the wasps (Herre & West 1997).

Market value

The incorporation of the effect of supply and demand makes the market approach different from all other theories of cooperation used in biology. For the moment our game theoretical market model (Noë & Hammerstein 1994) can only predict in which direction the market value of a commodity will shift when the supply/demand ratio shifts. More sophisticated models should be able to make more precise predictions about the exchange ratio of commodities. When, for example, food is traded against protection, as in the ant – lycaenid example above, it is interesting to ask *how much* food is paid for how much protection. Such predictions will not be possible with a pure game-theoretical model. Hoeksema and Schwartz (this volume; see also Schwartz & Hoeksema 1998) show how this problem can be approached with the help of rather different techniques borrowed from the economic literature.

An example of human mating markets can make clear how the supply/demand ratio affects the market value of a commodity. On the basis of an analysis of 'Lonely hearts' advertisements, Waynforth and Dunbar (1995) showed how women trade youth and attractiveness against the material benefits men are offering. One explanation for this phenomenon is that Fisher's reproductive value (expected number of offspring produced in the future) determines the market value: healthy young women and wealthy middle-aged men have the best chances to raise children successfully (see also Voland & Engel 1990; Voland & Dunbar 1995; Voland & Chasiotis 1998). The individuals with the highest reproductive value pair off first, followed by those with slightly lower values and so on. In biology this phenomenon is known as 'assortative mating'. One result was puzzling, however: judging from their modest demands, the members of the youngest class of women seemed to value themselves less than would be expected under the assumption that their market value declines with age.

In a later study Pawłowski and Dunbar (1999; this volume) defined the 'market value' for each age cohort of each gender as the proportion of advertisers seeking individuals of that cohort by the number of members of that cohort advertising. The modest demands of the youngest class of women could be explained, if reproductive value would indeed be the decisive parameter for men. In the present-day population of industrialised countries the reproductive value peaks around the age of 25. However, further analysis showed that fecundity (the number of births per female per year) is much more important for a woman's market value than reproductive value – and fecundity declines monotonically with age (Pawłowski & Dunbar 1999). That men are selected to pay attention to age is not too surprising, of course, since both fecundity and reproductive value are likely to have declined with age for women over 20 over most of human evolutionary history. Thus the question remains: why do women in the youngest age class estimate their bargaining power lower than expected on the basis of age? Pawłowski and Dunbar (1999) show that this is due to a market effect: the number of women advertising from the youngest class was high relative to the number of men that expressed a preference for that class. In the next two age classes the supply : demand ratio was much more in favour of the women.

Signals on markets

The choosing class has to be able to assess or estimate the (relative) value of the commodity offered in order to make market selection work. In some cases the commodity on offer can be assessed directly. For example, when ants protect plants for a reward in the form of food bodies (see review by Beattie 1985 and contributions in Huxley & Cutler 1991), the plant can determine the number, size and nutritional value of the food bodies it puts on the market. The ants can assess them just as any other source of food. The plant cannot retract its food bodies easily, at best it is able to change their nutritional value with a relatively short delay. In many markets, however, commodities cannot be assessed directly and a signal is used as an intermediate between the commodity and the chooser (see Box 5.2). Signals can help to find a reward, but also hinder its accurate assessment. For example, the pheromones produced by the tentacle organs of Lycaenidae larvae described above may correlate with the presence of nectar, but may also be used to manipulate the behaviour of the ants (Axén *et al.* 1996; Fiedler *et al.* 1996). One can thus distinguish two types of markets: those in which commodity values are measured directly and those in which signals play an intermediating role.

The issue of 'honest signalling' has been at the centre of a long and heated debate (reviewed by Johnstone 1995, 1997, 1998), especially in the context of sexual selection. There is growing consensus that the handicap principle, first proposed by Zahavi (1975, 1977) and formalised by Grafen (1990a,b), explains why many signals can be honest most of the time. Simply put, the handicap principle predicts that in the context of mate choice, agonistic competition or predation, receivers of signals only pay attention to those signals that are costly to produce. This is predicted, because only individuals that are fit enough to back-up the signal will produce it at high intensity. Examples are large antlers in deer, long tails in birds and high jumps of antelopes chased by predators. Note that the handicap principle only works in the context of a market in which individuals are chosen: a cheetah does not hunt a Thomson gazelle that signals superior condition by stotting high, because it is an economical decision given that there is other prey available that is easier to catch. A cheetah would probably give it a try when the same vigorously jumping gazelle was the only prey around. The handicap principle in the context of a pollination market is discussed in Box 5.2. For a discussion of the idea that partners are chosen on the basis of their altruistic behaviour, which itself functions as a signal in the sense of the handicap principle, see Zahavi (1995) and Roberts (1998).

Applications of the biological market paradigm

Biological markets can be found in rather diverse systems. Since the publication of our market papers (Noë *et al.* 1991; Noë & Hammerstein 1994, 1995) the market paradigm has been used to explain (1) the value of grooming for female baboons (Barrett *et al.* 1999; Henzi & Barrett 1999, Barrett & Henzi this volume), (2) exchange of grooming against information about reproductive status in mice (Stopka & Macdonald 1999), (3) the value of human mating partners and the resources they offer (Pawłowski & Dunbar, 1999, this volume, (4) the exchange value of protection and nutrients in ant–lycaenid markets (Weith 1998, as discussed above), (5) the market value of nutrients exchanged between plants and fungi in mycorrhiza (Schwartz & Hoeksema 1998, this volume), and (6) the interaction between cleaner fish and their hosts (Bshary this volume).

A market can be formed by two traders, as is discussed by Hoeksema and Schwartz (this volume, see also Schwartz & Hoeksema 1998), and a biological market with a choice among trading partners in the sense of the present chapter can be formed by three traders, but the use of the paradigm makes more sense when the number of traders is large. A typical biological market has two distinct classes of traders, such as: males and females, breeders and helpers, or plants and pollinators. The market logic can also be applied to systems with other characteristics, such as: (1) markets with only one mono-morphic class of trader, for example coalition formation among group members in primates (Noë 1990); (2) markets in traders offer commodities that have to compete with commodities from abiotic sources or from organisms that do not trade on the market, for example plants that provide hiding places for the insects that protect them, so-called 'domatia', compete on a market with alternative hiding places; and (3) markets in which many different kinds of organisms take part that can nevertheless be lumped together into distinct trading classes, for example pollination and seed-dispersal networks.

Analogies and differences with other models of cooperation

The purpose of game theoretical models is not to describe the real world in as much detail as possible, but rather to provide a caricature of the real world system with all confounding factors removed. The model should behave in the same way as the system it mimics as far as the feature of interest is concerned. It is therefore likely, or even desirable, that several models of cooperation coexist, even to analyse one and the same system (see also Bshary this volume). Models presently used in biology can roughly be classified in the following way:

1 Varieties of the two-player Repeated Prisoner's Dilemma

The use of the RPD puts the cheating problem under the magnifying glass. The model functions best for two, and not more than two, individuals in a dilemma between cooperation and conflict (for a concise overview of the many derivatives of the two-player RPD, see Table 3.1, pp. 42–44 in Dugatkin 1998). An example is the interaction between two territorial neighbours that must agree over the location of a common border. Examples are given by Whitehead (1987; mantled howler monkeys) and Godard (1993; hooded warblers). Conflict resolution is probably a better label than cooperation in such cases.

2 Extensions of the RPD with some form of partner choice

Some of these models (e.g. Dugatkin & Wilson 1991; Enquist & Leimar 1993) combine the focus on the cheating problem with the possibility of changing partners to explain the spread of free-riding and exploiting strategies. Batali and Kitcher (1995) show that if willing cooperators can actively seek each other, cooperation can evolve more easily.

3 Spatial models

Most of these models are based on the concept of cellular automata (e.g. Nowak & May 1992; Grim 1995). The emphasis is on the spread of a cooperation strategy through a population. As above, these models are based on the Prisoner's Dilemma, but have multiple players who interact with their neighbours in a lattice. Recently a new form of such models was presented by Doebeli and Knowlton (1998) that resembles the biological market concept in a crucial aspect: two classes of mutualists, for example hosts and symbionts, are separated into different lattices. The competition between the members of each class is modelled as an interaction within each lattice, and the mutualistic cooperation as an interaction between nodes in separate lattices.

4 Skew models

Skew models concentrate on the division of reproduction and labour between dominant and subordinate individuals in communally breeding groups. The original models by Vehrencamp, (1983a,b) were developed with cooperatively breeding vertebrates (notably birds and mammals) in mind. In recent years these models have been extended considerably and applied to social and eusocial invertebrates, especially insects, as well (see Keller & Reeve 1994 and Clutton-Brock 1998 for reviews). Important factors that determine the degree of reproductive skew are assumed to be: (1) ecological constraints that prevent subordinates from breeding elsewhere, an idea that goes back to earlier models by Emlen (1982a,b); (2) the group's overall reproductive output; (3) the genetic relatedness among the group members; and (4) the relative fighting abilities of dominants and subordinates (cf. Keller & Reeve 1994).

Together with Carel van Schaik and Jan van Hooff, I have proposed that 'market effects' also determine the degree of skew: the relative numbers of dominants and subordinates, the possibility of the dominant to discriminate between subordinates, and the ability of the dominant to evict one or more subordinates on the basis of their relative contribution (Noë *et al.* 1991). Our example was based on breeder–helper systems in birds. We proposed that, if the number of helpers is such that an additional helper adds little to the fitness of the breeder, the breeder can play off the helpers against each other by threatening to evict the least productive one. Our paper had little influence on the way skew models were developed, however. Fortunately the idea that partner choice is important was introduced nevertheless in a recent paper by Reeve (1998). Note that exactly the same mechanism would also influence the power differentials between parents and offspring and thus be relevant to the theory of parent–off-spring conflict as well.

5 Market models based on Ricardo's law of comparative advantage

Mark Schwartz and Jason Hoeksema (1998) developed a market model of mutualistic interaction on the basis of an economic principle first described by the British economist Ricardo (1817): the law of comparative advantage. This model of biological markets is rather different from the game theoretical models presented in Noë & Hammerstein (1994) and this chapter. The approach of Hoeksema and Schwartz is explained in their chapter in this volume.

An example of the use of multiple paradigms

Egg-trading in hamlet fish (Fischer 1980, 1988) is an example of a case in which the use of multiple models helps to understand a single phenomenon. Black hamlets are simultaneously hermaphrodite fish that trade small packages of costly eggs against cheap sperm in short, alternating bursts at the end of the day. The ins and outs of the egg-trading itself can be modelled on the basis of a game like the RPD (Fischer 1988). But one has to consider the market in the background to fully understand the strategies played (see Friedman & Hammerstein 1991). The timing of spawning is essential: since the eggs go bad overnight and alternative partners are usually far away, the chance to switch to another partner is low. This timing probably results from a strategy to prevent mates from switching to other partners. Even the tit-for-tat-like alteration of providing egg-parcels itself only makes sense in a market context: it would not pay to economise with eggs, when there would not be a chance to use them in a trade with another partner (see also Connor 1992, 1995b).

Conclusions: what is gained by a theory of markets?

Sticking a label 'biological market' on a certain phenomenon will in itself not help us to understand it better, but recognising the common features of biological markets may increase the awareness of analogies with other phenomena, studied in the following disciplines:

- Economics. A wealth of 'classical' supply–demand models as well as game theoretical models of human markets on which commodities are traded have been developed. Other markets that are studied by economists and that are important in this context are: 'mating markets' and 'job markets'.

- Anthropology. Human mating markets have been studied in the sub-disciplines of cultural and of evolutionary anthropology. In addition there is an extensive literature on human bargaining in many different societies.
- Biology. At least three relatively disjointed sub-disciplines are relevant: empirical as well as theoretical work on mating markets has been done in the context of sexual selection, students of intra-specific cooperation have a strong bias towards the development of models based on game theory, and interspecific mutualism has been studied in the less theoretical and more empirical tradition of ecologists.

Biologists can borrow a lot more from the economic literature than the other way around, although, economists may learn from evolutionary biology to pay more attention to strategies at an individual level.

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LOUISE BARRETT *AND* S. PETER HENZI

6

The utility of grooming in baboon troops

Periodically through the day – most obviously early in the morning and late in the afternoon – an individual member of a wild baboon group will approach another and begin to comb meticulously through its pelage with dextrous fingers or, equally likely, solicit such behaviour by lying down in front of the other animal. Such grooming, for other monkeys and apes, as well as baboons, is the defining act of sociality. Its dynamics are therefore likely both to reflect current ecological circumstances and to illuminate historical selection for attributes that enable successful performance in the social world. The broad question then, with which to begin, concerns the function of grooming.

To the observer, two things are immediately apparent. First, grooming clearly has hygienic value, since an animal also puts effort into grooming itself and because the grooming it receives from others is directed at those parts of its body that it cannot easily reach (Barton 1985). The targets of this grooming are ectoparasites, such as lice and their eggs (Saunders 1988; Tanaka & Takefushi 1993). The diligence and concentration that groomers apply to this task underscore the fact that grooming is more than just a pretext for tactile contact. Nevertheless, the second observation is that this physical contact is manifestly pleasurable for the recipient; it is, in fact, associated with the increased production of β-endorphins (Keverne *et al.* 1989). Presumably, this hedonistic benefit is a derived feature and serves, proximately, as the primary reinforcer sustaining participation. The analysis of function cannot, however, end here. The fact that monkeys put considerable effort into grooming relationships, groom some group members more than others, and work to sustain time for grooming in the face of opposing pressures (Sade 1972; Dunbar & Sharman 1984), suggests that grooming also subserves an individual's social goals. Determining how grooming functions in this context is a central concern for primate socio-ecology.

Savannah baboons (*Papio cynocephalus*), like most other cercopithecine monkeys and some New World species (O'Brien 1993), have grouping patterns that are categorised as 'female-bonded' (Wrangham 1980). Generally, this means that females are philopatric, with males dispersing at puberty. Social groups are therefore composed of natal females, all relatively closely related to one another, and one or more immigrant, unrelated adult males. A suite of traits characterising female relationships has co-evolved with this condition. These include strong dominance relationships, allomothering, evident competitive and cooperative relations together with strong grooming relationships (Di Fiore & Rendall 1994). An understanding of these behavioural propensities hinges on an understanding of what initially led to female philopatry. Putting to one side the issue of their evolutionary precedence, two factors extrinsic to the relationships among females are likely to underpin the initial selection for and subsequent maintenance of female groups. These are an increased risk of predation (van Schaik 1983; van Schaik *et al.* 1983; Hamilton 1971) and vulnerability to infanticidal males (van Schaik & Kappeler 1997; van Schaik 2000). The unavoidable corollary of this selection for female grouping in the face of external threats, however, is that such females find themselves in conflict with one another over access to scarce local resources, such as food or predator risk-reducing spatial positions (Barton & Whiten 1993; Ron *et al.* 1996). Although the effects may be ameliorated by kinship, females thus find themselves trapped squarely between the Scylla of predation risk and the Charybdis of competition. It is this dilemma, in both ultimate and proximate perspective, that generates the subtle and complex patterns of interaction with which we associate female-bonded systems.

Foremost amongst these are the coalitions that females form to contest resources (Silk 1987). As with male coalitions (Noë this volume), partner choice is crucial and it has been argued that this is where the social function of grooming can be seen most clearly. In this view – which has been the prevalent one – grooming serves to counteract the centrifugal force of cheating (van Hooff this volume). It is suggested that it does this either by building relational strength and thereby establishing the trust on which coalitions may be built (Dunbar 1988) or by acting as a currency that can be exchanged in anticipation of future coalitionary support (Harcourt 1988; Silk 1992). We have examined these two proposals in detail elsewhere, concluding that there is little evidence to support them (see Henzi & Barrett 1999 for a fuller account). In addition, it is apparent that the dyadic 'tit-for-tat' (Axelrod 1984) nature of the latter mechanism is inappropriate for primate social groups (Barrett *et al.* 2000. See Box 6.1). Furthermore, this lack of evidence for the 'grooming for support' model serves to corroborate a more immediate problem, one which initiated our own interest in the application of biological market theory (Noë & Hammerstein 1994; Noë this volume) to the dynamics of primate social encounters.

The problem is this: chacma baboons (*P. cynocephalus ursinus*), our chosen study animals, do not form coalitions despite the fact that females sustain grooming relationships and compete over access to resources (Ron *et al.* 1994, 1996; Barrett *et al.* 1999; Silk *et al.* 1999). Even more pertinent, chacma females from the Drakensberg Mountains continue to form grooming relationships and adjust their time budgets to conserve grooming time (Henzi *et al.* 1997a,b), despite the fact that the distribution of resources in this environment means that they experience no competition for food and show almost no aggression (Henzi *et al.* 1992). Obviously, then, no account of grooming that hinges on coalitions or agonism can provide a general explanation for the phenomenon. Consequently, we have argued that a comprehensive explanation should begin with an understanding that grooming is valuable in and of itself (Barrett *et al.* 1999). That is, grooming should be considered as a valuable service for one animal to provide to another since there are areas of the body that individuals are unable to groom themselves with any efficiency (the top of the head; middle of the back) and keep clean. Grooming can therefore be considered as a commodity since an animal cannot obtain all the grooming it requires by its own actions: it must trade with other individuals. Thus, within primate groups, animals should trade grooming with each other on a reciprocal, cooperative basis in order to reap the benefits that grooming itself offers. That is, it will be possible to distinguish a 'trader class' of females that exchange grooming with each other ('reciprocal traders': Hemelrijk & Ek 1991). If this were so, and grooming could be considered as a valuable service in its own right, it would explain the persistence of grooming among females in the Drakensberg Mountains.

By the same token, if grooming is valuable, the possibility exists for it to be traded for some 'value equivalent'. That is, grooming may be exchanged for other commodities besides grooming in return. This would lead to the formation of another trader class consisting of

Box 6.1 Raising the stakes in the market place?

The use of the Iterated Prisoner's Dilemma (IPD) to investigate the occurrence of altruism between unrelated individuals has been very successful at keeping theoretical biologists in work, but less successful at explaining the patterns found in nature. This is partly a consequence of the difficulty in quantifying precisely the costs and benefits of particular actions (e.g. Seyfarth & Cheney 1988) as well as problems in determining the nature of the payoff matrix (e.g. Milinski 1987; Godin & Davis 1995; Milinski *et al.* 1997). However, it also seems likely that, for permanently social animals like primates, the IPD is, quite simply, inappropriate for the system under study (Noë 1990).

The biological markets approach that we advocate here is more suitable for primate groups since it assumes that there is both partner choice and competition between individuals for the best partners. The basic IPD game recognises neither of these complicating factors. However, efforts have been made recently to make the IPD approach more amenable to empirical testing and more relevant to real-life situations. Roberts and Sherratt (1998), for example, allowed individuals to 'test the water' before embarking on a full-blown cooperative relationship and so avoid defection and exploitation. Cooperation could gradually build up over time as individuals gained 'confidence' or 'trust' in their partners. A strategy known as 'raise the stakes' (RTS) proved very successful under these conditions. An individual playing RTS increases its investment in a cooperative interaction if its partner matches or betters its own last move. Cooperation therefore increases over time if both players use RTS. Keller and Reeve (1998), reviewing the potential impact of this model, suggested that primate grooming patterns could represent an example of a system where RTS applies. Indeed, the results of one of our studies (see Fig. 6.1; Barrett *et al.* 1999) appear to conform to the RTS strategy. In this view, the short bouts we observed could represent individuals just beginning on a cooperative relationship – and therefore investing relatively little – while longer bouts represent those dyads with established partnerships.

However, when we explicitly tested for RTS among the grooming dyads in our study troops, we found no evidence that this was the case (Barrett *et al.* 2000. Instead, there was no tendency to increase the contribution across bouts (order of occurrence vs. bout length) and individuals tended to time-match their grooming contributions within a bout (Groomer 1 vs. Groomer 2), regardless of previous levels of cooperation (Table 6.1). This provides support at the individual level for our original group level finding. Even when we tested for RTS in the short-term within single grooming bouts, relaxed the definition of RTS or applied it to only a sub-set of 'unfamiliar partners' in our study troops, there was no indication that females were 'testing the water' in their grooming interactions (Barrett *et al.* 2000).

Table 6.1: *Spearman rank correlations between (i) individual contributions to grooming bouts and (ii) the date of a grooming bout and its length*

		Groomer1 vs Groomer 2		Order of occurrence vs. Bout length	
Dyad	*N*	r_s	*P*	r_s	*P*
1	7	0.5	0.1	−0.4	0.1
2	6	0.7	0.03	0.3	0.2
3	23	0.5	0.002	−0.09	0.3
4	16	0.4	0.05	−0.04	0.4
5	8	0.6	0.03	−0.4	0.1
6	6	0.8	0.02	0.1	0.4
7	5	0.5	0.2	−0.3	0.3
8	10	0.4	0.09	−0.4	0.1
9	6	0.1	0.4	−0.4	0.2

Notes:
N: number of grooming bouts per dyad. We analysed only those dyads for which we had five or more reciprocated grooming bouts.

This should actually come as no surprise since, despite Keller and Reeve's (1998) claims to the contrary, strategies such as RTS will inevitably fail to explain patterns of grooming in primate groups because the very nature of the social system renders them inapplicable. Within social groups, females do not initiate relationships at a single definitive point in time. Individuals interact with many others from a very young age, and these relationships are necessarily one-sided since young animals lack the skill and coordination to groom effectively. Although the nature of

Box 6.1 (*cont.*)

these relationships changes significantly through time, there is no point at which individuals can suddenly choose to initiate a completely new relationship and use RTS to establish whether cooperation is likely to be forthcoming. A model of relationship formation that makes no allowance for these kinds of effects is not appropriate for permanent social groups. If we are ever to make any progress in modelling and predicting the interactions of social animals, it will be necessary for theoreticians to recognise the limitations of dyadic games and tackle social groups in all their complexity, using models like biological markets as their basis. The bias towards dyadic models seems to arise because theoreticians continue to model systems that are tractable – but that does not help those of us trying to understand the real world. The concept of the biological market – in conjunction with other alternatives to IPD-based reciprocity, like parcelling (Connor 1995) and competitive altruism (Roberts 1998) – offers the most promising directions to take the analysis of complex social behaviour. All we need now are some brave, theoretically minded individuals to rise to the challenge.

'interchange traders' (Hemelrijk & Ek 1991). Since baboon females, in the absence of alliances, gain access to resources on the strength of their own 'power' (females can generally be placed in a linear, transitive dominance hierarchy, which describes priority of access to resources), interchange trading will occur only when the power differential between the two participants is great enough that the commodity gained could not be achieved by the less powerful individual alone. Power differentials among adult female primates can be expressed in terms of the distance between the animals' respective dominance ranks, and the 'gradient' (or steepness) of the dominance hierarchy (Henzi & Barrett 1999). In situations where resources are monopolisable and within-group competition is high, gradients are expected to be steeper than in situations where competition is relaxed, and the effect of rank distance is therefore expected to exert a stronger influence. Consequently, the rank distance required to produce a given power differential will differ according to the slope of the dominance gradient, with the result that the power differential between the highest- and lowest-ranking females in a group where

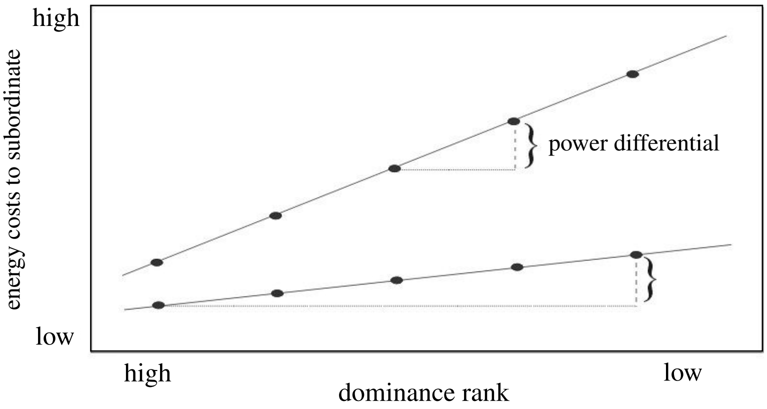

Fig. 6.1 The relationship between competitive gradient, dominance rank and power differentials. The Y-axis represents the notional energy costs of competition for the lower-ranking female, and slopes indicate steep (upper line) and shallow (lower line) competitive gradients. We illustrate power differentials of equal magnitude, produced between adjacently ranked and distantly ranked individuals as a consequence of a difference in competitive gradient (see text for details).

gradients are shallow may be identical to that between two mid-ranking individuals in a group where gradients are steep (see Fig. 6.1). This is important because market effects may only develop where gradients are steep enough for one animal to exert a much stronger negative effect on others by withholding access to commodities. In groups with shallow gradients, access to commodities may have little influence on reproductive success and individuals will be able to exert little leverage over others (see also Vehrencamp 1983).

Adopting a biological market stance in the analysis of female baboon relationships requires both the demonstration that grooming is a commodity and an assessment of how the structure of the marketplace – that is, the relative availability of traders or shifts in commodity value – affects transactions. Clearly, the latter, dealing as it does with supply and demand, is more important since it is central to the distinctiveness of the biological markets approach (Noë this volume). Nevertheless, our focus for the remainder of the chapter is on the former. This is partly because there is still a need for a formal elaboration of the theory, but also because the assumptions that grooming is a commodity and that it is exchanged for goods in other domains must be satisfied before more detailed tests of biological markets theory can be performed.

Is grooming a commodity?

To reiterate our argument, grooming can be exchanged for itself in a reciprocal manner or it can be interchanged for another, equally valuable, service. The ability to interchange will depend on the power differentials between individuals within the troop, which in turn will depend on ecological circumstances.

Reciprocal grooming

When grooming is traded for itself, two females should reciprocate grooming in a manner that minimises cheating and equalises value. We have found that about 40% of all female grooming in baboons is reciprocated immediately (Barrett *et al.* 1999). Females never groom each other simultaneously, but divide grooming up into a series of reciprocal, parcelled bouts (Connor 1995), where one female grooms for a while then stops, after which her partner reciprocates. A grooming bout is made up of a number of such episodes and one can predict that where grooming is traded for itself, the total time spent grooming, summed across episodes, should be the same for each female. This should be true regardless of bout length. That is, both short and long bouts should be time-matched, and there should be a positive correlation between the contributions of each individual to a bout at both the individual and the group level.

Interchange grooming

In primate social groups, potential interchange commodities include:

- **Tolerance at feeding/drinking sites**

When food resources are patchily distributed and it is possible for more powerful animals to monopolise them (see e.g. Barton & Whiten 1993; Ron *et al.* 1996), low-ranking females may trade grooming for tolerance at feeding sites. This need not involve the higher-ranking animal actively supporting the lower-ranking animal against competitors or giving up food itself. It may be enough for dominant individuals merely to tolerate subordinates within food patches, with the level of tolerance determined by the amount of grooming provided. As in all the examples we give here, we envisage grooming by subordinates to be a short-term, immediate response to (potential) lack of tolerance by dominant females (e.g. Silk 1982; O'Brien 1993). We do not expect it to be characterised by sustained levels of grooming over time between particular individuals. This is particularly likely to be the case in the wild, where females have more leeway simply to keep out of the way of intolerant animals. In other words, interchange grooming represents a short-term tactic, rather than a long-term strategy.

- **Coalitionary support**

Although we have questioned the prevalence of coalition formation among female primates (Henzi & Barrett 1999), it is theoretically possible that grooming can be exchanged for support. Nevertheless, we still question whether this would represent strategic behaviour, and would expect it to occur over a much shorter time frame than is usually suggested (see e.g. Dunbar 1988). We also regard coalitionary support as just one of many available commodities, and not the sole underlying reason for grooming.

- **Mating opportunities**

Exchange of grooming for sexual access would seem very likely. Male baboons tend to groom females only when the latter are fertile and possess a sexual swelling (personal observation; Weingrill 2000). Males may use grooming to ensure females tolerate them in close proximity so that they can exclude other males and achieve a high frequency of mating. The key to understanding the market effect here, as in all these examples, is to recognise that individuals may be prepared or forced to pay different prices for the commodities they wish to obtain. Naïve interpretations of the relevance of trading are often made because researchers fail to appreciate the crucial interaction between supply and demand.

For example, Hemelrijk & Ek (1991) stated that they could find no evidence that males traded grooming for fitness benefits within a captive chimpanzee colony. This conclusion was based on the fact that there was no correlation between the realised paternity score per male and his investment in a female in terms of the grooming services he provided. However, Hemelrijk & Ek (1991) failed to take account of the fact that males differed in dominance rank and quality and that the price males paid to achieve matings may have differed.

As Stopka *et al.* (in press) point out, within a mating marketplace, low-quality males are expected to overcompensate for their quality by providing more allogrooming bouts to oestrous females. By the same token, and perhaps more importantly, a male of high quality may be preferred by the females, and will therefore pay a lower price before he gains mating access. Data from wild chimpanzees in the Mahale Mountains, for example, indicate that adult males are more successful at courtship overall than adolescent males. In addition, the courtships of adolescent males failed more often than those of adult males whenever there were higher-ranking males present. This was not just a result of male–male competition but due also to females acceptance or refusal of a courting male (Matsumoto-Oda 1999). At the beginning of oestrus, females at Mahale mated promiscuously with many males, but, as they reached peak fertility, they tended to copulate repeatedly with only higher-ranking males and their rate of grooming of these males increased substantially. The fact that females increased their rate of grooming and appeared willing to 'pay' for increased mating with their preferred partners suggests that high-ranking, good-quality males need pay only a very small price to obtain matings. Given that females are not passive vessels but active traders in the mating marketplace, a simple relationship between male grooming of females and high fitness benefits is not to be expected. Finally, the relative availability of fertile females will lead to prices dropping or becoming highly inflated depending on whether supply can meet demand or is exceeded.

- **Infant handling**

Many cercopithecine monkeys are reluctant to allow their newborn offspring to be handled by other individuals. New mothers receive much more grooming than other females (Altmann 1980; Kenyatta 1995) and it seems possible that grooming is exchanged for short-term tolerance around infants. Females may be able to increase a mother's tolerance and willingness to allow her infant to be handled by providing grooming. In this case – and probably in all the other examples here – the release of endogenous opiates may help to reduce tension levels in the mother (or more dominant) female and increase her tolerance thresholds.

At any one time, there may be only 1 or 2 infants 'available' but many more interested females. The outstripping of supply by demand should generate a strong market effect. Market effects over infant access may also be found in species where infant handling is encouraged (e.g. vervets; langurs) but this will not be related to grooming frequency, since females are not buying tolerance from the mothers. In fact, in some instances, a reverse market effect may develop as mothers compete for good 'babysitters'.

Grooming and exchange in chacma baboon females

Since female chacma baboons do not form coalitions, we suggest that grooming will be exchanged for itself or for tolerance around food sources and infants. (They may also exchange grooming for sex, but we will not deal with male–female interactions here). We expect market effects to be stronger for interchange trading than for reciprocal trading, since demand will exceed supply: there will be fewer individuals able to 'sell' tolerance and more individuals wishing to 'buy' it.

As the designations of animals to particular trader classes within primate groups are relative and not absolute (i.e. they depend on the balance of power between two potential traders), individuals can be both types of trader simultaneously. However, the relationship between any particular pair of individuals will be fixed and limited to only one type of exchange. Individuals can thus make choices regarding with whom to form grooming-based or tolerance-based relationships depending on their standing in the marketplace, and their ability to 'outbid' the competition. From this, it follows that, when competition for resource access is high and dominance gradients are steep, relationships between distantly ranked individuals (such as they exist) will be based on grooming as an interchange currency (since power differentials will be large), whereas relationships between more closely ranked individuals will be based on reciprocal grooming. Differences in rates of food-related aggression between groups living under different ecological conditions should therefore lead to differences in the levels of reciprocated grooming observed. Within groups, individuals will differ in the relative proportions of time that they devote to reciprocal versus interchange grooming depending on their rank and therefore their standing in the marketplace.

We predict that the majority of female–female dyads in any troop will be characterised by reciprocal, rather than interchange, grooming. This is because interchange grooming will occur less frequently since there are fewer individuals able to offer tolerance effectively as a commodity, whereas all individuals will be able to trade grooming. It is also likely that individuals will trade grooming more frequently than they trade for tolerance, even though the latter is a more valuable commodity. This is because we view tolerance as a short-term tactical response to a current situation, whereas reciprocal grooming for hygienic (or hedonistic) reasons is an ongoing requirement. As a result, females can be expected to spend most of their time grooming females of similar rank to themselves, since this is the class of females that will trade grooming for itself on a frequent basis. This, in turn, means that a large proportion of grooming in any troop should be reciprocal, regardless of the level of competition in the population.

Box 6.2 Methods

In addition to collecting data on the protocols of grooming (who initiated, who ended, reasons for termination etc.), we timed each of the episodes making up a grooming bout, using stopwatches or hand-held computers. Two things need to be noted about our analyses of these data. First, we confined our attention to grooming bouts that contained at least two episodes, i.e. where there was immediate reciprocation. We did so because our work in the Drakensberg indicated clearly that, as groups grow in size, females come to set an upper limit on the size of their grooming clique (Henzi *et al.* 1997a). They do so because attempting to groom all other females reduces the amount of time available to any dyad. Specifically, they cap clique size to prevent bout duration dropping below that which is sufficient for reciprocation, suggesting that this is a fundamental requirement of grooming interactions. It is, at the same time, difficult to determine the timescale over which reciprocation might operate in the case of those bouts that are not immediately reciprocated. This makes non-reciprocated bouts problematic to analyse in a meaningful way: for example, a time interval could be chosen, based on an educated assessment of the likelihood of reciprocation within a certain time-window. However, if the results do not indicate that reciprocation occurs, this could either be a result of a true lack of long-term reciprocation or an artefact produced as the result of selecting an inappropriate time frame.

Second, despite the wealth of information, we conducted our analyses by pruning the data severely. For each female, we extracted all grooming bouts in which she was designated as the initial groomer, and from these selected at random a single grooming bout for each of the dyads of which she was a member. This gave us a maximum of $N(N-1)$ dyads per cohort of females. Although this seems wasteful of data, it does control for the overrepresentation of particular dyads and consequent inflation of N. Using the full data set, while analytically invalid, gives the same results.

Is grooming traded for itself?

In this light, we tested the notion that grooming represents a commodity by using data from two populations of South African chacma baboons (Barrett *et al.* 1999). Two troops were observed in each population, with the size of the female cohort matched across populations. There were highly significant differences in the levels of food-related aggression and the strength of the dominance hierarchy observed in the study populations. In the Drakensberg Mountains, the sparse and relatively even distribution of food (Henzi *et al.* 1992) meant that agonistic events between female baboons occurred at a rate of only one every 500 hours, whereas at De Hoop in the Western Cape, females were engaged in aggression at least once per hour. Consequently, females at De Hoop could be ranked in a strong linear dominance hierarchy, whereas this was not possible for the two mountain troops. We inferred from this that interchange trading would be possible at De Hoop since power differentials were likely to be high, whereas this was unlikely to be the case in the Drakensberg with the result that females would be limited to reciprocal exchange alone. More details on the methodology used are given in Box 6.2.

In line with our prediction that reciprocal traders should dominate the marketplace, we found a significant positive correlation for all four groups between the amount of time that each individual contributed to a dyadic grooming bout, despite the differences between groups in the potential for interchange trading (Fig. 6.2). That is, the longer one individual (Groomer 1) spent grooming another within a bout, the longer their partner (Groomer 2) groomed them in return. We suggested that this came about because individuals were seeking partners who provided good value in the marketplace. Time-matching of this kind has also been observed in blue monkeys (*Cercopithecus mitis*) (Payne *et al.* unpublished material).

Do 'market forces' influence grooming reciprocity?

As Fig. 6.2 shows, the slopes of the lines differed between the matched pairs in each population (WA2 vs. ST and HT vs. VT). That is, the relationship between individual partners' contributions was much stronger for both the Drakensberg troops than for the De Hoop. We suggested that this was because the potential for interchange trading was minimal in the Drakensberg. The lack of feeding competition meant that power differentials were low and that females were able to exchange grooming only for itself. Thus, the marketplace contained only reciprocal traders and the

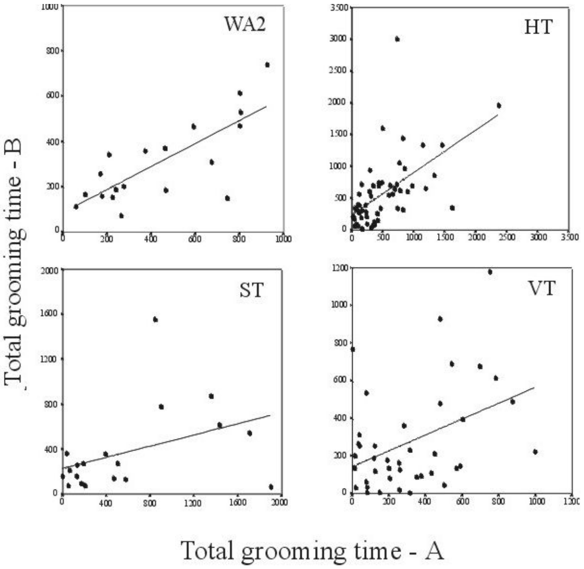

Fig. 6.2 Relationship between individual grooming contributions towards a bout for four groups of baboons from two populations. WA2 (6 females) and HT (12 females) are from the Drakensberg mountain population. ST (7 females) and VT (12 females) are troops from De Hoop, Western Cape. (*From* Barrett *et al.* 1999.)

emphasis was on finding grooming partners who would provide good value (offer as much grooming as they were given: see Box 6.1 for another test of time-matching in these study troops). The regression coefficient was higher for this population than for De Hoop where the potential for interchange introduced more noise into the relationship. In other words, market forces could predict the strength of grooming reciprocation in the two populations.

In addition to this difference between populations, we also found a significant relationship between rank distance and time-matching of bouts in the De Hoop population – although only the larger of the two troops showed this pattern. That is, subordinate individuals tended to groom for much longer than dominant individuals within bouts, suggesting that dominant individuals were able to use their control of other commodities to extract a higher price in grooming from their subordinate counterparts. The absence of a relationship between rank distance and time-matching for the smaller De Hoop troop suggests that there may be a group size effect on power differentials. The small female cohort size may mean that power differential effects do not operate as powerfully as they do in the large troop. This would imply that rank distance may have an absolute effect on females' ability to interchange. In a small troop where rank distance can never be very high, the difference between the highest- and lowest-ranking female may still be insufficient to lead to an interchange relationship. Overall, the data suggest that the asymmetry in the payoff for grooming bouts between distantly ranked animals compared to closely ranked animals within and between populations could be attributed to the operation of market forces within the group.

The notion that competition among subordinates for grooming 'rights' to dominant animals could lead to increased levels of grooming, as they attempt to 'outbid' each other, is similar to Seyfarth's (1977) model of grooming competition. In this model, grooming is directed up the hierarchy because dominant animals are more 'attractive' grooming partners. Thus, dominant animals receive more frequent grooming from a greater number of partners because they can offer the exchange of goods in other domains.

Adopting a market perspective takes this idea further since this predicts that dominant animals should receive, not only more frequent grooming, but longer grooming bouts from each of their grooming partners relative to less dominant females. The precise degree to which grooming time is elevated will depend on the number of subordinates competing with each other. This is interesting because there is generally a very poor relationship between the frequency of grooming received (number of grooming events per unit time) and the overall amount of time spent grooming (see e.g. Henzi *et al.* 1997a). That is, measuring the frequency with which an animal is groomed does not necessarily predict how long each animal is engaged in grooming with each partner. This may be because market effects are in play and the strength of these will vary across time, both within and between days. Thus, during periods when a high proportion of subordinate animals are free to groom, high-ranking females may be able to increase the amount of grooming received because subordinates are sensitive to the presence of rivals. In this case then, increased grooming is achieved by the operation of the market effect alone and dominant females remain 'passive'.

However, dominant females could increase the amount of grooming they received by taking a more active role and 'punishing' subordinates, in the sense of Clutton-Brock and Parker (1995) (see also Bshary, this volume, for a possible example of punishment within the cleaner-fish market). If dominant animals punish subordinates that do not supply 'sufficient' grooming (how this would be determined is a thorny issue that we will leave aside for the present), then the dominant will be able to force subordinates to groom for longer than they would in the absence of such coercion.

The original formulation of biological market models (Noë *et al.* 1991; Noë & Hammerstein 1994) stated that commodities were 'inalienable' and could not be taken by force. Punishment and partner control were therefore considered to be outside the scope of market-based models. However, it is clear that, while grooming is inalienable and requires the cooperation of another animal, punishment could not only increase the amount of grooming that an animal receives, but also create a very strong market effect, depending on how many subordinates are available for dominant animals to coerce (we thank Ronald Noë for pointing this out). That is, the threat of punishment would lead subordinates to increase the amount of grooming they supplied, again as a means of outbidding the competition, so that their rivals, rather than themselves, were punished.

The total amount of coercion performed and the strength of the market effect produced in this way depends on the number of subordinates an animal could bully. Given that an animal needs only a finite amount of grooming within a certain time period, the higher the number of competing subordinates available, the smaller the increase in grooming time that each will have to perform. When there are fewer subordinates available, each one will have to provide relatively more grooming to dominant animals in order to avoid aggression. The effectiveness of punishment could be tested empirically by using matrix correlations to determine the relationships between aggression, tolerance and grooming within dyads.

If coercion can be shown to be a market force, then we have an alternative explanation for the lower time-matching seen in the De Hoop baboons. As stated above, we suggested that the noise in these relationships was created by the potential for interchange trading in these troops (Barrett *et al.* 1999). However, it seems possible that high power differentials would give dominant animals the ability to extract more grooming during strictly reciprocal bouts, due to the market effect created by coercion or partner control. This latter explanation may, in fact, be more likely since our analyses dealt only with immediately reciprocated grooming bouts, whereas most interchange grooming is expected to be associated with non-reciprocated grooming of dominants by subordinates.

To date, there are very few studies on other primate species that have investigated grooming patterns from a market perspective. However, Muroyama (1991), working on Japanese macaques (*Macaca fuscata*), did find a difference between closely versus distantly ranked females in the level of reciprocation observed. However, this study focused on the proportion of reciprocated versus non-reciprocated bouts for particular dyads, and did not investigate the level of reciprocation (time-matching) within dyads. The data showed that partners of high relatedness, and therefore similar rank, were less likely to reciprocate grooming immediately than were distantly related dyads. Thus, the overall proportion of reciprocated bouts was higher for kin than non-kin. In light of the results we obtained from the baboons, it would be interesting to see how patterns of time-matching fit in with these results. We would predict that, although kin may show overall levels of reciprocation that are lower than those of non-kin, the level of time-matching observed in those bouts that are reciprocated will be closer than in the reciprocated bouts of distantly related (and distantly ranked) dyads. If this were the case, it would suggest that the higher levels of reciprocation by distantly ranked dyads do not reflect the avoidance of cheating (as suggested by Muroyama 1991) but the operation of market forces forcing subordinates to spend more time grooming dominant animals. If, on the other hand, this were not the case and close kin were less likely to time-match and reciprocate bouts, it would suggest that the rank-related effects seen in our baboons were attenuated in macaques. Since Japanese macaque females generally have steep dominance gradients (Matsumura 1999), this would be surprising. However, Muroyama's study troop was artificially provisioned (Yamagiwa & Hill 1998) and it may be that this reduces power differentials to a point where grooming can only be exchanged for itself. Further investigation of this troop and other non-provisioned groups would be very valuable.

Can grooming be traded for something else?

The data presented here support the view that monkeys, by being sensitive to the identity and capabilities of their partners, are using grooming as a commodity and that it is most commonly traded for itself. While our findings on the relationship between rank and within-bout reciprocity imply that interchange trading occurs, it is still necessary to demonstrate that this is so. (The manner in which females 'negotiate' regarding the kind of exchange they are seeking also requires investigation and clarification. See Box 6.3). In fact, it is crucial to further development of the biological markets model, which is built on the interaction of two trader classes and the competition that this engenders as supply and demand

Box 6.3 Grooming behaviour and bargaining tactics

One important component of forming a successful collaboration is the bargaining process. This constitutes the conversion of the power balance between individuals into a payoff distribution (Noë *et al.* 1991). As regards grooming, this is expected to take the form of signals to indicate that an animal wishes to engage in grooming with another, and that the reason for grooming (reciprocal or interchange) is made clear. With regard to reciprocal grooming, individuals need to establish that grooming given will be returned. The onus is on the individual initiating the bout to indicate what is expected of the other.

The most reliable and effective way of conveying the information that an individual wishes to engage in reciprocal grooming is to solicit grooming from the chosen partner. This may seem to place the first groomer at risk of being cheated. However, cheating may not be an overriding factor within permanently social groups (see e.g. Roberts 1998), and individuals may be more concerned with obtaining good value for their services than avoiding cheating *per se*. If this is the case, then soliciting for grooming would make it abundantly clear that grooming itself is required and not some other commodity. This may also allow the solicited animal to signal back how much it is prepared to invest in the other animal by timing the first grooming bout accordingly (although we found no evidence that this was the case in chacma baboons: Barrett *et al.* 2000). Solicitation also allows an animal to signal that it does not require grooming by ignoring the soliciting animal's request, stopping negotiations swiftly. Alternatively, vocalisations could also be used to signal whether an individual intends to groom or is seeking grooming itself. Muroyama (1991), for example, found that Japanese macaque females use specific variants of a vocalisation – the 'girney' – to indicate either an intention to groom or an intention to be groomed (see also Masataka 1989). It would be interesting to test if female baboon contact grunts also differ acoustically depending on whether a female is seeking or offering grooming.

Knowledge of rank may also be important in differentiating reciprocal from interchange requests, since it is possible that high-ranking animals could initiate interchange trading by demanding grooming from subordinates. A solicitation from an animal of adjacent rank can therefore be safely assumed to represent a request for reciprocal grooming, whereas an equivalent request from a dominant is most likely to represent interchange. We can therefore predict that time-matched reciprocal grooming bouts should begin with the solicitation of grooming of one animal by another of adjacent rank but that grooming for interchange should be characterised by non-reciprocated or highly mismatched bouts in which the grooming individual did not initially solicit for grooming itself. Grooming bouts are initiated through both solicitation and immediate grooming of the selected partner and individuals differ in the tactics used across partners (Barrett & Henzi, unpublished data) suggesting that these predictions are worthy of consideration. The potential for females to use vocalisations in addition to physical solicitation may also help to illuminate the negotiation process for reciprocated versus interchange bouts.

fluctuate. Although it is possible that individuals differ in their grooming ability, and may therefore invoke competition for their services, this seems unlikely. It is the time for which one is groomed that determines the benefits of grooming, and baboon females are known to be able to reduce the size of their grooming cohort in order to increase the length of individual grooming bouts (Henzi *et al.* 1997a).

Nevertheless, it is still possible to demonstrate interchange grooming in the De Hoop baboon population and to show that it is geared towards eliciting increased tolerance in the partner. To do this, we exploited the fact that baboon mothers are very reluctant to expose their young infants to the attentions of other group members, and measured the impact of grooming on an individual's ability to interact with another females' new infant. As mentioned above, infants are a source of great attraction for female baboons, and they frequently attempt to interact with both the infant and the mother in the first few months postpartum, despite maternal reticence. We found, as had Muroyama (1994) before us for patas monkeys (*Erythrocebus patas*), that in order to handle young infants that are not their own, most females had to groom the mother and thereby 'buy' her tolerance (Fig. 6.3).

All grooming bouts associated with infant handling were non-reciprocated and the length of the grooming bout was dependent on the rank

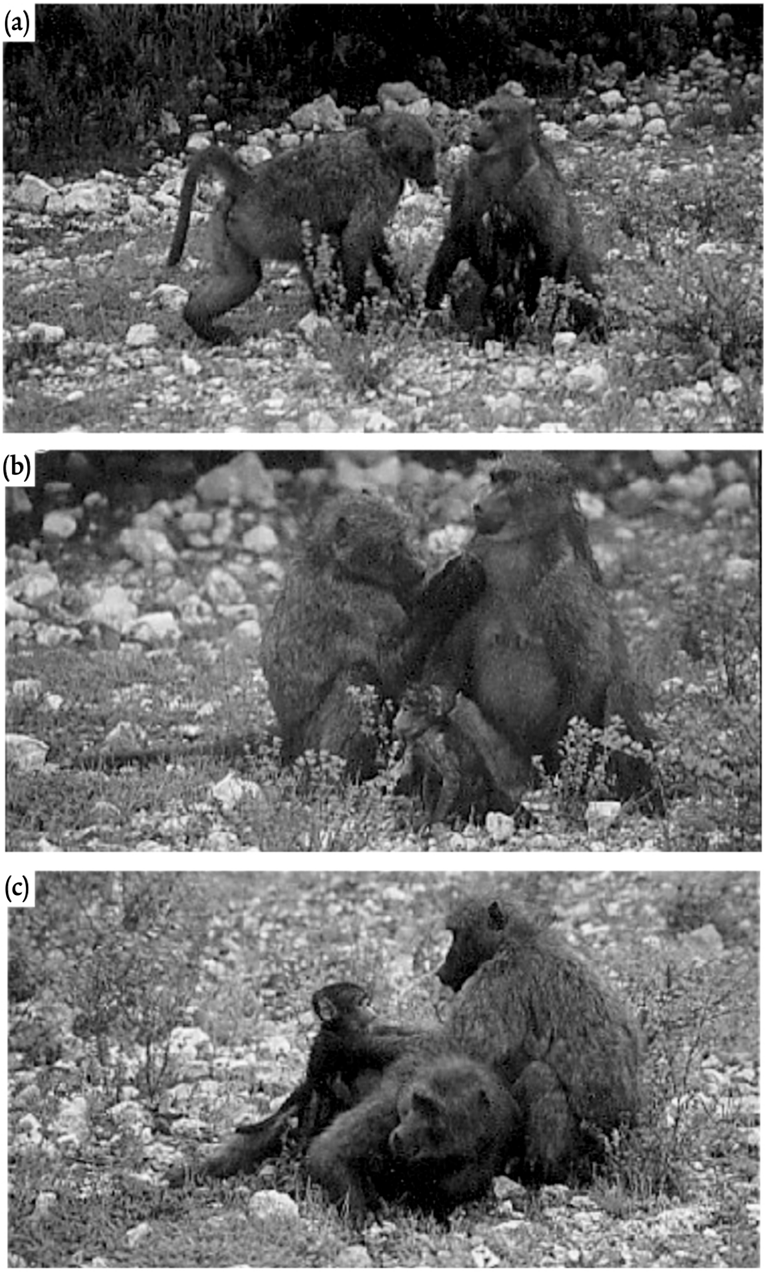

Fig. 6.3 Sequence showing infant handling and grooming. (a) individual QU approaches mother AC and infant KE, lipsmacking (b) QU initiates grooming with AC (c) AC tolerates QU handling KE.

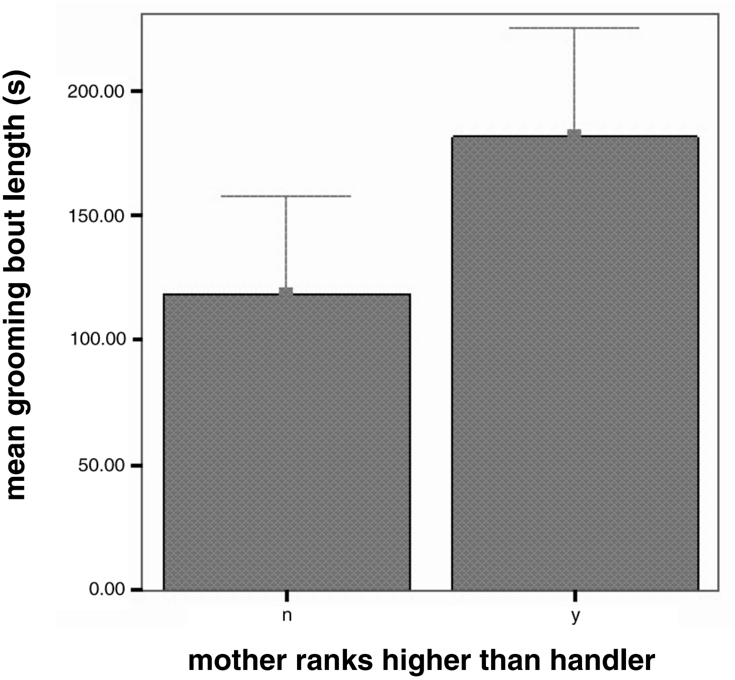

Fig. 6.4 Mean time spent grooming before handling for individuals who ranked below versus above the mother in the dominance hierarchy.

difference between the mother and the groomer: the lower ranking the handler compared to the mother, the longer the grooming bout ($r_s = 0.4$; $N = 19$; $p < 0.05$; see also Fig. 6.4). However, when the power differential between mother and handler was reversed, i.e., handlers ranked above mothers, market effects appeared to break down. Very high-ranking females (ranks 1–3) were able to handle infants without having to pay with grooming. The possibility exists, however, that exchange actually occurs in the opposite direction in this case. Low-ranking females may not attempt to extract grooming from high-ranking animals because they are, in fact, trading handling for tolerance from the dominant animal in another domain. This explanation seems unlikely, since the threat of force was always present when dominant individuals handled low-ranking infants and resistance by the subordinate female would have been useless and potentially dangerous for her and her offspring. At the same time, the exchange value of grooming was also influenced by whether the handler could offer other commodities in exchange for handling. Mothers with new infants of their own were less likely to groom before handling another female's infant than were non-mothers, effectively trading access to each other's infants (Henzi & Barrett unpublished material).

Prospects for a baboon market

Our data show, first, that baboons are capable of both reciprocal and interchange trading. Although the trading of grooming for participation in coalitions remains possible for other subspecies of baboon and for other species of monkey, we must assume that chacma females will swap it, in the main, for tolerance. As pointed out above, individuals can be both reciprocal and interchange traders simultaneously and individuals can thus make choices regarding with whom to form grooming-based or tolerance-based relationships depending on the supply and demand within their groups. Second, then, is the fact that the emergence of two trader classes will hinge on the local dominance gradient. When competition for resource access is high and dominance gradients are steep, relationships between distantly ranked individuals (such as they exist) will be based on grooming as an interchange currency (since power differentials will be large) whereas relationships between more closely ranked individuals will be based on reciprocal grooming.

As we have shown, power differentials are affected primarily by habitat. Within habitats, the size of the female cohort will alter the pitch of the gradient (Dunbar 1992) as will the extent of short-term ecological variation. This last is likely to be especially useful in the empirical demonstration of a baboon market since the value of interchange grooming will co-vary with resource availability and dispersion. Whereas, in the Drakensberg, for example, the monthly allocation of available time to grooming does not vary that much (8–12%; Henzi unpublished data), this is not so for De Hoop, where a need to move between small food patches and the associated thermoregulatory costs (Hill 1999) can reduce time budget allocation to grooming to 3% in the hot, dry summer months (Barrett & Henzi unpublished data). At the same time, diurnal patterns of grooming can also be structured by the habitat. Drakensberg females snatch grooming opportunities when they can throughout the day (Henzi *et al.* 1997a) whereas those at De Hoop follow the more conventional baboon pattern of concentrating social time early in the morning and late in the afternoon. This, too, will affect the short-term availability of partners, since choice may be limited to those who are either close by or who are not already engaged in grooming. Questions of supply and demand, and competition for engagement with desired trading partners, will need to be explored within these parameters.

Conclusions

Although there is still much work to be done, it seems reasonable, at this stage, to pursue the idea that primate social groups function as market places, and that variation in female grooming behaviour represents short-term tactical solutions to current events within the trading arena. The results of our work (Barrett *et al.* 1999; Barrett *et al.* 2000. See also Henzi & Barrett 1999) suggest that female chacma baboons deal with events within the social arena over a very short time-scale, and that they optimise their access to grooming partners and other commodities, on a daily (or even shorter-term) basis. In so doing, they are likely to be optimising in the long-term as well, and at a lower risk of failure than if they were to devote their efforts to a long-term strategy at the expense of immediate opportunities.

This view of primate groups as market places not only provides an alternative means of analysing patterns of cooperation, but also questions traditional notions of primate sociality. These often see grooming relationships between individuals as a manifestation of long-term strategic goals designed to alleviate the negative effects of resource competition within groups (see e.g. Wrangham 1980; Dunbar 1984; van Schaik 1989; Barton *et al.* 1996). In addition, social strategies are perceived as species or group-level characteristics. Thus, within a species or group (van Schaik 1989; Barton *et al.* 1996), females are all constrained to respond to the world in the same way. It is much more in keeping with recent theoretical thinking (Sutherland 1996) to assume that individual animals make decisions that will differ adaptively from those being made by other members of the group (see Henzi *et al.* 2000a,b). More detailed data on animals' social interactions and cognitive abilities are needed to resolve these issues, but it is clear that biological markets provide the most promising direction to take in research on the complex social groups both of primates and other taxa.

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REDOUAN BSHARY

7

The cleaner fish market

Introduction

The interaction between 'cleaners' and their 'clients' is one of the most amazing interspecific interactions one can witness on coral reefs. Cleaners are small fish and shrimps that inspect the body surface and the inside of the gill chambers and mouth of larger fish, the clients, in search for ectoparasites and dead or infected tissue (Eibl-Eibesfeldt 1955; Randall 1955; Limbaugh *et al.* 1961, reviews: Feder 1966; Losey 1987; Losey *et al.* 1999). Cleaning seems to be ubiquitous in aquatic systems, and many fish species are known to be facultative cleaners as juveniles (review by Wirtz 1998). The highest degree of specialisation is found in coral reefs, where a few members of the Labridae and Gobiidae families evolved into highly specialised cleaners which feed almost exclusively on material they remove from clients (Losey *et al.* 1999). Most work has been done on the two cleaner wrasses *Labroides dimidiatus* and *L. phthyrophagus* (Losey *et al.* 1999). These cleaners live in small territories, the so-called cleaning stations. Clients actively visit these cleaning stations and often use special postures to signal their wish to be inspected (Randall 1958; Losey 1971). Clients visit cleaners several times a day, some up to an estimated 144 times a day for a total of 30 min. (Grutter 1995).

Since the 1950s, scientists tried to solve the puzzle of this apparent mutualism. After early descriptive work, the question of the impact of cleaning on client fitness was tackled. Experiments in which cleaners were removed from relatively small coral reef heads ('patch reefs') which are isolated by sand from other reef areas, yielded inconclusive results concerning changes in fish densities and parasite loads (Limbaugh 1961; Youngbluth 1968; Losey 1972; Gorlick *et al.* 1987; Grutter 1997a). It also became apparent that cleaners remove from their clients not only parasites and dead or infected tissue, but also mucus and scales (Randall 1958). However, Alexandra Grutter recently provided strong evidence that cleaners really do clean. Stomach analyses indicated that a cleaner wrasse *L. dimidiatus* eats about 1200 parasites per day (Grutter 1996). A field experiment with fishes in cages placed on patch reefs either with or without cleaners showed that clients without access to cleaners had a fourfold parasite load after 12 h compared to clients who had access to cleaners (Grutter 1999). Still, the net benefit probably differs between sites and seasons, as shown by Grutter (1994, 1997b). Applying the same methods for stomach analysis on cleaners caught around both Heron Island and Lizard Island, Australia, she found that cleaners fed almost exclusively on parasites around Lizard Island while stomachs contained significantly more mucus around Heron Island.

Losey (1977, 1979) investigated the proximate causes which make clients seek cleaners. Interestingly, clients also visit cleaners when they are not infested with parasites, obviously to receive a form of tactile reward: While inspecting clients, cleaners of the genus *Labroides* often touch their clients with their pelvic fins, and cleaners may even hover above specific sites of the clients' body to provide this tactile stimulation. They apparently do not search for parasites while hovering (Potts 1973). In response to this tactile stimulation clients often drift motionless. Moreover, clients react to other sources of tactile stimulation, like an automatically turning brush, with behaviour that resembles the behaviour they show in interactions with cleaners (Losey 1977). Providing tactile stimulation is thus a tool for the cleaner to manipulate a client's decision on how long to stay and how often to come back (Losey 1987).

The cleaner fish mutualism became famous as one of the examples Trivers (1971) used in his seminal paper on reciprocal altruism. He proposed that predators refrain from hunting cleaners only because repeated interactions yield accumulating benefits which eventually surpass the high but only once achievable benefit of cheating in a single interaction, especially after the cleaner finished the inspection. To my knowledge, no attempt has ever been made to quantify the payoffs clients obtain when they cooperate or cheat. However, Losey (1987) proposed that the cooperation of predators represents a form of pseudoreciprocity (Connor 1986), also called by-product mutualism (Brown 1983; Dugatkin 1997), as he observed a few times that predators seemed to refrain from hunting a cleaner which was severely wounded from a spearing attempt. The cleaner's perspective was ignored for a long time, and so it remained unclear whether it would pay cleaners to cheat, or whether the cleaners' optimal foraging strategy is to search for parasites, leading to pseudoreciprocity. Recent experiments by Alexandra Grutter and myself (submitted) contradicted the pseudoreciprocity hypothesis. Cleaners did not search for parasites in the absence of partner control (clients slightly anaesthetised) but mainly fed on mucus. Clients appeared to use three different control mechanisms. Following Trivers (1971), predators could cheat back on a cheating cleaner by trying to eat it. Harmless clients either chased the cleaner after a harmful bite or simply swam off. Market theory as developed mainly by Noë and colleagues (Noë 1990; Noë *et al.* 1991; Noë & Hammerstein 1994; Noë this volume; see also Bull & Rice 1991) was used to explain differences between client species in their likelihood to attack versus swimming off. Client species with small territories or home ranges which had access to one cleaning station only (hereafter called 'residents') reacted mainly aggressively, while client species with larger territories or home ranges, thus having access to two or more cleaning stations (hereafter called 'floaters') mainly swam off. Floaters then visited another cleaning station for the next inspection with a higher probability than after an interaction without cheating by the cleaner.

The aim of the present chapter is to test how far market theory can help to understand differences in the quality of service different client species receive from the cleaner fish *L. dimidiatus*. The cleaner fish mutualism certainly has the basic properties of a market. Cleaners and clients belong to two distinct classes of traders, offering the removal of parasites or an easy meal, respectively. Kin selection can be ruled out as the traders belong to different species. There is competition over access to partners as well: clients are known to queue at cleaning stations, particularly in the morning, waiting to be served (Eibl-Eibesfeldt 1955, own observations). From a cleaner's perspective, there are two different classes of clients, namely residents and floaters. In interactions with residents, the cleaner is in a so-called veto position (Kahan & Rapoport 1984; Noë 1990). It is the only cleaner these clients can seek to have their parasites removed, while it can interact with many clients. It is therefore expected that the payoffs in these interactions are very asymmetric, with the clients having to accept a relatively bad service (as long as the payoff is higher than the payoff for not interacting at all) while the cleaner can increase its energy gain by feeding not only on parasites but also on client tissue. In contrast, floaters can, in principle, select the cleaner which gives the best service within their home ranges, and one would therefore expect that cleaners try to outcompete each other with a good service to attract floaters. The cleaning market therefore does not have two distinct classes of 'choosing' and 'chosen' traders, since both cleaners and floaters can exert choice. An important assumption of market theory is that members of each class try to outcompete each other through their offer but not through aggressive interference. This assumption is fulfilled in the cleaner market. While cleaners cannot interfere with each other because they remain at their respective cleaning stations, it remains unclear why clients aggregating at cleaner stations hardly use this option. But, as a matter of fact, out of 2133 interactions analysed for the present chapter, only 17 (0.8%) ended due to aggressive interference from other clients, and in 14 of these 17 cases the aggression was due to territorial behaviour and not because of competition over access to the cleaner.

Previous work on cleaner–client interactions has not acknowledged the possible influence of clients' choice options on cleaner fish service but has focused on another potentially important factor, namely the clients' quality as a food source. There is experimental evidence that cleaning duration correlates positively with parasite load within species (Gorlick 1984; Bshary & Grutter unpublished material). Both within and between species, the size of a client, which correlates positively with the number of parasites (Grutter 1995; Grutter & Poulin 1998a), seems to influence cleaning duration (but see Grutter & Poulin 1998b). Gorlick (1980) proposed that the amount of mucus might be an important factor, as he found a positive correlation between amount of mucus and cleaner preference in an interspecific comparison. Yet the results remain inconclusive as they are even better explained by client size (see text on p. 867 and Table 2 in Gorlick (1980)).

A third factor which might influence service quality is the potential harm the client would inflict on a cheating cleaner. The majority of clients are plankton feeders or grazers of algae, hence species which do not potentially feed on cleaners. There are, however, also a few piscivorous species. While both harmless and predatory clients can impose costs on cleaners through chasing and ramming (resembling 'punishment' see Clutton-Brock & Parker 1995), only predators have the option to switch from co-operation to cheating and to gain in metabolic currency by consuming a cleaner, while a harmless client would perform a purely spiteful act by killing a cleaner. With harmless clients the cleaners therefore simply trade the removal of parasites against a food source, but with predatory clients the cleaners in addition have to buy the willingness of the clients to refrain from attack. One would therefore expect that predators receive a better service than harmless clients. In addition, one would expect that harmless resident species which respond mainly aggressively to cheats by cleaners receive a better service than harmless floater species which respond mainly by swimming off as the former impose immediate costs on the cleaner. Note that market theory and partner control mechanisms are closely linked in this subject.

To summarise, I will combine information on clients' quality, clients' partner control options and clients' partner choice options to investigate how these three factors interact in determining the course of interactions between the cleaner fish *L. dimidiatus* and its clients. I use client size as a correlate for the quality of the food patch it offers to a cleaner, as size strongly correlates with amount of parasites and mucus (Grutter 1995). To look at the effects of partner choice options and partner control mechanisms, four categories of clients are distinguished: harmless residents, predatory residents, harmless floaters and predatory floaters. It is important to note that market theory predicts a good service to floaters and predators which may contradict predictions based on size and thus partner quality alone. This is because the latter is a kind of optimal foraging approach and treats clients as passive food patches, while market theory assumes that clients are active players which use strategies to maximise the service quality rendered by cleaners. Floaters and predators have strategic options which harmless residents are lacking, namely to play off cleaners against each other or threatening to prey on a cleaner. These strategic options could lead to a better service for smaller floaters or predators compared to larger residents despite the larger residents being the better food patch.

I will investigate the following aspects which should represent the quality of the service rendered by the cleaners: (1) Duration. Long duration should lead to the removal of more parasites or infected material. (2) Harmful bites per time unit interaction. Low rates would reflect low cheating by the cleaner. (3) Amount of tactile stimulation provided by the cleaner. Tactile stimulation is obviously appreciated by clients (Losey 1979), thus the more the cleaner gave tactile stimulation, the better I considered its service. (4) Distribution of interactions over the day. Field experiments by Grutter (1999) revealed that infection rates by gnathiid isopods were about twice as high during the night than during the day. Cleaner fish are only active during daytime. It is thus important for clients to get serviced for the first time soon after sunrise to have the parasites which infested them overnight removed. (5) Switching by the cleaner from one client to another. (6) Queuing for an interaction with a cleaner while the cleaner services another client. Aspects 1–3 reflect the quality of the service itself, while aspects 4–6 reflect the willingness of cleaners to interact with a certain client compared to other clients. Cleaning in the morning, high switching rates to the client species and low queuing rates indicate that a client has to invest little in terms of time and energy to get serviced by a cleaner. Methods are explained in Box 7.1.

Results

Cleaning duration

(a) Correlations between cleaning duration and client length

Data for all client species yield a significant positive correlation between client length and cleaning duration (Spearman's Rank correlation coefficient, $r_s = 0.76$, $n = 76$ species, $p < 0.0001$. When correlations are calculated separately for each client category, there are significant positive correlations for harmless residents ($r_s = 0.80$, $n = 24$ species, $p < 0.0001$), for harmless floaters ($r_s = 0.39$, $n = 37$ species, $p < 0.05$), and for floating predators ($r_s = 0.78$, $n = 9$ species, $p < 0.05$), and a high but unsignificant correlation for predatory residents ($r_s = 0.6$, $n = 6$ species, ns). The combined probability of these four correlations is highly significant ($\text{chi}^2 = 33.8$, $df = 8$, $p < 0.001$).

(b) Cleaning duration in the four client categories

There are significant differences in cleaning duration between harmless residents, predatory residents, harmless floaters and predatory floaters (Kruskal–Wallis test, $\text{chi}^2 = 25.1$, $df = 3$, $\text{n} = 76$ species, $p < 0.0001$, Fig. 7.1a). *Post-hoc* comparisons show that floaters interact longer with cleaners than residents do, independently of whether they are predatory or harmless clients (all differences are significant on the level $p < 0.01$). Testing only client species which are on average 10–20 cm in length to control for size effects, it appears that harmless floaters still have longer cleaning interactions than harmless residents. Predators, however, are cleaned for a shorter time than non-predatory clients when corrected for size (Kruskal–Wallis test, $\text{chi}^2 = 12.4$, $df = 2$, $n = 32$, $p < 0.01$; for all *post-hoc* comparisons $p < 0.05$, Fig. 7.1b).

Cleaners could interact longer with floaters than with residents due to

Box 7.1 Methods

Study site

All original data presented were collected at Ras Mohammed National Park in Sinai, Egypt. The study site was at Mersa Bareika, a bay which is well protected against surge. In this area, incoming sand through wadis led to the formation of patch reefs which are separated from each other by sand rather than to the formation of a continuous reef. Each of the 14 cleaners studied inhabited a separate patch reef which was separated from other patch reefs by at least 5 m of sand. The estimated volume of the patch reefs varied from 3.2 m^3 to 22.3 m^3, and the depth at the bottom varied between 2 and 6 m.

Data collection

Data were collected in April to June 1998 and May to July 1999. Four cleaners were observed in 1998 and 10 in 1999. All cleaners were adults. Single individuals were present at 7 cleaning stations, while pairs lived at the other 7 cleaning stations. When a pair was present, the smaller individual was observed. As cleaner wrasses are protogyneous hermaphrodites, individuals start their reproductive career as females and eventually switch into males. It is thus very likely that single individuals and the smaller fish in a pair are females, so probably all individuals observed were females.

Observations were made by scuba diving. I sat 2–3 m in front of a cleaning station on the surrounding sand. In 1998, the schedule was to make observations lasting 30 min. at 07:00, 09:00, 11:00, 13:00, 15:00 and 17:00 h. Thus, a total of 3 h observations are available for each cleaning station. In 1999, the schedule was to make 60 min. lasting observations at 07:00, 10:00, 13:00 and 16:00 h. Thus a total of 4 h observations are available for each cleaning station. Total observation time is 52 h. No cleaner was observed more than once on the same day. An interaction between the cleaner and a client was first observed over the entire duration, and, immediately afterwards, the following information was noted on a plexiglas plate:

1 client species. Species were determined according to Randall (1983).

2 client length. The length of the client, including the caudal fin, was compared to a reference measuring stick and estimated to the nearest cm.
3 duration. The duration in seconds was measured with a stopwatch.
4 harmful bites and client reaction. Whenever a client showed a short jolt while the cleaner was in mouth contact, a 'harmful bite' was scored (see also Randall 1958). Note that most often clients remain relaxed when cleaners are in mouth contact (and take 'bites') and that the removal of parasites is not linked to client body jolts (Bshary & Grutter forthcoming).
5 tactile stimulation. Tactile stimulation was defined as the cleaner hovering, usually at the dorsal fin of the client, and touching the client with the pelvic and pectoral fins, while the cleaner's head was pointing away from the client into the open water. Alternatively, the cleaner could hover underneath the client's belly, touching it with its dorsal fin. Cleaners provide tactile stimulation under a variety of circumstances (Bshary & Würth, unpublished data), but, for the present data analysis, tactile stimulation is considered only if the client did not move before and while the cleaner was hovering. In these cases, tactile stimulation occurred due to the cleaner's initiative, not as a reaction to the client's behaviour.
6 switching. When a cleaner left a client and swam directly to another client, switching was scored and the species and length of the new client was noted as well.
7 queuing. If two clients sought cleaning simultaneously, the one which had to wait was noted as queuing, together with species identity and length, while the interaction of the other one with the cleaner was noted as usual.

When the observation session was finished, data were transcribed on paper, together with information on date, hour and cleaner identity. All data were analysed either with the statistical program SPSS-X or with the program SsS, except for combined probabilities which were calculated according to Sokal & Rohlf (1995). The phylogenetic regression was calculated using phylo.glm, written by Grafen (1991).

Box 7.1 (*cont.*)

Data analysis

As the vast majority of clients could not be recognised individually, data are analysed on the basis of client species. For each client species and cleaning station, the mean value was calculated for client length, cleaning duration and harmful bite rate, and the percentage of interactions with tactile stimulation determined. The values for each species and variable were added and divided by the number of patch reefs where individuals of the species were observed to interact with cleaners. Thus, for each species and variable, a single (mean) value was used for the calculations. These final values were used in all Spearman's rank correlations to determine the effect of client size on the quality of service rendered by cleaners and in all Kruskal–Wallis tests and *post-hoc* comparisons which test the influence of client category (resident or floater, harmless or predator, see below) on cleaner fish behaviour.

For another calculation, the percentages of harmless residents and harmless floaters cleaners interacted with was calculated for each cleaning station and for four different times of day, namely 07:00–08:00, 10:00–11:00, 13:00–14:00 and 16:00–17:00 h. Only the data from 1999 exactly fit this schedule. For data from 1998, data collected from 09:00 to 09:30 and 11:00 to 11:30 h were used for the 10:00–11:00 h value, and data collected from 15:00 to 15.30 and 17:00 to 17:30 h were used for the 16:00–17.00 h value. The percentage values were used to calculate Friedman tests and *post-hoc* comparisons to detect differences in client composition interacting with cleaners between different times of day.

Cleaner switching between clients and client queuing were relatively rare events. These data were not analysed per cleaning station, but were lumped together into one data file. G tests were used to analyse these data further.

Client categories

Information on clients' diet provided by Randall (1983) was used to determine which fish species observed to interact with cleaners feed on live fishes of the size of cleaners and which do not. To be able to distinguish between residents and floaters, ten patch reefs were observed continuously from 15 min. before dawn until 15 min. after

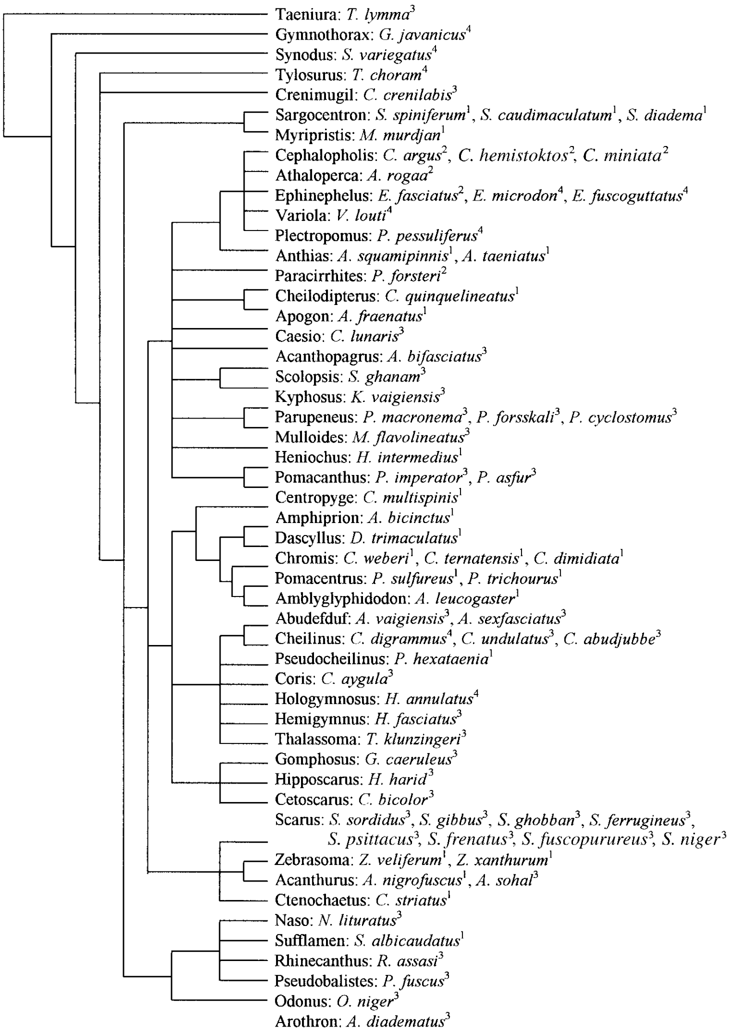

Fig. 7.7 Phylogenetic tree according to Nelson (1994) of client species observed to interact with *L. dimidiatus* at Mersa Bareika. ^{1}: harmless resident, ^{2}: predatory resident, ^{3}: harmless floater, ^{4}: predatory floater.

dusk in November 1997. At the beginning, all species present on the patch reef were noted. Then all fishes which came to the patch reef or left it were noted. Additional information was collected on individually recognisable fishes (due to specific colour patterns or wounds) whenever possible. Only a few fish species could not be

Box 7.1 (*cont.*)

classified exclusively into one of the two categories. Butterfly fish species especially could spend hours or even whole days repeatedly at a particular patch reef if the size of the patch reef was large enough, but would switch regularly at other patch reefs. All the fish species which could be termed facultative floaters on the basis of my observations were omitted from the present analysis. Two things are important to note: first, the classification as resident does not imply that individuals of these species cannot move between patch reefs. I observed rare short excursions by surgeon fishes. Still, these individuals were reliably found at the same patch reefs day after day. Second, the classification of residents with access to one cleaning station only and floaters with access to two or more cleaning stations would be much more difficult to make at a continuous reef, where there are no dangerous open areas to cross in order to visit another cleaning station. The classification presented with the phylogenetic tree (Fig. 7.7) might thus be one that applies to a patch reef area only.

market effects, but there is also the alternative explanation that floaters stay longer than residents because they pay more in travel time to visit cleaning stations, which would make longer services more efficient. For the same reason, floaters might visit cleaning stations less often than residents and could therefore have more parasites than residents. Data on visit frequencies are not available. However, floaters are inspected for longer than residents of similar size also when only data collected early in the morning are analysed (Fig. 7.2), i. e. when all clients are full of parasites which infested them overnight. In addition, interactions between cleaners and residents tended to be longer when the resident terminated the interaction, while interactions between cleaners and floaters tended to be longer when cleaners terminated the interaction (Fig. 7.3).

Harmful bite rates

(a) Correlation between harmful bite rates and client length

All data together yield a significant negative correlation between harmful bite rates and client length (Spearman's rank correlation coefficient, $r_s = -0.32$, $n = 76$ species, $p < 0.01$). However, if data are analysed for

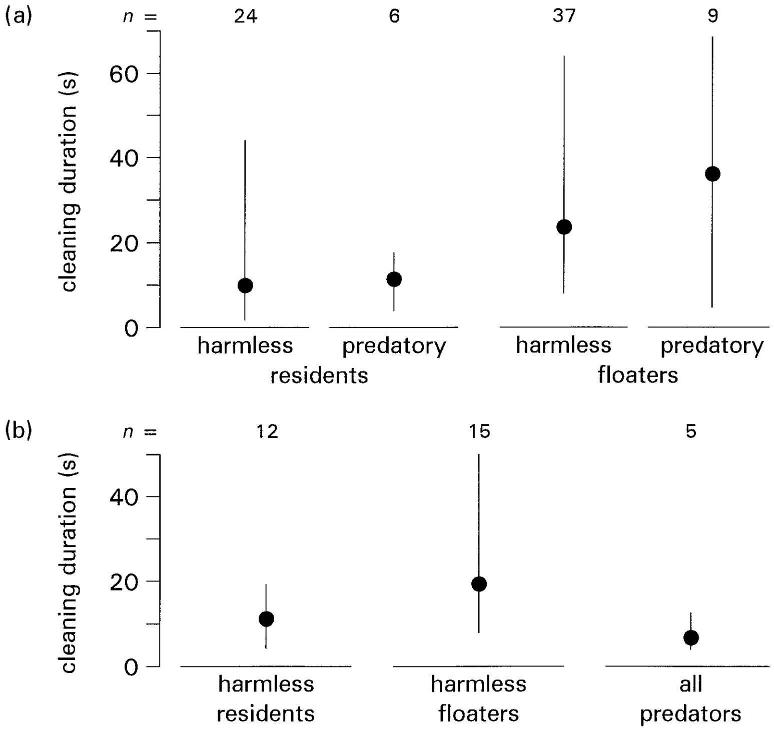

Fig. 7.1 Cleaning duration of interactions between cleaners and harmless residents, predatory residents, harmless floaters and predatory floaters. *n* = number of species which fall into each client category. Shown are the means and ranges of the mean values calculated for each species. (a) all client species included, (b) only client species included with a mean body length of 10–20 cm. Here, no distinction is made between predatory residents and predatory floaters, due to small sample size.

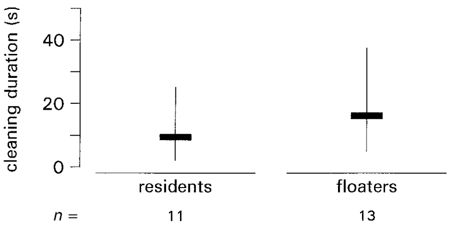

Fig. 7.2 Cleaning duration of interactions observed 07:00–08:00 h between cleaners and harmless client species with a mean body length of 10–20 cm. *n* = number of species which fall into each client category. Shown are the means and ranges of the mean values calculated for each species.

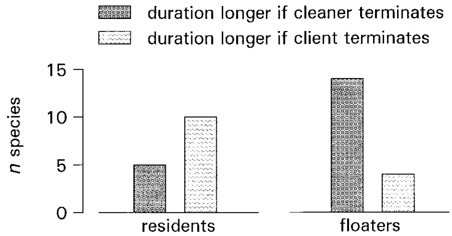

Fig. 7.3 Relation between terminator (harmless client or cleaner) and cleaning duration. Dark columns: *n* species for which mean duration was longer if the client terminated the interaction; light columns: *n* species for which mean duration was longer if the cleaner terminated the interaction.

each client category separately, no significant correlations are found except for a negative correlation between client length and harmful bite rate for harmless residents (Spearman's rank correlations: harmless residents: $r_s = -0.51$, $n = 24$ species, $p = 0.011$; predatory residents: $r_s = 0.72$, $n = 6$ species, ns; harmless floaters: $r_s = -0.09$, $n = 37$ species, ns; predatory floaters: $r_s = 0.05$, $n = 9$ species, ns). The combined probability of these four correlations is not significant ($chi^2 = 5.6$, $df = 8$, ns).

(b) Harmful bite rates in the four client categories

There are significant differences in harmful bite rates between the four categories (Kruskal–Wallis test, $chi^2 = 26.6$, $df = 3$, $n = 76$ species, $p < 0.0001$, Fig. 7.4a). *Post-hoc* comparisons show that harmless residents are bitten more frequently than harmless floaters ($p < 0.05$), and predators are bitten less often than harmless clients, independent of whether they are residents or floaters (all $p < 0.01$). These differences remained when I controlled for size (Kruskal–Wallis test, $chi^2 = 6.2$, $df = 2$, $n = 33$ species, $p < 0.05$, Fig. 7.4b). A significant difference between predators and harmless clients remains while the difference between harmless floaters and harmless residents is far from being significant (*post-hoc* comparisons: predators–harmless residents and predators–harmless floaters $p < 0.05$; harmless floaters–harmless residents $p > 0.1$).

Tactile stimulation

(a) Correlations between client length and tactile stimulation

All data together yield a significant positive correlation between client length and percentage of interactions in which cleaners provide tactile stimulation (Spearman's rank correlation coefficient, $r_s = 0.49$, $n = 76$

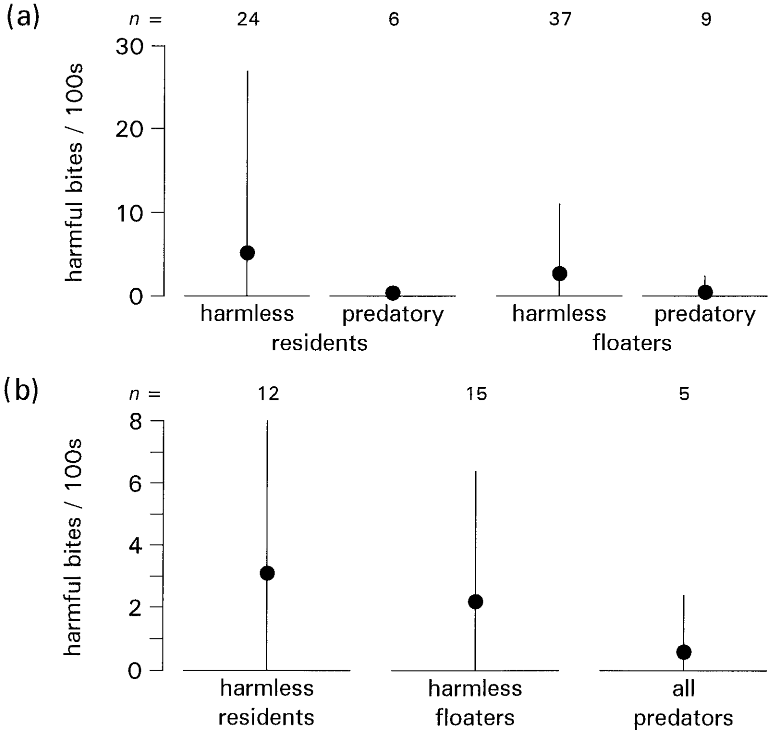

Fig. 7.4 Harmful bite rates during interactions between cleaners and harmless residents, predatory residents, harmless floaters and predatory floaters. n = number of species which fall into each client category. Shown are the means and ranges of the mean values calculated for each species. (a) all species included, (b) only species included with a mean body length of 10–20 cm. Here, no distinction is made between predatory residents and predatory floaters, due to small sample size.

species, $p < 0.0001$). However, if data are analysed for each client category separately, only the correlation for harmless residents is still significant while the others are not (Spearman's rank correlations: harmless residents: $r_s = 0.55$, $n = 24$ species, $p < 0.01$; predatory residents: $r_s = -0.52$, $n =$ 6 species, ns; harmless floaters: $r_s = 0.18$, $n = 37$ species, ns; predatory floaters: $r_s = 0.53$, $n = 9$ species, ns). The combined probability of these four correlations is not significant (chi$^2 = 14.4$, $df = 8$, ns).

(b) Tactile stimulation in the four client categories

There are significant differences between the four categories in the percentages of interactions in which cleaners provide tactile stimulation

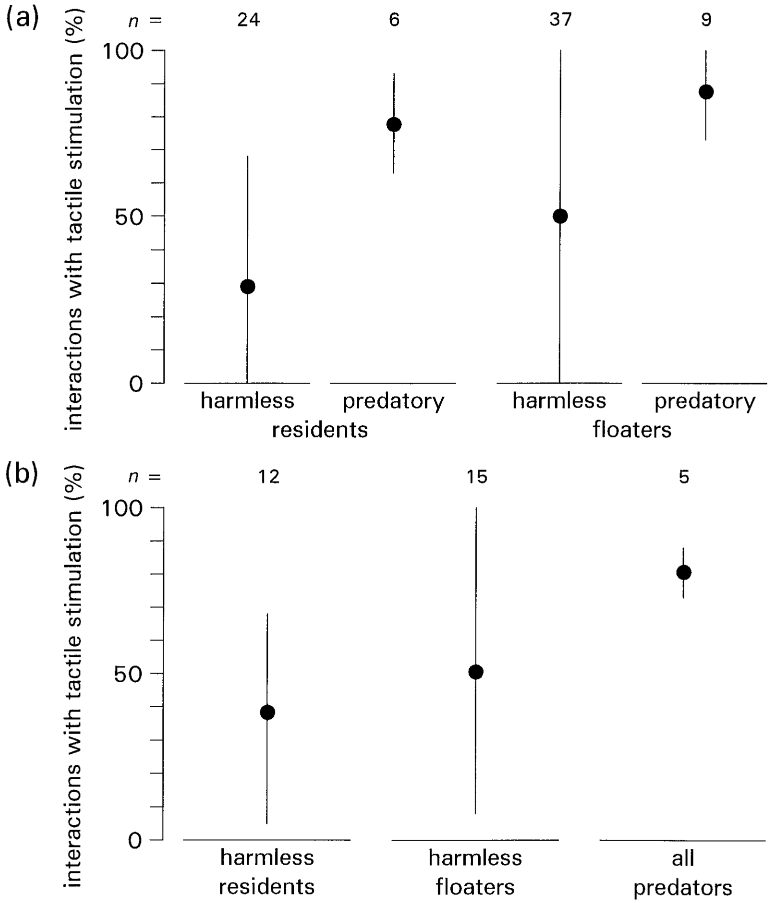

Fig. 7.5 Percentage interactions during which cleaners provided tactile stimulation when interacting either with harmless residents, predatory residents, harmless floaters or predatory floaters. *n* = number of species which fall into each client category. Shown are the means and ranges of the mean values calculated for each species. (a) all species included, (b) only species included with a mean body length of 10–20 cm. Here, no distinction is made between predatory residents and predatory floaters, due to small sample size.

(Kruskal–Wallis test, $chi^2 = 28.2$, $df = 3$, $n = 76$ species, $p < 0.0001$, Fig. 7.5a). Predators receive more tactile stimulation than harmless clients independent of home range size effects (*post-hoc* comparisons, all differences between predators and harmless clients $p < 0.01$). Harmless floaters receive more tactile stimulation than harmless residents (*post-hoc* comparison, $p < 0.01$). When controlling for size, the difference between predators and harmless clients remains while only a strong but non-significant trend remains that floaters receive tactile stimulation more often than residents (Kruskal–Wallis test, $\text{chi}^2 = 8.2$, $df = 2$, $n = 33$, $p < 0.05$; and *post-hoc* comparisons: predators–harmless residents and predators-harmless floaters $p < 0.01$; harmless floaters–harmless residents $0.05 < p < 0.1$, Fig. 7.5b).

Distribution of interactions over the day

Harmless floaters comprise a higher percentage of all clients cleaned in the morning compared to other times of day (Friedman test, $\text{chi}^2 = 9.0$, $df = 3$, $n = 14$ cleaning stations, $p < 0.05$; *post-hoc* comparisons: all comparisons 07:00–08:00 h against other times of day $p < 0.05$, Fig. 7.6a). This effect remains when client size is controlled for by analysing only data for clients with a mean body length of 10–20 cm (Friedman test, $\text{chi}^2 = 8.1$, $df = 3$, $n = 13$, $p < 0.05$; *post-hoc* comparisons: 07:00–08:00 against 10:00–11:00 and 13:00–14:00 h $p < 0.05$, 07:00–08:00 against 16:00–17:00 h, $0.05 < p < 0.1$, Fig. 7.6b). There are only few data available for predatory clients. These interactions are about equally distributed over the day (Friedman test, $\text{chi}^2 = 1.8$, $df = 3$, $n = 14$, ns, Fig. 7.6a). There are not enough data for a separate analysis for predators of 10–20 cm body length. As a logical consequence, harmless residents mirror the results for harmless floaters and are cleaned less often in the morning compared to the other times of day (Friedman test, $\text{chi}^2 = 9.6$, $df = 3$, $n = 14$, $p < 0.05$; *post-hoc* comparisons: 07:00–08:00 h against all other times of day $p < 0.05$, Fig. 7.6a), though the results are not significant if client body size is controlled for (Friedman test, $\text{chi}^2 = 5.3$, $df = 3$, $n = 13$, ns, Fig. 7.6b).

Switching between clients

Data are shown in Table 7.1. All data together yield a significant tendency of cleaners to switch from a smaller client to a larger client (G test, $G = 8.2$, $n = 205$ cases, $df = 1$, $p < 0.01$). Within each category, however, size does not seem to influence to whom a cleaner switches (G tests, harmless residents: $G = 0.1$, $n = 36$ cases, $df = 1$, ns; harmless floaters: $G = 1.6$, $n = 105$ cases, $df = 1$, ns). The combined probability of these two results is also not significant ($\text{chi}^2 = 3.8$, $df = 4$, ns). The overall significant size effect is due to cleaners switching significantly more often from harmless residents to harmless floaters than the other way round (G test, $G = 61.6$, $n = 52$ cases, $df = 1$, $p < 0.0001$), as in most of these cases (40 out of 51), the floaters are longer than the residents. Still, cleaners switch more often from a larger resident to a

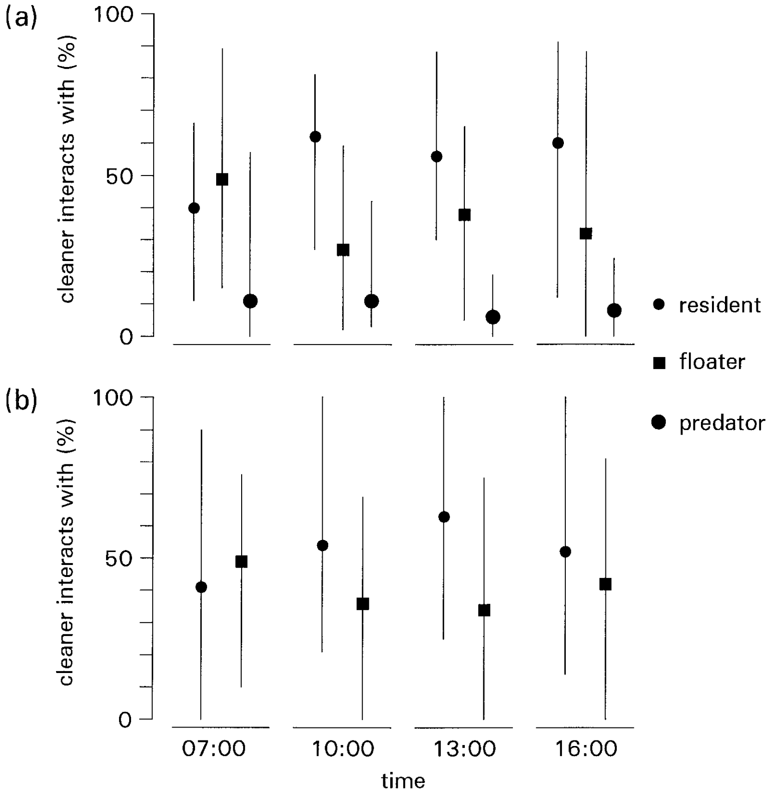

Fig. 7.6 Relative frequencies (means and ranges) of interactions between cleaners and either harmless residents, harmless floaters or predators, at different times of day. $n = 14$ cleaning stations. Shown are the means and ranges of the mean values calculated for each cleaning station. (a) all species included, (b) only species included with a mean body length of 10–20 cm. Here, predators are excluded due to small sample size.

smaller floater than the other way round (Binomial test, $n = 12$, $x = 1$, $p < 0.01$). A predatory client was involved in only 12 cases. Cleaners switched to a predatory client in 4 cases and left predatory clients to interact with a harmless client in 8 cases.

Queuing

Data are shown in Table 7.2. All data together yield a significant tendency that in a pair of clients seeking cleaning simultaneously, the smaller client has to queue more often than the larger one (G test, $G = 4.7$, $n = 133$ cases,

Table 7.1: *Influence of client size and partner choice options on the likelihood of cleaners switching between clients*

	cleaner switches	observed	expected	G test: p
all data	to larger	123	102.5	
	to smaller	82	102.5	<0.01
harmless residents	to larger	19	18.0	
	to smaller	17	18.0	ns
harmless floater	to larger	59	52.5	
	to smaller	46	52.5	ns
between categories	to harmless floater	51	26.0	
	to harmless resident	1	26.0	<0.0001

Table 7.2: *Influence of client size and partner choice options on the likelihood of clients having to queue when more than one client seek cleaning simultaneously*

	client queuing is	observed	expected	G test: p
all data	larger	54	66.5	
	smaller	79	66.5	<0.05
harmless residents	larger	8	8.5	
	smaller	9	8.5	ns
harmless floater	larger	18	20.5	
	smaller	23	20.5	ns
between categories	harmless floater	1	33.0	
	harmless resident	65	33.0	<0.0001

$df = 1, p < 0.05$). Within each category, however, size does not predict which of two clients that simultaneously seek the service of a cleaner must wait (G tests, harmless residents: $G = 0.1$, $n = 17$ cases, $df = 1$, ns; harmless floaters: $G = 0.6$, $n = 41$ cases, $df = 1$, ns). The combined probability of these two results is also not significant ($\text{chi}^2 = 2.0$, $df = 4$, ns). The overall significant size effect occurs because when a resident and a floater compete simultaneously over access to a cleaner, residents have to queue significantly more often than floaters (G test, $G = 80.5$, $n = 66$ cases, $df = 1$, $p < 0.0001$), and floaters were larger in most of these cases (44 out of 65). Still, a larger resident has to queue significantly more often while a smaller floater is inspected, rather than the other way round (Binomial test, $n = 21$ cases, $x = 0$, $p < 0.0001$). In only 9 cases, a predatory client was involved. In 8 of these 9 cases, the predator had to queue.

Table 7.3: F-*values for phylogenetic regressions, using client length as independent variable, and cleaning duration, harmful bite rate and percentage of interactions with tactile stimulation as dependent variables*

	cleaning duration	harmful bites	tactile stimulation
all client species	$F_{1,38} = 110.4^{***}(+)$	$F_{1,38} = 4.3^{*}(-)$	$F_{1,38} = 1.25$, ns
harmless residents	$F_{1,14} = 49.4^{***}(+)$	$F_{1,14} = 5.6^{*}(-)$	$F_{1,14} = 4.0^{x}(+)$
predatory residents	$F_{1,1} = 10.7$, ns	$F_{1,1} = 0.1$, ns	$F_{1,1} = 0.1$, ns
harmless floaters	$F_{1,16} = 6.8^{*}(+)$	$F_{1,16} = 0.1$, ns	$F_{1,16} = 0.8$, ns
predatory floaters	$F_{1,5} = 3.6$, ns	$F_{1,5} = 0.1$, ns	$F_{1,5} = 0.1$, ns

Notes:
***: $p < 0.0001$, *: $p < 0.05$, ^{x}: $0.05 < p < 0.1$, (+): regression between client length and variable is positive, (−): regression between client length and variable is negative.

Table 7.4: F-*values for phylogenetic regressions, using client choice categories (resident or floater) or client control options (harmless or predator) as independent variables, and cleaning duration, harmful bite rate and percentage of interactions with tactile stimulation as dependent variables*

Comparison	Cleaning duration	harmful bites	tactile stimulation
residents-floaters	$F_{1,32} = 39.7$, $^{***}(+)$	$F_{1,32} = 1.60$, ns	$F_{1,31} = 1.37$, ns
residents-floaters (length controlled)	$F_{1,31} = 3.64$, $^{x}(+)$	$F_{1,38} = 0.36$, ns	$F_{1,38} = 0.24$, ns
harmless-predators	$F_{1,38} = 0.57$, ns	$F_{1,38} = 10.5$, $^{**}(-)$	$F_{1,36} = 13.8$, $^{***}(+)$
harmless-predators (length controlled)	$F_{1,37} = 6.40$, $^{*}(-)$	$F_{1,37} = 9.34$, $^{**}(-)$	$F_{1,37} = 13.1$, $^{***}(+)$

Notes:
***: $p < 0.0001$, **: $p < 0.01$, *: $p < 0.05$, ^{x}: $0.05 < p < 0.1$, (+): regression between client length and variable is positive, (−): regression between client length and variable is negative.

Testing the influence of phylogenetic dependencies

Several authors (Felsenstein 1985; Grafen 1989; Harvey & Pagel 1991) have pointed out that one has to take phylogeny into account when one compares data from different species to investigate the effect of one variable (i.e. body size) on another variable (i.e. tooth length). Significant results might be due to a group of closely related species which have a distinct morphology or behave differently compared to other species because of a feature they share through common ancestry. I used the phylogenetic comparative method (Grafen 1989, 1991) to test whether the results of all

Table 7.5: *Summary of the results*

	cleaning duration	harmful bites	tactile stimulation	switching	queuing	morning service
client length	yes	no	no	no	no	no
harm. res. length	yes	yes	yes	no	no	no
market	yes	no	no	yes	yes	yes
partner control	no	yes	yes	no	no	no

Note:
Significant influences of investigated factors are indicated with 'yes', non-significant influences are indicated with 'no'. harm. res. length: harmless residents length.

Spearman's rank correlations are stable when phylogenetic effects are taken into account. This is generally the case. There are a few exceptions, however. There is no significant positive regression between client length and frequency of tactile stimulation ($F_{1,38} = 1.25$, ns), and the regression between harmless resident client length and tactile stimulation only approaches significance ($F_{1,14} = 3.99$, $0.05 < p < 0.1$). The results are summarised in Table 7.3. The four client categories used in the Kruskal–Wallis tests are not suited for the calculation of phylogenetic regressions as the distinction between resident and floater, on the one hand, and harmless and predatory clients, on the other hand, cannot be brought into a logical sequence. I could therefore only compare harmless residents with harmless floaters, and harmless clients with predatory clients. The results are summarised in Table 7.4.

Discussion

The aim of this chapter is to investigate whether the quality of service rendered by cleaners is better explained by optimal foraging theory ('client as food patch') or by cooperation theory. In the latter category there are again 2 options: (2–player) partner control theory and (n-player) market theory. The results are summarised in Table 7.5.

Methodological considerations

Two factors might have influenced the results in an undesired way, namely phylogenetic dependencies (significant results might be due to a group of closely related species which are treated differently compared to other species because of a feature they have from common ancestry) and the fact that clients could not be recognised individually. The phylogenetic regressions calculated to investigate the relation between (1) client body length, (2) client choice options, (3) partner control mechanisms and service quality, indicate that the results presented in this chapter are hardly affected by phylogenetic dependencies. Thus, client length, market effects and partner control mechanisms have to be considered to explain significant results. As clients could not be recognised individually, it was not possible to calculate one value per individual client. This would be desirable because individual differences in client behaviour can increase the variance in the results if some individual clients interact with a cleaner more often than with others. I tried to minimise such unwanted variance by calculating one value per client species per cleaning station, and each of these values has the same weight in the calculation for an overall species value. It is important to note that the remaining uncontrolled variance has a conservative effect, i.e. it reduces the likelihood of getting significant results. In addition, I was interested in analysing the *relative* importance of client length, market effects and partner control mechanisms on service quality, and all three factors should be equally affected by the variance. Finally, I did not explicitly use the Bonferroni technique (Rice 1989) to lower the α-level when several tests were made either with the same data-set or to test the same question. I refrained from using Bonferroni corrections where the different α-levels and explanations as to which data-sets are used repeatedly in different analyses would lead to considerable confusion. However, I will not build any argument on a result that would disappear when the Bonferroni technique is used.

The data show that in the absence of market effects and special partner control options, client length as an indicator of partner quality affects service quality in the predicted way: in harmless residents, client length is correlated with cleaning duration, harmful bite rates and amount of tactile stimulation in the predicted way. Otherwise, client quality alone is a poor predictor for cleaner fish behaviour. Within client categories, client length correlated consistently with cleaning duration only. For all other tests within each of the three client classes – harmless floaters, predatory residents and predatory floaters – client length failed to explain harmful bite rates, cleaning of floaters in the morning, cleaner switching between clients, clients queuing and the amount of tactile stimulation provided by the cleaner. The lack of significant results is not an effect of the naturally smaller sample sizes of the fractionated data sets compared to the complete data set, as the combined probabilities of the results for the four different client categories were not significant either. The overall positive influence of client size on the service rendered by cleaners was thus mainly a spurious result and caused by the fact that both floaters and predators, which both get a better service than residents, tend to be larger than residents. However, floaters and predators receive a better service than harmless residents independently of their size. Authors of earlier papers (Gorlick 1984; Grutter & Poulin 1998b) assumed that cleaner preference occurs because some clients yield a higher energy gain per inspection time. The fact that cleaners (1) prefer to interact with a smaller floater rather than with a larger resident in the morning when all clients have many parasites, and (2) are responsible for the longer duration of interactions with floaters, indicates that cleaners try to maximise their daily energy intake rather than their momentary intake: floaters leaving the cleaner station without being inspected or after a short inspection are a potential food patch that might not be available at a later stage due to floaters switching between cleaner stations. An ignored resident, however, will come back for sure. Thus the optimal foraging strategy for a cleaner seems to be to service floaters whenever they are available, and to service residents when there is no floater around.

The priority of access for floaters (cleaner switching to floater, floaters not having to queue, floaters being serviced early in the morning) was predicted by market theory. Floaters can potentially choose between different cleaners, and cleaners therefore have to outcompete each other by a better service. Floaters indeed use their choice option and visit another cleaning station for the next interaction with a higher probability either if they have been ignored by a cleaner or if the interaction ended negative, i.e. they swam off because they were bitten (Bshary & Schaeffer unpublished data). Also the result that cleaning interactions were longer than with residents, due to the behaviour of the cleaner and also independently of client length, fits the prediction from market theory. In contrast, the amount of tactile stimulation provided, and in particular harmful bite rates, did not differ significantly between harmless residents and harmless floaters when client length was controlled for. This indicates that the cleaner's decision to manipulate a client (by providing tactile stimulation, Losey 1987) and to cheat (by taking harmful bites) is relatively independent of the clients' choice options.

While cleaners apparently do not give priority to predatory clients, predators receive more tactile stimulation and are bitten less often than harmless clients, independently of whether they can choose between cleaners or not. Cleaners thus appear to provide the best service to those clients which could potentially profit from cheating them. This shows that in this case the partner control mechanism is more important for the course of an interaction than the clients' choice options. Choice options, on the other hand, are more important in determining which client has priority of access to a cleaner. Interestingly, cleaning duration was shorter for predators than for harmless clients when client length was controlled. There are several potential explanations for this phenomenon. First, cleaners might keep the duration short because they are still at risk of predation attempts by the client during interactions. This risk should increase during the course of an interaction due to diminishing returns for the client from being cleaned, while the value of a cleaner as food source remains constant. Second, cleaners cannot gain additional energy from harmful bites during interactions as they cannot cheat on predators. Third, I often observed predators, mainly groupers, to spend considerable time with cleaner shrimps, either *Stenopus spp*. or *Periclimenes spp.* (see also review by Feder 1966). Therefore, the need for these predators to interact with a cleaner fish might be lower. However, harmless clients also interacted with shrimps, and my impression that groupers especially spent relatively more time with shrimps still needs quantification. The whole cleaning market might prove to be more complex than the way it is presented in this chapter. Cleaners might compete not only with other cleaner fish over access to floaters, but also with cleaner shrimps which are visited by both floaters and residents. A further complication is due to juveniles of facultative cleaner species. Like many other authors (reviews: Feder 1966; Wirtz 1998), I observed interactions between both residents and floaters with juvenile facultative cleaners several times. The interactions were elaborate in the sense that clients often swam directly towards the cleaner, inviting it to clean them ('posed', see Côté *et al.* 1998) before the interaction began. Detailed studies on cleaner shrimps and facultative cleaners are lacking. It would be interesting to know whether they are real competitors of the 'professional' cleaners or whether they are visited by different client species. Cleaner shrimps might remove different items from clients, thus competition might be low because of different foraging niches.

In conclusion, the results on the cleaner fish mutualism show the cleaning mutualism cannot be fully understood if one ignores the market effects involved. Partner choice options determine which pairs form first. The results thus add to the accumulating evidence that market effects are a widespread phenomenon in co-operative and mutualistic interactions (Barrett *et al.* 1999; Henzi & Barrett 1999; Stopka & Macdonald 1999; see also examples in Noë *et al.* 1991; Noë & Hammerstein 1994, 1995; Noë this volume). On the other hand, it is important to note that the various partner control mechanisms used by clients influence the course of interactions relatively independently of the clients' choice options. Predators which could gain in energetic currency by cheating on cleaners receive a better service than harmless clients which do not pose a threat to a cleaner's survival, no matter whether the predators are residents or floaters. The high risk which cleaners face when interacting with predators might lead to an unconditional cooperative strategy of cleaners towards predators which overrides all potential market effects. Another important result is that the harmless floaters' option to play cleaners off against each other hardly leads to lower cheating rates by the cleaners compared to cheating rates towards harmless resident clients, as would have been predicted by market theory. Again, partner control mechanisms might account for this unexpected result. Residents but not floaters impose costs on cheating cleaners by chasing them around, and this seems to compensate for the lack of choice options. Thus, the market assumption that traders of one class cannot force members of the opposite trader class to increase their offer does not apply to the cleaner fish mutualism. Overall, the results therefore emphasise the need to integrate partner control theory and partner choice theory into a single coherent framework in order to understand payoff distributions in cooperative and mutualistic systems.

Another important topic for future research will be to investigate the cognitive abilities of both cleaners and clients. Trivers (1971) assumed that individual recognition is crucial for the evolution and maintenance of cooperation in repeated interactions despite cheating being the more profitable option in any single interaction. Clients might have a relatively easy task to recognise a couple of cleaners they interact with, either individually or on the basis of the location (as Trivers (1971) proposed). Cleaners, on the other hand, sometimes share a patch reef with more than 300 potential resident clients, plus the floaters which pass by once in a while. This makes individual recognition of clients by cleaners very unlikely. How, then, can client aggression work as a control mechanism against cleaners cheating, as clients of the same species face a 'tragedy of the common' problem (Hardin 1968), if the cleaner does not recognise them individually: the client which is chasing the cleaner has the costs of this behaviour but all individuals profit from its behaviour. It also remains unclear how cleaners distinguish between residents and floaters, and harmless and predatory clients. The data show that cleaners certainly do distinguish between client categories, and it will be interesting to find out how much brain is actually needed to handle seemingly complex cooperative interactions.

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JASON D. HOEKSEMA AND MARK W. SCHWARTZ

8

Modelling interspecific mutualisms as biological markets

Introduction

Mutualistic interactions between species are diverse and widespread, and are becoming well documented empirically (Bronstein 1994b). The partners involved in mutualistic interactions range from bacteria to fungi to plants and animals. Early mathematical models of mutualisms predicted that they should be rare in nature (e.g. May 1973). Since then, modellers of mutualisms have focused on defining conditions and mechanisms that could account for the prevelance of mutualistic interactions in nature. Recently, mutualisms have been modelled as biological markets (Noë & Hammerstein 1994, 1995; Schwartz & Hoeksema 1998).

Mutualisms are characterised by complexity and variation, with multiple, varying individuals and species on both sides of the interaction, species engaged in multiple types of mutualism simultaneously, and costs and benefits of the interaction changing over time and space. Biological market models address this complexity in a number of ways, and as such may be appropriate for modelling many types of mutualistic interactions. The central mechanism of market models is that the price of trade is negotiated, with individuals choosing partners who are offering the best price. This partner-choice mechanism incorporates variation among potential partners in a mutualism, and recognizes that mutualisms operate in a complex community context.

Many mutualisms may be best seen as interactions in which individuals of one or both species exploit individuals of the other species, but that none the less result in net benefits to each of the individuals involved (Thompson 1982; 1994; Futuyma & Slatkin 1983; Janzen 1985; Herre & West 1997). A modelling approach that explicitly outlines the costs and benefits of the interaction to the individuals or species involved, such as

Box 8.1 The economic law of comparative advantage

Classical western economists of the late eighteenth and early nineteenth centuries were primarily concerned with economic growth, in particular trying to understand the influences on the 'wealth of nations' (Leighton 1970). Adam Smith, in his well-known treatise by this title in 1776, emphasised the role of free trade among nations in increasing the wealth of all nations, stating that 'it is a maxim of every prudent master of a family never to attempt to make at home what it will cost him more to make than to buy. What is prudence in the conduct of every private family, can scarce be folly in that of a great kingdom' (Smith 1937). This analogy between international trade and the workings of a family illustrates the idea of 'absolute production advantage', which hypothesises that if one nation produces commodity A better than commodity B, and another nation perceives the opposite production possibilities, then the total wealth of two nations will be increased if they each specialise in production of the commodity that they produce more efficiently, and then trade for the other commodity. The achievement of economist David Ricardo, in the early nineteenth century, was to show that trade is advantageous for both nations even if one nation is better at producing both commodities than the other nation. The only requirement for trade to be beneficial is that the two nations perceive different ratios of costs of the two commodities, i.e. they perceive different relative costs of the two commodities. Trade will always benefit both nations as long as the exchange rate for the two goods lies between the ratio of costs that each country experiences individually. The economist John Stuart Mill reformulated Ricardo's theory to make specific predictions about the mechanisms determining the international exchange rate for two commodities. This principle worked out by Ricardo and Mill has been termed the 'law of comparative advantage'. The history of the development of these economic principles is well detailed by Ellsworth and Leith (1975). The law of comparative advantage, and its associated graphical depiction of the market conditions of two countries potentially engaging in trade, forms the basis of the biological market approach to modelling species interactions presented in this chapter and previously (Schwartz & Hoeksema 1998). Many of the graphical tools and terms we employ in the biological market approach have direct counterparts in the basic literature of the economics of international trade (e.g. Leighton 1970; Ellsworth & Leith 1975; Grubel 1977). For example, our 'isolation acquisition isocline' corresponds directly to the classic 'production possibilities curve'. Similarly, our 'optimal consumption vector' is equivalent to the economist's set of 'consumption indifference curves'. We suggest that the basic economic principles of international trade are useful in understanding the specialisation and trade that may occur between two interacting biological species.

the biological market approach discussed here, is useful in analysing these types of mutualisms (Keeler 1985; Thompson 1986; Addicott & Tyre 1995; Connor 1995; Joshi & Thompson 1995; Pellmyr *et al.* 1996; Herre & West 1997; Pellmyr 1997). Such models will be useful for making predictions about conditions under which benefits of an interaction outweigh the costs.

We have previously presented a biological market model to analyse the specific situation in which two species in a mutualistic interaction both require the same two resources (Schwartz & Hoeksema 1998). The economic principle that is the basis for this model is relatively simple. Classic economic theory tells us that nations can benefit by specialising in production of certain goods and trading with other nations rather than producing all commodities themselves (Mill 1877; Ricardo 1891; Box 8.1). The biological equivalent of this theory is that individuals or species that are more efficient than others at one aspect of resource capture (e.g. carbon fixation) ought to specialise and trade with others for other resources (e.g. soil water and macro-nutrients). Specialising individuals acquire their resource at a discount relative to other trading partners and can trade the surplus for more of other resources than they could acquire on their own. The principle of increasing total resource acquisition through specialisation and trade, however, can be extended beyond *absolute* production advantage to include *relative* production advantage. In this case, an individual may be less efficient than its trading partner at the production of all commodities and still benefit from trade as long as it is more efficient at the production of one commodity than it is at another (Ricardo 1891).

Basic model of specialisation and trade

Individuals of two species (A and B) require both of two resources for growth, and experience a tradeoff in acquisition of these resources. The tradeoff in resource acquisition is described by a resource acquisition isocline representing the maximum annual amount of the two resources individuals of each species can acquire in *isolation* (Fig. 8.1a,b, solid lines). This *isolation acquisition isocline* intercepts the axes at the maximum amount of resources each species could obtain in a year if the species completely specialised in acquisition of one resource (R_{max}). The negative of the slope of the isolation acquisition isocline is equal to the resource cost ratio (the *isolation cost ratio,* or *I*). We allow individuals to choose to acquire resources at any point along their isolation acquisition isocline.

We define an individual's fitness to be maximised for a specific combination of acquired resources. The set of points defining this specific combination of resources is a straight line, beginning at the origin, that lies in the plane of the relevant resources. We call this line the *optimal consumption vector.* In the absence of resource exchange, a species optimises its fitness by acquiring resources at the intersection of the isolation acquisition isocline and the optimal consumption vector (points 1 in Fig. 8.1a,b).

Example 1: Simple trade between a plant and a mycorrhizal fungus

We illustrate the simplest application of this model by analysing a common mutualism, that between a plant and a mycorrhizal fungus. In this example, individuals of species A (a vascular plant) are more efficient than those of species B (a mycorrhizal fungus) at acquiring both of two resources (phosphorus and carbon). Individuals of species A perceive an isolation cost ratio of 1 : 1, while B perceives an isolation cost ratio of 4 : 1 (Fig. 8.1). Thus, the fungus is less efficient at acquiring either resource than the plant, but is better at acquiring phosphorus (R2) than carbon (R1) (Fig. 8.1b). In reality, fungi are likely better at acquiring phosphorus than plants; however, for illustrative purposes we assume plants are more efficient at acquiring phosphorus than fungi.

The principle illustrated by this simple model is that, if the poorer resource competitor perceives a lower isolation cost of one resource than the other resource, it will always benefit by specialising (with respect to acquisition) on the resource that it acquires more efficiently and trading for the other resource. By trading, individuals of both species experience a more favourable cost ratio than without trade. Thus, they are able to

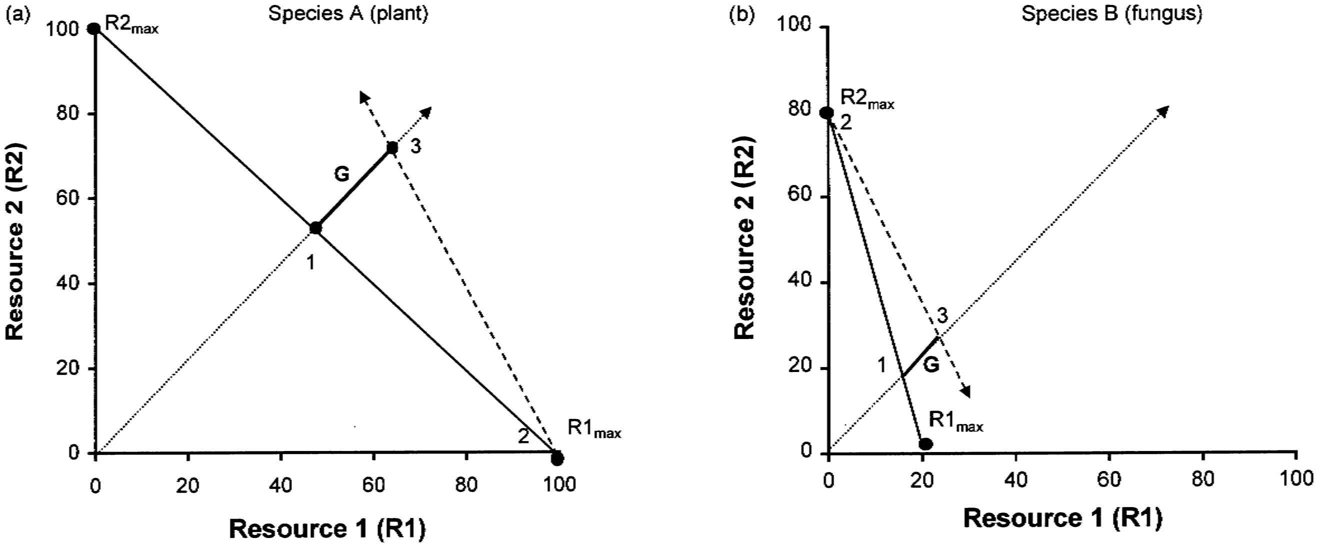

Fig. 8.1 Market conditions for a simple model of resource specialisation and trade between two species (species A, a plant, and species B, a mycorrhizal fungus). Each have an optimal consumption vector (........), which represents combinations of resource 1 and resource 2 that maximise individual fitness, and an isolation acquisition isocline (-----), which represents the maximum combined amount of resources 1 and 2 that can be acquired without trade. In the absence of resource exchange (trade), the optimum resource acquisition is represented by point 1. With trade, species B specialises on acquisition of resource 1 (phosphorus; b, point 2, $R1_{max}$), which it acquires more efficiently than resource 2 (carbon). Species A, in turn, specialises in acquisition of resource 2 (carbon; a, point 2, $R2_{max}$). Each species then trades a portion of one resource for the other required resource to end up along a trade acquisition isocline (- - - -). The optimum resource acquisition with trade, for each species, is represented by point 3. The gain from trade (*G*) is the distance along the optimal consumption vector between its intersections with the isolation acquisition isocline and the trade acquisition isocline.

acquire additional resources along a new *trade acquisition isocline,* which is analogous to the isolation acquisition isocline introduced earlier, except that it represents all possible combinations of the two resources that a species can acquire with specialization and trade (Fig. 8.1a,b). The negative of the slope of this line is the *trade cost ratio* (*T*). Under conditions of resource specialisation and trade, individuals will acquire resources at the intersection of this trade acquisition isocline and the optimal consumption vector (points 3 in Fig. 8.1a,b). We can define the *gain from trade* (*G*) to be equal to the distance along the optimal consumption vector from its intersection with the isolation acquisition isocline to its intersection with the trade acquisition isocline. An individual's fitness is assumed to be greater the more resources it can acquire, and thus the further away from the origin it is along the optimal consumption vector. Therefore, it is to the advantage of all individuals to specialise in the acquisition of the commodity for which they experience an acquisition advantage relative to potential trading partners. This result holds even under the condition that, in isolation, individuals of one species obtain both resources more efficiently than those of the other species, and perceive no difference in the cost of obtaining the two resources (Schwartz & Hoeksema 1998). Under any conditions where the trade cost ratio (*T*) lies between the isolation cost ratios (*I*) for the two trading partners, trade will be beneficial to both partners (Schwartz & Hoeksema 1998). Graphically expressed, the intersection of the optimal consumption vector and the trade acquisition isocline will always be farther from the origin than the intersection between the optimal consumption vector and the isolation acquisition isocline (Fig. 8.1).

Applicability of the biological market approach

The market model described above, based on the example of mycorrhizal interactions, involves two species requiring the same two resources, and the benefits exchanged involve costs to both species. In nature, however, many mutualisms do not fit this description. Often, the benefits exchanged between two species are services (e.g. seed- or pollen-dispersal), rather than resources. Furthermore, the benefits in mutualisms are often by-products of selfish actions (e.g. pollen movement among plants by a flower-feeding herbivore, Connor 1995) and as a result involve little or no cost to the organism giving the benefit. The following example illustrates the applicability of market models of mutualisms by showing how the market model framework can incorporate the exchange of services, as well

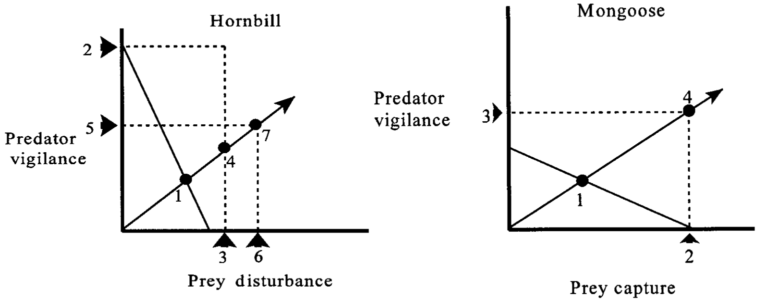

Fig. 8.2 Market model representation of a mutualism involving hornbills and the dwarf mongoose. Dashed lines represent trade acquisition isoclines, solid arrows represent optimal consumption vectors, and other solid lines represent isolation acquisition isoclines. (a) Market conditions of the hornbill where: (1) represents the amount of vigilance and prey disturbance experienced by the hornbill in isolation; (2) represents the amount of vigilance by a hornbill when in association with the mongoose; and (3) represents the amount of prey disturbance received from the mongoose in exchange for vigilance against shared predators. In this case, when hornbills are not vigilant against mongoose-specific predators, they experience (4) with specialisation and trade. If, however, hornbills are also vigilant against mongoose-specific predators, they are slightly less vigilant against their own predators (5), but receive more prey disturbance (6) from the mongoose than in the first situation, and thus experience increased resources (7). (b) Market conditions of the mongoose where: (1) represents the amount of vigilance and prey capture experienced by the mongoose in isolation; (2) represents the amount of prey capture when the mongoose specialises in prey capture; (3) represents vigilance received from hornbills in exchange for hornbill prey disturbance. Thus, under specialisation and trade the mongoose experiences increased vigilance and prey capture (4).

as benefits that are by-products. As in the first example above, we employ a graphical approach. The mathematics behind this graphical approach is simple algebra and is detailed elsewhere (Schwartz & Hoeksema 1998).

Example 2: Mixed-species foraging flocks

Rasa (1983) describes an interesting mutualistic association between the hornbill (a bird) and the dwarf mongoose. The two species form mixed foraging flocks, in which each performs a service that benefits the other. The hornbills take advantage of prey disturbed by the feeding activities of the mongoose, while the mongoose benefits when the hornbill warns of predators. This interaction is described by a market model when we consider the hornbill to require both prey disturbance and predator vigilance (Fig. 8.2a). Similarly, the mongoose needs both prey capture and predator vigilance

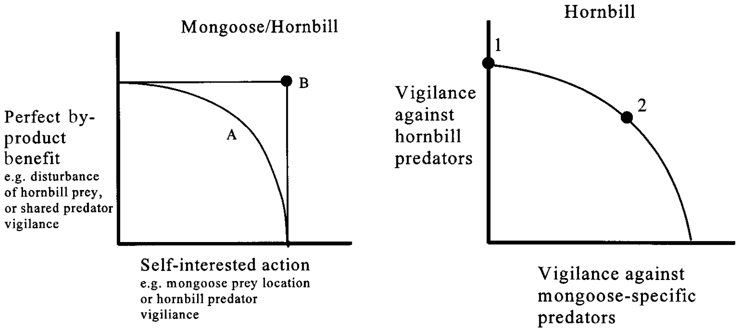

Fig. 8.3 By-product relationships for hornbill and mongoose resources and services. (a) Mongoose prey location results in prey disturbance for hornbills as a perfect by-product. Similarly, hornbill predator vigilance of shared predators results in a perfect by-product benefit of vigilance for the mongoose. (b) Market conditions of hornbill, in which vigilance against mongoose-specific predators is perceived as a partial by-product of vigilance against all hornbill predators because vigilance against additional predators may reduce the efficiency of vigilance against hornbill predators. Hornbills may, in theory, choose to be (1) vigilant specifically against hornbill predators, or (2) vigilant against both hornbill and mongoose predators.

(Fig. 8.2b). In isolation both species must expend energy on both activities. The hornbill could be considered to perceive vigilance against predators that prey on both the mongoose and the hornbill as a perfect by-product of vigilance against only its own (hornbill) predators, since, in watching for all of its own predators, the hornbill is also watching for some of the mongoose predators. Similarly, the mongoose perceives disturbance of hornbill prey as a perfect by-product of foraging for its own food. We can model these by-product relationships between commodities by changing the shape of the acquisition isoclines from the straight line used in the basic model above. We use a convex acquisition isocline (Fig. 8.3a, line A) when the acquisition of one resource is partially a by-product of the acquisition of the other resource. When acquisition of one resource is a perfect by-product of the acquisition of another resource, the isocline is square (Fig. 8.3a, line B). As discussed above, if the acquisition or production of one resource results in a by-product that is not needed by the acquiring species, then all of that by-product resource or service may be available for trade.

This situation favours hornbills that specialise in vigilance, and trade mongoose predator vigilance for disturbance of its prey by the mongoose. The situation also favours the mongoose that trades disturbance of hornbill prey to the hornbill for vigilance against predators. With specialisation and trade, both the hornbill and the mongoose perceive trade acquisition isoclines that are more favourable than their isolation acquisition isoclines (Fig. 8.2). These new trade isoclines are not straight sloped lines because in each case, individuals are trading perfect by-products to receive benefits, and thus do not need to give up important resources. The point of intersection of the trade acquisition isocline with the consumption vector is determined by the amount of benefit received for the by-product traded.

Connor (1995) suggests that if the hornbills warn about predators that do not prey on hornbills, they are 'investing' in by-product benefits received from the mongoose. This investment is described by our model if we consider the hornbill to perceive vigilance against mongoose-specific predators to be a partial by-product of vigilance against all of its own predators (Fig. 8.3b). Such a hornbill may be slightly less vigilant against its own predators, but can trade vigilance against all mongoose predators for more prey disturbance by the mongoose (Fig. 8.2a). It is important to point out that we are not hypothesising that the organisms involved are consciously 'trading'. Further, it may be difficult to quantify specific values of services rendered. We are instead suggesting that a market model is a useful context for describing interactions in which two organisms both provide services for the other that have little cost to themselves.

As Connor (1995) discusses, by-product benefits are important in many abundant present-day mutualisms, including such well-studied examples as pollination and seed-dispersal. Furthermore, present-day interactions that do not involve by-product benefits may well have evolved from interactions that began as by-product mutualisms or commensalisms. Despite the potential importance of by-product benefits, models of mutualisms have not considered them explicitly. As we show here, by-product benefits are conceptually straightforward to model, and can affect the predictions of mutualism models in significant ways.

Discussion

Mutualisms are increasingly being understood as mutually exploitative interactions that happen to result in net benefits to both species involved (Thompson 1982, 1994; Futuyma & Slatkin 1983; Janzen 1985; Herre & West 1997). The interaction is considered a mutualism if the benefits and costs involved add up to a net benefit for both species. From this perspective, market models are useful for understanding mutualisms, since they are explicit about the specific costs and benefits being exchanged. This feature allows us to make specific predictions about the conditions required for mutualism.

Bronstein (1994a) pointed out that mutualisms are not static, but rather they commonly change over space and time depending on a number of factors. One example is that of resource availability. Changing resource availability has been shown to strongly change the nature of the mycorrhizal mutualism, with the relationship being less favourable for the plant at higher soil nutrient availability (e.g. Johnson 1993). Market models are useful for modelling such changes in mutualistic interactions, since they are explicit about how the market conditions of the interaction change as supplies and demands of the the benefits involved change (Schwartz & Hoeksema 1998).

The first example of a market model presented here, that of resource trade between a plant and a mycorrhizal fungus, suggests how exchanges of goods or services between species will be favoured in many situations. The economic principle of specialisation and trade forms the basis for this idea. The model shows that some type of trading relationship is favoured as long as the two species involved perceived different ratios of acquisition costs of two resources. The second example presented here, that of the hornbill and mongoose mixed foraging flocks, shows how the market approach can incorporate mutualistic benefits that are services rather than resources. It also demonstrates how the degree to which one resource or service is a by-product of another can be modelled explicitly in the biological market approach.

It should be remembered that specific conditions are required for the functioning of a market mechanism in nature. Most importantly, mutualistic interactions may be less likely to function as biological markets if access to a partner's benefits is determined forcibly by those receiving the benefits, rather than by a choice of the giving partner (Noë & Hammerstein 1994). It would be useful to quantify the extent that partner-choice determines the distribution of benefits in mutualisms. That type of data would suggest the extent to which biological market models can be applied usefully to natural systems.

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Part III

Mating markets

Mating usually involves a bilateral decision of two individuals to accept each other as partners. However, depending on the species and on socio-ecological circumstances, females can differ strongly from males in how choosy they are and what principles govern their choice. In many animal species females are far more choosy than males. Evolutionary explanations of this phenomenon are typically based on the idea that competition for access to mates is stronger in males than in females. This asymmetry seems to be induced by differences in reproductive potential and, ultimately, by differences between eggs and sperm (anisogamy). Now, whenever there is strong choosiness in one sex, it pays the other sex to advertise desired properties and hide the undesired ones. Assuming that different advertisements are indeed compared by potential mating partners, the success of an advertisement will depend on how one's own signal compares to that of the competitors.

This competitive situation creates a mating market where individuals have different market values because they differ in their signalling potential. The higher an individual's market value, the larger its scope for being choosy itself. Therefore, Pawłowski and Dunbar study the heterosexual human mating market and explore how sensitive individuals are to their own market value. By analysing written advertisements they demonstrate a positive correlation between market value and aspiration level. They also show that, with an interesting exception, advertisers behave as if they know the choice criteria of the opposite sex. This is an important requirement for the mating scene to operate as a market.

In animals the criteria of female choice seem to vary considerably between closely related species, and within a species over evolutionary time. This raises an interesting question about the dynamics of female mate preferences and male secondary sexual characters: what causes the long-term instability of advertising signals and choice criteria? Pomiankowski and Iwasa study this problem by using a quantitative genetics model. The rationale behind this approach is as follows. In order to discuss the instability of basic mating market characteristics, it is essential to analyse non-equilibrium behaviour. From the theory of population genetics we know that this requires more attention to genetics than in the equilibrium models of a static market that can be related more easily to game theory. Based on their model analysis, Pomiankowski and Iwasa argue that advertising signals have a *fashion aspect* related to Fisher's runaway process and a *condition-dependent aspect* related to the so-called handicap process. They also argue that both processes can easily operate simultaneously. However, it is the runaway process that seems to cause the instability under investigation. Fashions seem to change in animal markets as they do in human markets – in both cases it is a certain degree of arbitrariness of the signal which causes this effect.

Participation in the mating market requires various kinds of investments. As far as the advertising is concerned, cost obviously plays an essential role in the understanding of why some individuals give stronger signals than others. Natural selection will disfavour those who 'bid too high' with the signal they choose. The same is true with regard to another aspect of the mating market, the allocation of sperm. Whenever females have multiple matings, sperm from different partners will compete for fertilisation. This resembles an auction where males are bidding for egg fertilisation: the more sperm a single male invests in an ejaculate, the higher the chances of getting access to the egg. Parker and Ball study the nature of these auctions. They show that depending on properties of the mating market, animals have to use different principles of sperm allocation. This tells us that market analysis is a crucial key to understanding sperm competition. Turning now to another procedure of how animals deal with potential rivals, Dunbar demonstrates market effects in pre-and post-copulatory mate guarding. Depending on the spatial distribution of females, there will be different numbers of male competitors on 'local' mating markets. This, in turn, should influence an animal's tendency to search for receptive females or to stay and defend a future mating partner until it becomes sexually receptive again. The temporal distribution of reproductive periods will also shape this market.

BOGUSLAW PAWŁOWSKI AND ROBIN I. M. DUNBAR

9

Human mate choice strategies

Introduction

In many species, the process of mate finding begins with advertising. As such, advertising is an opening bid that is often made in the absence of any information about the quality (and sometimes even the identity) of potential mates. These bids will, however, often reflect a trade-off between the individual's assessment of its own preferences and its experience of what the marketplace in general has to offer. This is as true of human beings as it is of other species (Grammer 1989). In humans, bids of this kind are often contingent on the advertiser's perception of his/her own bargaining hand; in consequence, the level of demands that an advertiser makes may vary according to what he/she has to offer (Waynforth & Dunbar 1995).

Advertisements in personal columns provide one outlet where human mate choice criteria are explicitly elaborated. Analyses of the content of such advertisements have consistently shown that the words used in these advertisements reflect a small number of key dimensions that have strong evolutionary valency (Kenrick & Keefe 1992; Wiederman 1993; Greenlees & McGrew 1994; Waynforth & Dunbar 1995; Bereczkei *et al.* 1997). All these studies concur that the single most important criteria by which men assess the mate quality of women is age (or, as a surrogate of this, physical attractiveness), while women tend to emphasise a wider range of criteria, including wealth/status and commitment (Borgerhof Mulder 1988a; Buss 1989; Voland & Engel 1990; Kenrick & Keefe 1992; Waynforth & Dunbar 1995; for a review of the more general literature, see Grammer 1989). Age in women is significant because it is a direct correlate of both fertility and future reproductive potential (Fisher's reproductive value). In contrast, resources and commitment are significant for women because they represent alternative forms of paternal investment (with the first at least known to have a very significant impact on the success with which women can rear their offspring in pre-industrial societies: Borgerhof Mulder 1988b, Voland 1989). Miller (1998) has suggested that the ability to entertain a mate may also be an important criterion used in human mate choice: the ability to entertain may act either as a proximate mechanism that helps to keep the mate bonded or at the ultimate level as an index of the actor's genetic quality, or both.

While we know a great deal about the patterns of such advertisements, we know very much less about how effective they are as a form of advertising. Rajecki *et al.* (1991) obtained response rates from individual advertisers and found that advertiser's age was the only variable that significantly affected the number of responses received, with younger women and older men receiving the most replies. Advertiser's looks and status were only weakly related to response rates. In a subsequent study, Baize and Schroeder (1995) reported a similar relationship for age, but also found that the number of replies received by male advertisers was influenced by their income and education, while reply rates to women's advertisements were influenced by cues of attractiveness. Our present concerns focus much more on the question as to whether advertisers understand the requirements of potential respondents so as to give appropriate emphasis to those traits that are most sought after by members of the opposite sex.

In this chapter, we first summarise the results of a previous analysis (Pawłowski & Dunbar 1999a) to show that advertisers are sensitive to their market value (their standing in the mating market) and then present new data that explore the accuracy of these perceptions.

Market value

We define the market value of an age cohort as the proportion of advertisers seeking individuals of a given age (the demand for individuals of that age) divided by the proportion of advertisers of that age in that segment of the population actively engaged in mate searching (the supply). For the purposes of our analysis, we take the relevant population to be that in our personal advertisements sample (see Box 9.1). Market value so calculated is a measure of the relative selection pressure placed on individual age cohorts, in the same sense that selection ratios are used in foraging ecology. (Note that in calculating a market value for males, we restricted our analysis to advertisements made by females in the reproductive period (20–44 years of age) since this is the age cohort on which males principally focus their own interest.)

Box 9.1 Analysing personal advertisements

Personal advertisements provide a vignette of an individual's ideal mate at a particular moment in his/her life, as well as a statement of what the advertiser has to offer at that particular time. Because courtship is inevitably a process of negotiation, the traits offered may be adjusted in the light of the perceived demands of the target population.

In our study, heterosexual personal advertisements for 445 male advertisers and 454 female advertisers aged 20–59 years were extracted from eight issues of the *Observer* newspaper published during winter 1995 and spring 1996 (for full details of the database, see Pawłowski & Dunbar 1999b).

Advertisers usually specify their own age by giving their exact age, an approximate age (e.g. early, mid or late 30s), or age by decade (e.g. '30s'). In contrast, advertisers usually specify age sought as a range (e.g. 'seeks 35–45 year old' or 'seeks partner in 30s'). Following conventional practice in the analysis of personal advertisements (e.g. Greenlees & McGrew 1994; Waynforth & Dunbar 1995), age sought was coded as the mid-point of the age range.

Advertisers typically list both a number of words to describe themselves and a number of traits that they seek in a prospective partner. A total count was made of all traits sought (i.e. demanded of any prospective mate) that have previously been identified as having evolutionary significance (see Thiessen *et al.* 1992; Waynforth & Dunbar 1995). These include all trait terms for age, physical attractiveness, resources, commitment, social skills and sexual behaviour (for detailed definitions, see Waynforth & Dunbar 1995; Pawłowski & Dunbar 1999b).

Age-specific values of mean weekly income, survivorship, fecundity and divorce rates for 5-year age cohorts were obtained from the most recent UK census statistics (OPCS 1993, 1995, 1996, 1997). Since most of the advertisers in the *Observer* newspaper are likely to be middle class, we restricted the data on income to that for non-manual workers. All other statistical data are for the UK population as a whole.

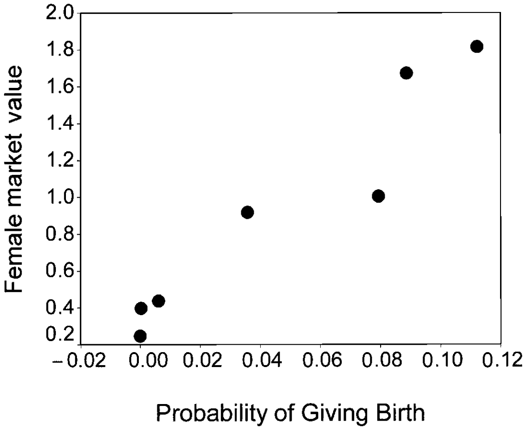

Fig. 9.1 Market value of female advertisers plotted against age-specific fecundity for five-year age cohorts. (Reprinted, with permission, from Pawłowski & Dunbar 1999a).

Fig. 9.1 shows that female market value is linearly related to female fecundity (as determined from contemporary national UK birth-rate statistics). In contrast, male market value is determined by a combination of a male's wealth (measured by his current weekly income) and the probability that he will still be married to the same woman 20 years later (i.e. at the end of the main period of parental investment) (Fig. 9.2). The probability of still being married for a male of any given age is calculated as the conjoint probability of still being alive and not being divorced in 20 years time. In each case, the independent variables explain 97% and 82% of the variance in female and male market value, respectively. These results thus suggest that surprisingly simple criteria explain almost all the selection pressure placed on each sex.

Individuals seem to have an intuitive understanding of their own market value. This can be shown by plotting the choosiness of individuals (measured as the mean number of traits sought in a prospective partner) against their market value (Fig. 9.3). With the exception of males in the 45–49 year age cohort, both males and females seem to adjust the number of traits sought in line with their market value (linear regressions: males, $b=0.42$, $F_{1,4}=7.76$, $r^2=0.66$, $P=0.049$; females, $b=0.46$, $F_{1,5}=9.50$, $r^2=0.66$, $P=0.027$).

Optimal choice strategies

Our next question is whether the traits that advertisers emphasise are those valued by individuals seeking mates. We know from previous

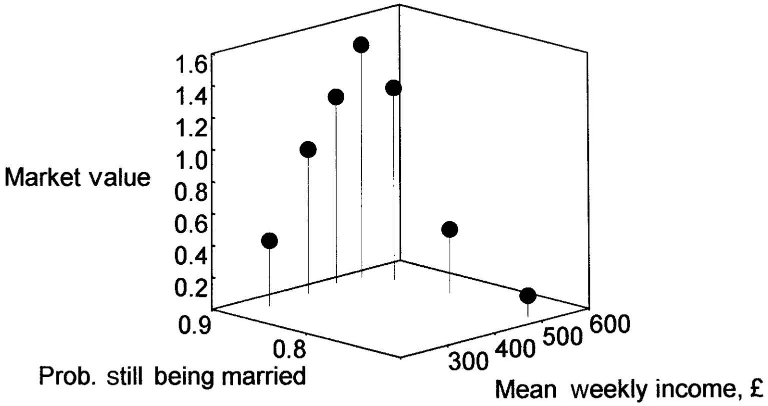

Fig. 9.2 Market value of male advertisers plotted against (a) the mean age-specific weekly income and (b) age-specific probability of still being married to the same individual at the end of the period of parental investment (defined as the conjoint probability of not being divorced in 20 years time and still being alive then). The data points are the mean values for 5-year age cohorts.

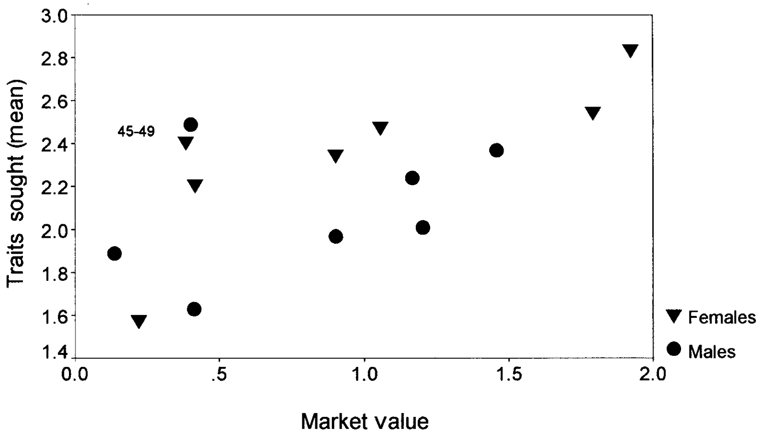

Fig. 9.3 Mean number of traits sought in prospective mates by male and female advertisers, plotted against their maket value (for 5-year age cohorts). (Reprinted, with permission, from Pawłowski & Dunbar 1999a)

analyses (e.g. Waynforth & Dunbar 1995) that advertisers adjust their bids in line with the perceived strength of their bidding hand (as reflected in whether or not they offer traits presumed to be valued by the opposite sex). However, we do not know whether these are in fact the traits actively sought by the opposite sex. In order to examine this question, we looked at the preferences that each sex actively expressed for advertisements by members of the opposite sex. (see Box 9.2).

Box 9.2 Studying trait preferences experimentally

Our principal concern in this study was to determine whether those traits that advertisers choose to mention are in fact those to which the target population attaches greatest weight. Ideally, we would have liked to have done this by examining response rates to actual advertisements. Two considerations made this difficult. First, advertisements typically contain both traits offered and traits sought. Since our interest is specifically with traits offered, the confounding effects due to variance in traits sought would have necessitated a very large data-set and some complex statistical analyses to disentangle the two sets of effects. This problem is exacerbated by the fact that advertisements vary considerably in both their length and the traits listed, thereby adding a further source of confound. Second, our attempts to gain access to a publicly available data-set met with some resistance: understandably, the publishers of these columns do not want to jeopardise the privacy of their clients or even risk gaining a reputation for allowing that privacy to be invaded. We therefore adopted the next best strategy, namely using a questionnaire-style approach with conventional experimental subjects. This allowed us the additional advantage of being able to control the size and composition of the advertisements more effectively.

A questionnaire that listed 13 different personal advertisements for prospective mates was devised (see Appendix). Advertisements in personal columns usually consist of two parts: a series of words or phrases listing the characteristics of the advertiser and a series of words describing the kind of person the advertiser would like to meet. Since our interest was exclusivly in the successfulness of the terms that advertisers use to describe themselves, the second component of the advertisements was reduced to a standard format with very limited variation (but of a kind quite often seen in personal columns). The terms used in the main part of the test advertisements were those frequently used in the personal column advertisements of national UK newspapers (principally, the Sunday broadsheet *Observer's* 'Soulmates' column). In each case, the test advertisements consisted of three to five words, each referring to one of the principal trait characteristics that advertisers seek or advertise. These were physical attractiveness, resources (or status), commitment, social skills (including humour) and sexiness (see Wiederman 1993; McGrew & Greenlees 1994; Waynforth & Dunbar 1995; Bereczkei *et al.* 1997). The terms used in ten of the advertisements counterbalanced all combinations of the first four of these in pairs and triplets; the remaining three advertisements balanced sexiness against attractiveness, resources and commitment. A separate questionnaire was prepared for males and females: these differed, however, only in respect of the gender terms used and in some of the words used for trait characteristics (e.g. handsome vs. beautiful). No words referring to age were included in any of the advertisements in order to ensure that subjects' age-preferences did not confound the results. All advertisements were explicitly heterosexual. All subjects were required to declare their sexual orientation on the questionnaire and only the questionnaires completed by those describing themselves as heterosexual were used in this analysis.

All subjects were undergraduates taking first- and second-year psychology classes. Of those subjects who described themselves as heterosexual, 159 were women (age range 18–50 years; mean 22.2, SD = 5.08) and 41 were men (age range 18–49 years; mean 22.6, SD = 5.76). Three women who completed the questionnaire improperly were discounted from the analysis. The age distribution of the subjects was biased towards the lower end of the range: only 12% of men and 16% of women were older than 25 years, but that is fairly typical of that section of the population that is actively engaged in mate-searching. Out of 156 female subjects, 54 stated that they did not have a current partner, 99 that they had a partner and three gave no answer; among males, 17 had no partner and 25 had a current partner.

Subjects were asked to rank from 1 (highest) to 6 (lowest) the six most preferred advertisements that they felt offered the prospect of someone with whom they would like to form a relationship had they been looking through the personal columns of a newspaper. For analytical convenience, these rankings were then reversed (6 highest, 1 lowest) and a rating of 0 given to each of the remaining seven advertisements. The points ratings for all advertisements that included a term for a given trait were then summed, to yield a mean

Box 9.2 (*cont.*)

score for that trait. This yielded a value that could range between 0 and 21 for the four main traits (attractiveness, resources, commitment and social skills) and 0 and 15 for sexiness. The resulting score for each subject was then standardised by dividing by the number of advertisements that included terms for that category (6 for the first four traits and 3 for sexiness: note that division is by 6 even though some categories include seven questions because at most six advertisements could be given a preference ranking) to yield a mean score; these values were then scaled to yield a standardised preference score that varied between 0 and 5.

The advertisements focused on the traits offered by the advertiser, with the traits sought in the advertisee held constant. Our concern is with five general categories of traits that have been identified in the literature as having evolutionary valency rather than with the individual trait words themselves. In the following analyses, we use the convention of identifying trait categories by their initial letters: A (attractiveness), R (resources), C (commitment), S (social skills) and X (sexiness).

Subjects were asked to rate the advertisements for preference. Figure 9.4 gives the mean scores for each test item in the questionnaire for the two sexes. Both sexes responded most strongly to those advertisements that included commitment (females: AC, CS, RCS; males: AC, ACS, CS, SX). However, the two sexes differed in their responses to the traits associated with commitment. Thus, when commitment is associated with either resources or social skills alone, females rate the advertisements higher than males do; but when these two traits are associated with attractiveness or sexiness, males rate the advertisements higher than females do.

In order to separate out the weightings given to each trait more clearly, a mean score for each trait was calculated by summing (and then standardising) the scores for all advertisements that included a given trait term (see Box 9.2). Table 9.1 gives mean preference scores for each trait for each sex. Females rated resources and social skills significantly higher than males did (one-way ANOVA: $F = 17.44$ and $F = 17.66$, $P < 0.001$ in both cases), while males rated attractiveness ($F = 33.20$, $P < 0.001$) and sexiness ($F = 3.59$, $P < 0.06$) higher than females did. Only in respect of commitment was there no significant difference between the sexes.

Table 9.1: *Standardised mean preferences for each trait for each gender (with higher values indicating greater preference)*

	Scaled means	
Trait category	Females	Males
Attractiveness	2.11	3.09**
Commitment	3.43	3.40
Resources	2.36	1.65**
Social skills	2.95	2.32**
Sexiness	1.15	1.54*

Note:
One-way ANOVA: ** $P<0.01$, * $P=0.06$

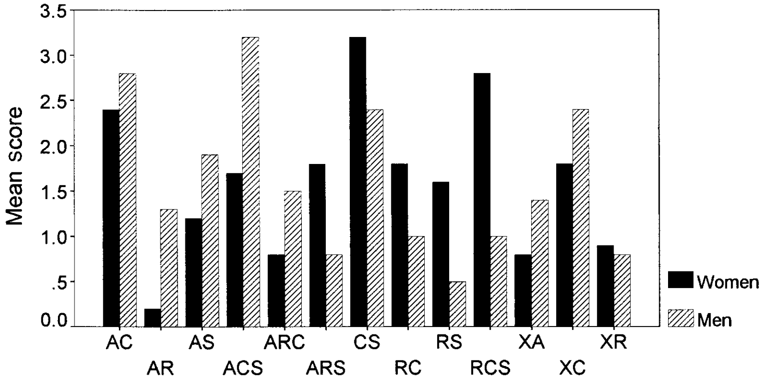

Fig. 9.4 Mean preference score for each test item in the questionnaire (as listed in the Appendix). A: physical attractiveness; R: resources (wealth/status); C: commitment; S: social skills (humour); X: sexiness.

A series of paired *t*-tests was then used to compare individuals' preferences for all pairwise combinations of trait categories. These data yield the following preference ranking for the traits:

Females: $C>S>R>A>X$
Males: $C\approx A>S>R\approx X$

(where the symbol $>$ denotes a significant difference at $P=0.05$ and $\approx$ denotes a non-significant difference with the expressed preference being higher for the first-listed trait). Aside from the common overriding preference for cues related to commitment, females show a striking preference

Table 9.2: *Pearson correlations between pairwise comparisons of individuals' expressed preferences for trait categories for (a) males and (b) females*

(a) Males

	Attractiveness	Resources	Commitment
Resources	−0.26		
Commitment	−0.22	−0.32	
Social skills	−0.27	0.28*	0.01
Sexiness	−0.09	−0.46*	−0.23

(b) Females

	Attractiveness	Resources	Commitment
Resources	−0.19		
Commitment	−0.46*	−0.39*	
Social skills	0.19*	−0.09	−0.15
Sexiness	−0.30	−0.11	−0.13

Note:
[a] Significant at $P < 0.05$ (see text for details)

for social skills and resources, whereas males show a strong preference for attractiveness. Sexiness scores low for both sexes.

Next we examined the data for evidence of trade-offs between trait categories by running pairwise correlations between them. The results are given in Table 9.2. These correlations need careful interpretation because scores in the upper right and lower left corners of the state space are not possible and, as a result, a randomly distributed data-set will tend to produce a slightly negative correlation rather than a slope of zero. In fact, the mean slope for the 18 correlations in this dataset is $r = -0.178$. If we take this to be a reasonable estimate of the null hypothesis, our question then becomes: how many of the observed correlations lie outside the 95% confidence intervals for this estimate (i.e. $-0.34 > r > -0.02$). On this criterion, there are five significant results in Table 9.2: two for males (sexiness correlates negatively with resources, while resources correlates positively with social skills) and three for females (negative correlations between commitment and both resources and attractiveness and a positive correlation between attractiveness and social skills).

Negative correlations in this context imply trade-offs. Surprisingly perhaps, males appear willing to trade sexiness against resources in women, though why they should be willing to do so from an evolutionary perspective remains unclear. Females' willingness to trade commitment against both attractiveness and resources by men is more understandable: paternal investment can come in two forms, direct investment (in the form of commitment to the relationship and the offspring) and indirect investment (in the form of resources which the woman can invest in her offspring). The positive correlation between social skills and attractiveness in women subjects probably reflects the fact that physical attractiveness and social skills are commonly perceived as going together, and may in fact be strongly correlated (Calvert 1988; Cann 1991; Hope & Mindell 1994).

We should consider two possible confounding variables in these analyses: subject age and their partnered status (i.e. whether or not they have a regular partner). We found only two significant differences when we compared subjects 24 years and under with older subjects. Older women chose advertisements which offered resources more often than did younger women (one-way ANOVA: $F_{1,153} = 13.9$, $P = 0.0003$) and they chose those advertisements that offered cues of sexiness less often than younger women (one-way ANOVA: $F_{1,153} = 4.81$, $P = 0.03$). Males exhibited no differences with respect to age.

Out of 156 female subjects, 54 did not have a partner and 99 had a partner (3 additional subjects failed to answer the question). For males, 17 did not have a partner and 25 did. For all categories and for both sexes, we found only one significant difference between those who had a partner and those who did not. Females having partners tended to choose advertisements with offers of commitment significantly more often than females who had no partner (one-way ANOVA: $F_{1,151} = 3.80$, $P = 0.05$).

Other than these three differences (all concerning female subjects), there were no differences in behaviour that could be attributed to age or partner status.

Finally, we consider the question of how well each sex understands the other sex's requirements. To examine this, we plotted preference scores for each of the five trait categories for one sex against the emphasis given to these trait categories in a sample of real advertisements by the other sex. We use, again, the standardised preference scores from the present study in the first case. For the second variable, we took two measures of trait preference from our personal columns database: the mean number of words listed for a given trait category and the proportion of advertisers who listed at least one word for that category. In practice, the two indices produced nearly identical results (mainly because the range in the number of words listed per category is very small), so we give only the latter data.

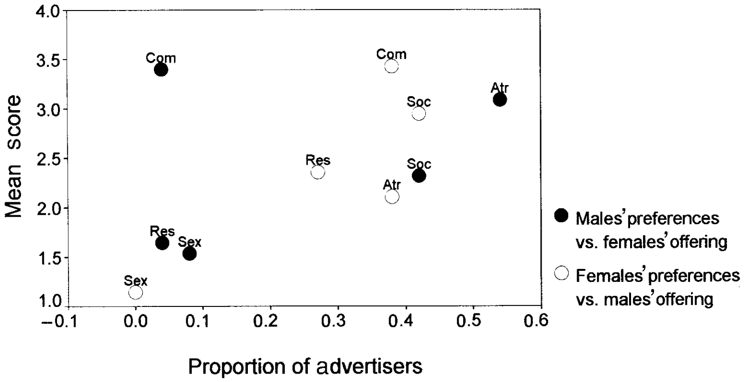

Fig. 9.5 Mean preference score for individual trait categories by questionnaire respondents of one sex plotted against the frequency with which that category was advertised by members of the opposite sex in a sample (matched for age and education) of actual personal advertisements from a national newspaper. Atr: physical attractiveness; Res: resources (wealth/status); Com: commitment; Soc: social skills (humour); Sex: sexiness

In the final step of the analysis, we compare the expressed preferences of these subjects with the traits actually offered by advertisers. The data for this sample derive from a database of personal advertisements placed in the *Observer* newspaper's 'Soulmates' column published during late 1995 and early 1996 (for background details see Pawłowski & Dunbar 1999b). We selected only those advertisements in which individuals sought heterosexual relationships. To maintain comparability with the undergraduate sample in terms of both age and educational level, we sampled only those advertisers aged between 18–29 who described themselves as students or graduates. We excluded all advertisements where it was difficult to decide whether the traits mentioned were being offered or sought, and those where use of literary and other allusions and/or a humorous style made the interpretation of the advertisement difficult, as well as those who stated that they were parents. This yielded a sample of 24 advertisements by women (mean age 24.8 years) and 26 advertisements by men (mean age 25.6 years). These advertisements were then coded for the number of words listed for each of the five traits as descriptors of the advertiser (traits offered).

Figure 9.5 shows the data for the two sexes separately. Two points emerge from these results. First, the two variables are positively correlated for both sexes: when constructing their advertisements, both males and females seem generally to be well attuned to the kinds of cues that most interest members of the opposite sex. Second, and perhaps surprisingly, female advertisers seem to underestimate the extent to which males are interested in commitment. As a check on the validity of these results, we checked the advertisements database itself for internal consistency. Plotting the proportion of advertisers of one sex that seek a given trait against the proportion of the opposite sex that advertise that trait yields virtually the same distribution of points: as in Fig. 9.5, females underestimate the extent to which the males in this age group are interested in commitment.

Conclusions

We have shown that, aside from a common interest in cues of commitment, males and females differ in their preference ratings for the cues that advertisers list. Males' interest in females seems to be dictated largely by their fertility (indexed by attractiveness and/or age), while females' interest in males seems to be dictated by the resource benefits they offer (indexed by status and/or actual or future wealth). In the women's case, this emphasis on wealth (or earning potential) is also moderated by the male's age, apparently in an attempt to ensure that the resourcing benefits on offer continue to accrue throughout the period of primary parental investment (in modern industrial societies, approximately the first 20 years of the relationship). These findings imply that male and female mate interests focus on contrasting criteria (the woman's fertility in the case of males and the males' ability to invest in offspring in the case of females).

In general, the patterns that emerge confirm those previously noted in many studies of personal advertisements: males offer cues associated with resources and seek attractiveness, whereas females offer attractiveness and seek cues associated with commitment and resources. Both males and females thus seem to be sensitive to the demands of their target populations (in the case of heterosexual advertisers, members of the opposite sex).

None the less – and perhaps surprisingly – females seemed to underestimate males' concerns with commitment. This result is puzzling, since in none of the analyses of personal-column advertisements does commitment come out as a strong interest of males: males typically seek commitment much less often than they do traits like attractiveness. One possible explanation is that males' interest in commitment here is a reflection of mate-guarding behaviour and the problems of paternity certainty. The rather young age-bias of the present sample (with its mean age of 23 years for males) might lend itself to such a distortion. This suggestion is given added weight by the fact that, in the full *Observer* sample of some 400 male advertisements, males in their 20s were more likely to seek commitment than males in their 30s and 40s, though not those in their 50s.

If this emphasis on commitment does reflect males' concerns about paternity certainty, we might expect there to be a cross-cultural relationship between the level of interest in this trait category and the degree of promiscuity: in societies or sub-cultures that are particularly promiscuous, males may be especially interested in cues of commitment, but in societies where sexual behaviour is more strictly controlled they may show less interest in this trait.

An alternative (but perhaps less plausible) explanation for the apparently high level of interest in cues of commitment might be that the words used as indices of commitment in the questionnaire (*caring, sincere, sensitive*) conveyed other meanings (for example, sensuousness) to male respondents. In contrast, females interest in commitment is less surprising, since it is likely to reflect their concerns with ensuring a flow of paternal investment (irrespective of whether this comes in economic or social terms).

Of particular significance were the analyses suggesting that females were more likely to trade-off between different trait categories than males were. Most of the research on mate preferences in humans has suggested that females are more choosy than males and use a larger number of criteria by which to judge prospective mates (see Grammer 1989). The present results confirm this general pattern, but emphasise the fact that females may actually be willing to trade-off one dimension against another. However, the basis of the trade-off remains unclear. Table 9.2 suggests that women are willing to trade commitment against attractiveness. The emphasis on attractiveness might reflect the fact that physical attractiveness and (future) socio-economic success do appear to be correlated (see e.g. Mueller & Mazur 1997), but it might equally reflect a desire for good genes (since attractiveness is directly related to structural symmetry). It is also possible that these contrasts in female mate choice patterns reflect a contrast between short- and long-term strategies: females seeking long-term relationships might prefer commitment, but those seeking short-term relationships might prefer attractiveness and/or social skills. For males, on the other hand, attractiveness (with or without commitment) remains the overriding concern for both short- and long-term relationships (presumably because of its association with age and thus fertility) and males show little evidence of being willing to trade attractiveness against any other trait category.

Appendix

The 13 advertisements listed on the questionnaire in the study of response preferences. For present purposes, only those pertaining to male subjects are shown; an identical set, with opposite gender terms and appropriate wording, was given to female subjects. The listed trait categories are given in brackets at the end of each advertisement.

1 Attractive and independent female with attitude WLTM[a] that special male (AR)[b]
2 Beautiful, sincere and easygoing female seeks male for longterm relationship (AC)
3 Pretty, amusing and creative female WLTM uncomplicated male (AS)
4 Solvent, caring and sensitive female seeks relaxed male (RC)
5 Financially independent, winsome and lively female WLTM friendly male (RS)
6 Kind, sensitive female with good sense of social skills WLTM male to share good times (CS)
7 Attractive, warm and professional female seeks male for stable relationship (ARC)
8 Cheerful, pretty female with great job seeks that special male (ARS)
9 Affectionate, financially independent and witty female seeks interesting male (RCS)
10 Gorgeous, funny, warm and honest female seeks male to share good times (ACS)
11 Pretty and sensual female WLTM male for long term relationship (XA)
12 Finacially independent, cuddly and snoggable female seeks male for stable relationship (XR)
13 Sensual, passionate and sensitive female seeks male for stable relationship (XC)

Notes:

[a] 'would like to meet' in conventional abbreviated format

[b] A: physical attractiveness; R: resources (wealth/status); C: commitment; S: social skills; X: sexiness

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ANDREW POMIANKOWSKI *AND* YOH IWASA

10

How does mate choice contribute to exaggeration and diversity in sexual characters?

Introduction

Males of many species are typified by exaggerated secondary sexual traits and courtship displays (Darwin 1871; Andersson 1994). These sexual signals are highly variable amongst closely related species and appear to change very quickly in evolutionary time (Iwasa & Pomiankowski 1995). Two classic examples of exaggeration and diversity in sexual characters are the cichlid fish species flocks of the African Great Lakes (Fryer & Iles 1980) and the birds of paradise found in south-east Asia (Coates 1990).

In this chapter we will consider how female mating preferences cause the evolution of exaggeration and diversity in male sexual displays. As recognised by Fisher (1930) this requires an understanding of how female sexual preferences evolve. Two main hypotheses have dominated thinking on this question, Fisher's runaway and the handicap process. These ideas concern the benefits of mate choice. Fisher's runaway assumes that females select mates with exaggerated ornaments because they are attractive. Choosy females benefit as their male offspring inherit genes for attraction. The handicap process assumes that the degree of exaggeration reveals male quality. In this case, choosy females benefit directly because higher-quality males make better fathers or indirectly because quality is inherited by their offspring. These are not the only forces affecting the evolution of mate choice. For example, inbreeding avoidance and species recognition can be important. However, Fisher's runaway and the handicap process seem the best candidates for explaining exaggeration and diversity.

The evolution of female preferences for male sexual ornaments has been treated in a number of ways, using major gene, quantitative genetic and game theory models. In the following sections we will summarise our work using quantitative genetic models. We do not advocate one modelling style as more realistic or more illuminating than any other. In fact there is little dissonance between the different modelling strategies which have largely come to the same conclusions. However, the frequent use of economic modelling (game theory and optimisation) in other chapters in this book is not suited to some investigations. In particular, the non-equilibrium dynamics are more obviously captured by using models that incorporate genetic details. As we will see, these are potentially important in explaining the rapid diversification of sexual selected traits.

In the following section, we outline a basic model of sexual selection. Our strategy has been to reduce the process of mate choice to its most simple, and then add complexity when necessary. Our goal is to show the importance of the various forces acting on mate choice in causing the exaggeration and diversification of sexual characters.

Basic sexual selection model

The basic model of Fisher's runaway (Pomiankowski *et al.* 1991) follows evolutionary change in the mean value of the two traits, the strength of female preference ($\bar{p}$) and the size of a male sexual ornament ($\bar{s}$). The per generation change in the mean trait values ($\Delta\bar{p}$) is given by the effect of selection (β_s, β_p) on the genetic variation underlying the two traits (G_s, G_p, B_{sp}),

$$\begin{pmatrix} \Delta\bar{s} \\ \Delta\bar{p} \end{pmatrix} = \frac{1}{2}\begin{pmatrix} G_s & B_{sp} \\ B_{sp} & G_p \end{pmatrix}\begin{pmatrix} \beta_s \\ \beta_p \end{pmatrix} + \begin{pmatrix} -u \\ 0 \end{pmatrix}. \tag{10.1}$$

G_p and G_s are additive genetic variances of s and p respectively. Despite claims to the contrary (e.g. Taylor & Williams 1982), both traits have repeatedly been shown to be genetically variable (Bakker & Pomiankowski 1995; Pomiankowski & Møller 1995) and there is some evidence that sexual traits show higher levels of genetic variability than equivalent non-sexual traits (Pomiankowski & Møller 1995). Preferences and ornaments are predicted to covary because females with stronger preferences (larger p) tend to mate with males with bigger ornaments (larger s) resulting in a positive additive genetic covariance B_{sp}. As yet there have been few measurements, but a number of experimental studies have reported the existence of positive genetic covariances (Bakker & Pomiankowski 1995). The final genetic term u is the mutation bias acting on the male trait (Pomiankowski *et al.* 1991). We assume that u is small but greater than zero because most mutations affecting a complex trait will tend to disrupt production and therefore tend to make the trait smaller.

The male and female traits are assumed to be sex limited, hence the value of half in Eq. (10.1). The selection differential β_s is calculated from the effect of the male ornament on male fitness (W_m),

$$\beta_s = \frac{\partial}{\partial_s} lnW_m, W_m = \exp\left[a\bar{p}(s - \bar{s}) - cs^2\right]. \tag{10.2a}$$

Male fitness has two components: mating success and survivorship. Male mating success is determined by how much females prefer males with exaggerated sexual traits (first term). Females can favour males with larger or smaller than average ornament size dependent on $\bar{p}$, the mean female preference. If $\bar{p} > 0$ females prefer males with larger ornament size and if $\bar{p} < 0$ females prefer males with smaller than average ornaments (Pomiankowski *et al.* 1991). We assume that males can mate many times and that females have open-ended preferences (Lande 1981). The coefficient a defines the effectiveness of the male ornament in causing increased mating success.

In addition, male fitness is determined by how the ornament affects survivorship (second term). Most male display traits reduce survival chances because they are energetically costly to produce or maintain (Andersson 1994). We can assume that there is an optimum size for the sexual trait which maximises survival chances. By convention this natural selection optimum is set at $s = 0$. Survival chances decline symmetrically either side of this value at a rate c.

The effect of selection on female preference β_p is calculated from the effect of preference on female fitness (W_f),

$$\beta_p = \frac{\partial}{\partial p} lnW_f, W_f = \exp\left[-bp^{\gamma}\right]. \tag{10.2b}$$

We assume that choosing is costly, so females with stronger positive or negative values of p have lower survival chances (Pomiankowski 1987). This might relate to predation risks, time constraints or some other factor associated with mating behaviour. We further assume that female choice costs are minimised when females mate at random ($p = 0$) and increase symmetrically about this natural selection optimum at a rate b following the power exponent γ(we usually set $\gamma \geq 2$). In the Fisher model we assume that males mate with females but do not provide them with any resources, territory, parental care etc., so there is no direct effect of the male preferred on female fitness (hence Eq. (10.2b) has no s term). Any benefits of mate choice accrue indirectly to the female's offspring, via the inheritance of genes for attraction carried by the chosen male.

In the equations above, the effect of selection is calculated as the partial derivative of the logarithm of fitness with respect to the trait in question. Weak selection is the most important assumption we make in our calculations, which means that fitness changes slowly over the range of trait values in the population (i.e. $a, b, c, u \ll 1$). We adopt a particular set of assumptions about the magnitude of the parameter values. We assume that $b, u \ll a, c$ that is, the effect of mate choice on female survival chances (b) or the magnitude of mutation bias (u) are much smaller than the effect of selection on the male ornament through mate choice (a) and survivorship (c). These assumptions hold in most natural conditions. There is abundant evidence that male sexual traits are subject to relatively strong selective forces compared to direct selection on mate choice (Andersson 1994). In addition, mutation bias on phenotypic characters cannot but be small.

Using these assumptions, we can calculate the per generation change in the mean trait values according to the magnitude of the selective coefficients, by picking up the leading order terms. The procedure allows us to find some simple results that otherwise would be impossible to obtain. For example, we can show that the evolutionary equilibrium (see below) is independent of the additive genetic variances, as the genetic covariance term (B_{sp}) is approximately the product of the mate choice coefficient (a) and additive genetic variances (G_s & G_p) which then cancel out (Pomiankowski & Iwasa 1993). A full justification of our techniques is found in Iwasa *et al.* (1991), and Iwasa and Pomiankowski (1994).

Fisher's runaway

The evolutionary dynamics of Fisher's runaway are found by calculating the selection differentials,

$$\beta_s = a\bar{p} - 2c\bar{s},$$
$$\beta_p = -\gamma b\bar{p}^{\gamma-1},$$

and substituting these into Eq. (10.1) (Fig. 10.1). In the short term, Fisher's runaway can create large exaggeration of preferences and male ornaments. Equilibrium is found by setting $\Delta\bar{s}=0$ and $\Delta\bar{p}=0$ (Pomiankowski & Iwasa 1993). There is a single equilibrium at,

$$\bar{p} = \left(\frac{ua}{\gamma b}\right)^{1/(\gamma-1)}, \bar{s} = \frac{a}{2c}\bar{p}. \tag{10.3}$$

The degree of exaggeration increases with mutation bias (u), the effectiveness of the male ornament in causing increased mating success (a)

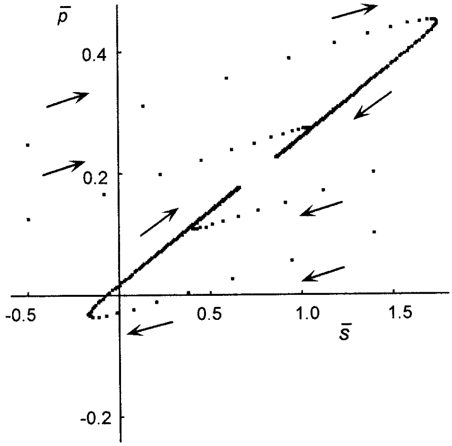

Fig. 10.1 The evolution of the mean female preference ($\bar{p}$) and male ornament ($\bar{s}$) by Fisher's runaway. Several trajectories are plotted every 20 generations, and the direction of evolution is indicated by arrows. There is a single equilibrium. Parameters are: $a = 0.4$, $b = 0.001$, $c = 0.05$, $\gamma = 2$, $u = 0.001$, $G_s = G_p = 0.5$. (Adapted from Pomiankowski & Iwasa 1993.)

but decreases with the cost of female choice (γ and b) and the cost of the ornament (c).

As previously noted (Pomiankowski *et al.* 1991), mutation bias (u) plays an indispensable role in maintaining a positive evolutionary equilibrium. Mutation bias (u) produces an excess of poorly ornamented males. Females that are choosy are favoured because on average they have more attractive male offspring with higher mating success and higher overall fitness. In the absence of mutation bias, $u = 0$, the equilibrium lies at the natural selection optimum $\bar{p} = 0$, $\bar{s} = 0$, and females mate at random. There are few reasons for thinking that the absolute value of mutation bias is large (Pomiankowski *et al.* 1991). So this leads to the conclusion that the degree of stable exaggeration created by Fisher's runaway is unlikely to be great.

Handicap models

The handicap model differs from Fisher's runaway as the size of male sexual ornaments reflect male quality. Females choosing to mate with males carrying large ornaments potentially benefit as their offspring inherit genes for high viability, so-called good genes. In addition, male quality can be correlated with male parenting ability, territory quality, better resources or other factors that directly benefit females. These consequences have been grouped together and called the 'good parent' effect, in contrast to the good genes effect (Price *et al.* 1993; Schluter & Price 1993). They bring direct benefits to females choosing males carrying large ornaments.

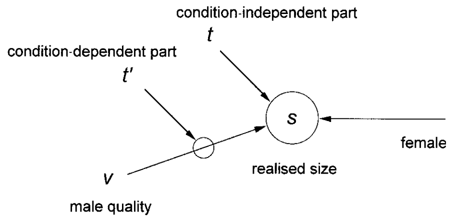

Fig. 10.2 Male ornament size *s* is composed of a condition-independent (*t*) and condition-dependent (*t′ v*) part which depends on male quality. Male quality *v* may be non heritable but improve female reproductive success (good parent model) or heritable and so improve offspring viability (good genes model). Females cannot assess quality directly, their mate preference *p* depends on male ornament size *s*. (Adapted from Iwasa *et al.* 1991.)

To model the handicap process, the expression of the male ornament must be made condition-dependent. As before *s* is the size of a male ornament used by females in their mate choice. But this now depends on male quality *v*. To capture this we allow ornament size to be $s = t + t'v$, which is composed of a condition-independent (*t*) and condition-dependent ($t'v$) part (Fig. 10.2). For simplicity we assume that ornament size is a linear function of quality. The degree of condition dependence of the male ornament depends on how costs vary with quality. Here we follow the handicap assumption that larger ornaments are more costly for individuals with lower quality (Zahavi 1977).

We can model these differences by making a few, simple changes to the basic Fisher model (Iwasa *et al.* 1991, Iwasa & Pomiankowski 1994). Let individuals vary in a quality trait *v*. This affects male and female fitness in three ways,

$$W_m = \exp[\mathrm{g}(\mathrm{v})] + \exp\left[a\bar{p}(s - \bar{s}) - \frac{cs^2}{1 + kv}\right] + \exp[hv], \tag{10.4a}$$

$$W_f = \exp[\mathrm{g}(\mathrm{v})] + \exp\left[-bp^2\right] + \exp\left[p\sigma_v{}^2 ha\bar{t}'\right]. \tag{10.4b}$$

First, both males and females with better quality have higher survival chances, given by an increasing function g(*v*). Second, males in better condition have lower costs associated with ornament size. This is the case if $k > 0$, where *k* is the condition-dependence of the survival cost. If $k = 0$, we recover the condition-independent costs that are typical of Fisher's runaway.

Third, male quality can affect paternal care. In Fisher's runaway and good genes handicap models, there are no direct benefits to female preference, $h=0$ and the third terms in Eq. (10.4a–10.4b) are zero. But, with the good parent model, we assume that males with higher quality enhance female reproductive success. The rate constant h is the effectiveness of male quality in improving female reproductive success. The effect of males on female fitness needs to be calculated with respect to the distribution of quality amongst the males with whom the female mates. This depends on the strength of her preference (p), the phenotypic variance of male quality amongst males ($\sigma_v{}^2$), the male signal efficiency (a) and the mean condition-dependence of male ornament size ($\bar{t}\,'$) (for derivation see Schluter & Price 1993; Iwasa & Pomiankowski 1999).

The evolutionary model for the handicap process needs to follow the evolution of these four quantitative traits,

$$\begin{pmatrix} \Delta\bar{t} \\ \Delta\bar{t}' \\ \Delta\bar{p} \\ \Delta\bar{v} \end{pmatrix} = \frac{1}{2}\begin{pmatrix} G_t & B_{tt'} & B_{tp} & B_{tv} \\ B_{tt'} & G_{t'} & B_{t'p} & B_{t'v} \\ B_{tp} & B_{t'p} & G_p & B_{pv} \\ B_{tv} & B_{t'v} & B_{pv} & G_v \end{pmatrix}\begin{pmatrix} \beta_t \\ \beta_{t'} \\ \beta_p \\ \beta_v \end{pmatrix} + \begin{pmatrix} 0 \\ 0 \\ 0 \\ -w \end{pmatrix}. \qquad (10.5)$$

Although this looks complicated it is just a four-trait version of Eq. (10.1). Finally, the model needs to take into account mutation bias on the quality or general viability trait, v. This is expected to be significant and negative, as for each generation there is an input of deleterious mutations that decreases quality. The intensity of mutation bias is expressed by $-w$.

The evolutionary dynamics of the handicap process are similar to those seen with Fisher's runaway (Iwasa *et al.* 1991; Iwasa & Pomiankowski 1994; Iwasa & Pomiankowski 1999), except there are two equilibria at,

$$\bar{p} = \pm\left[\frac{(\sigma_v^2 h + w)a\bar{t}'}{\gamma b}\right]^{(1/(\gamma-1))}, \bar{t} = \frac{a}{2c}\bar{p}, \bar{t}\,' = \frac{ak}{2c}\bar{p}, \qquad (10.6)$$

and a third when there is no exaggeration ($\bar{p}=0$, $\bar{t}=0$, $\bar{t}\,'=0$). Using the assumption of $\gamma > 2$, both positive and negative equilibria are locally stable and the null equilibrium is unstable (Fig. 10.3).

We can compare the handicap equilibria with that generated by Fisher's runaway. First, the handicap process creates equilibria with positive and negative exaggeration. This is expected as the fitness functions are symmetric (Eq. (10.4)), so quality can become associated with either greater positive or negative exaggeration. At the positive equilibrium, males with higher quality produce larger ornaments, so females benefit from selecting males with larger (more costly) ornaments. Likewise, at the negative equilibrium, males with higher quality produce smaller (more costly)

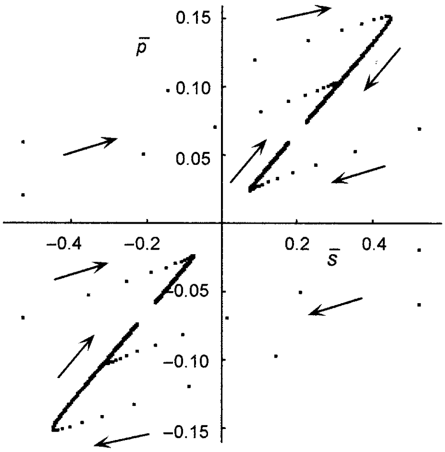

Fig. 10.3 The evolution of the mean female preference ($\bar{p}$) for a male ornament ($\bar{s}$) when the male trait is a handicap that reveals male quality. Population mean trait values are shown by dots every 10 generations, and the direction of evolution is indicated by arrows. There are three equilibria: positive and negative equilibria are stable, and the equilibrium at the origin is unstable. For simplicity we have assumed that there is no heritable component of quality, so there are only direct benefits to females from choosing a mate. Similar patterns occur when quality is heritable. Parameter values are $a = 0.4$, $b = 0.01$, $c = 0.1$, $h = 0.01$, $k = 0.5$, $\gamma = 3$, $w = 0.01$, $G_p = G_t = G_{t'} = 0.5$, $\sigma_v^2 = 0.5$. (Adapted from Iwasa & Pomiankowski 1999.)

ornaments, so females benefit from selecting males with smaller ornaments. In contrast, Fisher's runaway can occur in either direction, but it only produces a positive equilibrium as mutation bias acts unidirectionally, reducing ornament size (Fig. 10.2).

Second, the ecological–physiological parameters *a*, *b* and *c* have similar effects in both cases. The strength of handicap exaggeration depends on $(\sigma_v^2 h + w)\bar{t}'$, whereas the strength of Fisher's runaway exaggeration depends only on u. The former is likely to be much larger. First mutation bias on general viability (w) is known to be large (Rice 1988; Burt 1995), and is likely to be considerably larger than mutation bias on traits (u). Second, phenotypic variation in male quality (σ_v^2) will be even larger, and it is well established that males can contribute to female reproductive success (h) through parental effort, control of territory or resources etc. (Andersson 1994). Finally, condition-dependent expression ($\bar{t}'$) is a general phenomenon (Andersson 1994) and in some cases has been shown to be particularly strong in male sexual ornaments used by females in their mate choice (David *et al.* 1998). This leads to the conclusion that the handicap process, whether good genes or good parent, is a much more likely explanation of strong female preferences for exaggerated male sexual ornaments.

Extreme natural selection – Fisher's runaway

The conclusion drawn so far is one that implicitly or explicitly pervades many recent discussions of sexual selection and the evolution of signals. These have tended to neglect Fisher's runaway while extolling the power of the handicap process (e.g. Johnstone 1997). We now show that this viewpoint is premature.

Sexual ornaments and courtship displays show rampant diversity across species well in excess of the variation seen in non-sexual morphology and behaviour. This sexual diversity typifies a number of different groups and types of traits, for example the cichlid fish species flocks of the African Great Lakes (Fryer & Iles 1980), the highly species-rich Hawaiian *Drosophila* (Carson 1986), male insect genitalia (Eberhard 1985) and the birds of paradise (Coates 1990). Even sub-populations of the same species show sexual divergence where there is little apparent difference in other characters (e.g. sage grouse, Young *et al.* 1994; African Great Lake cichlids, Seehausen & van Alphen 1998).

These observations are a major challenge to the handicap-centred view of sexual trait evolution. If females prefer a male ornament that acts as a condition-dependent handicap and so reveals male quality, why have such traits diverged so rapidly across closely related species? It seems highly unlikely that each sexual trait reveals a different aspect of quality specific to each species. Most of the diversity seems arbitrary and lacking in specific meaning.

Diversity of sexual ornaments was recognised by Fisher in his original writing (Fisher 1930) and was an outcome in early mathematical modelling of Fisher's runaway (Lande 1981). We have formalised this by recognising how easily Fisher's runaway can give rise to diversity (Iwasa & Pomiankowski 1995; Pomiankowski & Iwasa 1998). In particular, we have investigated more extreme selection on the male trait in which the cost of the male trait is very small around the optimum but increases very quickly beyond a certain limit. This can be modelled by assuming that male survival decreases with the fourth power rather than a quadratic,

$$W_m = \exp\left[a\bar{p}(s-\bar{s}) - cs^4\right],\ \beta_s = a\bar{p} - 4c\bar{s}^3\,. \tag{10.7}$$

Under this more extreme fitness function, the population shows two general outcomes. First there is continual, cyclic evolution (Fig. 10.4).

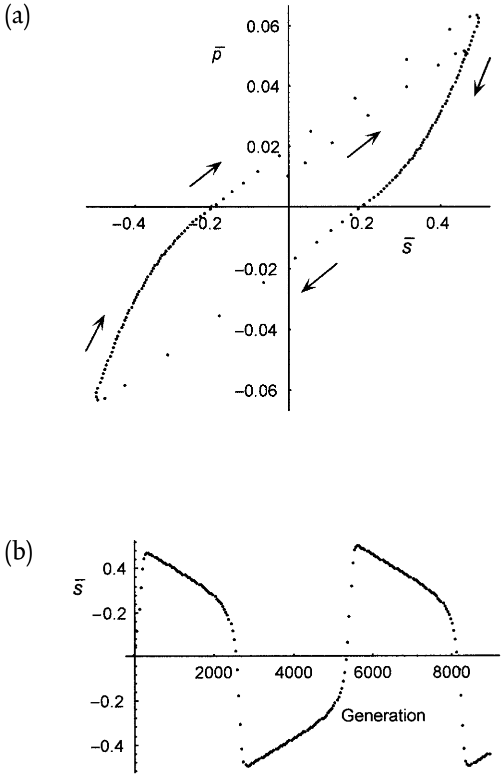

Fig 10.4 Cyclic evolution caused by Fisher's runaway is plotted as (a) the joint evolution of the mean female preference ($\bar{p}$) for a male ornament ($\bar{s}$) and (b) as change in the mean male trait ($\bar{s}$) per generation. The population is plotted every 20 generations. Parameter values are $a=0.4, b=0.001, c=0.05, G_t=0.5, G_p=0.5, u=0$. (Adapted from Iwasa & Pomiankowski 1995.)

Runaway exaggeration leads to semi-stable exaggeration of female preference and the male ornament. This is followed by a slow decline until runaway starts again but this time in a negative direction. This negative runaway stops and results in another semi-stable state in which preference and ornament are negatively exaggerated. Then a slow movement in a positive direction takes place until runaway is triggered again, this time towards positive values.

A second outcome is runaway to a stable equilibrium. The equilibrium is simply the cost–benefit maximisation for female preference given that male survival decreases with the fourth power,

$$\bar{p}=\left(\frac{ua}{\gamma b}\right)^{1/(\gamma-1)}, \bar{s}=\left(\frac{a}{4c}\bar{p}\right)^{1/3}. \tag{10.8}$$

This equilibrium is stable so long as the equilibrium mean preference ($\bar{p}$) lies beyond the point where runaway evolution is triggered. A number of factors promote cyclic evolution (Iwasa & Pomiankowski 1995). The most

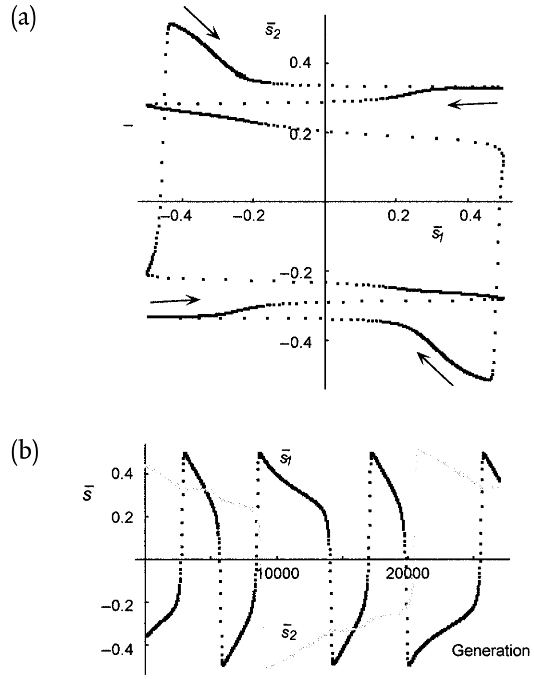

Fig. 10.5 Coevolution of two preferences for separate male ornaments. Evolution is represented as a phase-space of the mean male traits ($\bar{s}_1$ and $\bar{s}_2$) every 20 generations, and as $\bar{s}_1$ (black) and $\bar{s}_2$ (grey) values through time. The mean female preferences are not shown as they follow similar evolutionary trajectories. The cost of choosing s_1 is set to be larger than the cost of choosing s_2, causing $\bar{s}_1$ to change three times more quickly than $\bar{s}_2$. Parameter values are $a_1 = a_2 = 0.4$, $b = 0.001$, $c_1 = c_2 = 0.05$, $\lambda_1 = 1$, $\lambda_2 = 0.6$, $\theta = 0.2$, all $G = 0.5$. (Adapted from Pomiankowski & Iwasa 1998.)

important are weak mutation bias (u) and strong cost of choice (γ and b) which means that females gain little benefit from discriminating between males once runaway has stopped; and high additive genetic variation in female preference (G_p) which promotes Fisher's runaway.

The power of this result is better seen by increasing the dimensionality of the model to multiple female preferences for different male traits (e.g. colours, songs, feathers). This greatly increases the number of possible semi-stable states (Pomiankowski & Iwasa 1998). Each preference and ornament pair can reach either a stable equilibrium or cycle. If the mutation bias affecting each ornament is low, rather than simple cycles, we find a complex switching between different sexual phenotypes through evolutionary time (Fig. 10.5). The model predicts that allopatric populations will quickly diverge under sexual selection as small environmental differences are quickly amplified into large population differences.

Extreme natural selection – Handicap

The same cyclic evolution is possible when male traits are handicaps indicating either good genes or good parents (Iwasa & Pomiankowski 1999). A more extreme, fourth power, fitness function can easily be incorporated into the handicap model. There are two general outcomes. There are either stable positive and negative equilibria or the population cycles between semi-stable positive and negative exaggerated states (Iwasa & Pomiankowski 1999).

As with Fisher's runaway, the transition from stable to cyclic evolution is more likely if there is a high cost of preference (*b*) or a high additive genetic variance in preference (G_p). But cyclic evolution also requires that the handicap is ineffective: because the male ornament does not have condition-dependent expression (small $\bar{t}'$) and does not reveal heritable male quality (small *w*), or when male quality has no beneficial effect on female reproductive success (small σ_v^2 and *h*). Effectively this means that the more an ornament acts like a Fisher trait, the more it will cycle; and the more it acts like a handicap with condition-dependent expression, the more exaggeration will be stable.

Multiple preferences

We have already mentioned multiple ornaments above. These are typical features of many courtship displays. Here we consider how they have evolved in order to satisfy multiple female preferences. This topic is worth considering in more detail as it again brings out differences between Fisher's runaway and the handicap process (Pomiankowski & Iwasa 1993; Iwasa & Pomiankowski 1994).

To model the evolution of multiple female preferences, we will concentrate first on Fisher's runaway with two separate preferences. Consider two preferences p_1 and p_2, for two male traits, t_1 and t_2 respectively. Modifying Eq. (1), the evolutionary dynamics with Fisher's runaway become,

$$\begin{pmatrix} \Delta\bar{t}_1 \\ \Delta\bar{p}_1 \\ \Delta\bar{t}_2 \\ \Delta\bar{p}_2 \end{pmatrix} = \frac{1}{2}\mathbf{G}\begin{pmatrix} \beta_{t_1} \\ \beta_{p_1} \\ \beta_{t_2} \\ \beta_{p_2} \end{pmatrix} + \begin{pmatrix} -u_1 \\ 0 \\ -u_2 \\ 0 \end{pmatrix}. \tag{10.9}$$

G is a matrix of the additive genetic parameters (variance and covariance terms, details in Pomiankowski & Iwasa 1993). The effect of selection must now be considered for each ornament and each preference ($i = 1,2$),

$$\beta s_i = \frac{\partial}{\partial s_i}\ln W_m,\ W_m = \exp\left[\Sigma_{i=1}^{2} a_i\bar{p}_i(s_i - \bar{s}_i) - \Sigma_{i=1}^{2} c_i s_i^2\right],$$

$$\beta p_i = \frac{\partial}{\partial p_i}\ln W_f,\ W_f = \exp\left\{-b\left[\Sigma_{i=1}^{2}(\lambda_i p_i)^{1/\theta}\right]^{2\theta}\right\}. \tag{10.10}$$

The two ornaments are assumed to have independent effects on male attractiveness to females. Female preference for one male character does not extend to the other. We also assume that the cost of producing two ornaments is simply the sum of the cost of producing each trait independently. These linear assumptions are adopted to simplify the analysis.

The only non-linearity is in the cost of female choice. As before we assume that choice costs are minimized at $p_1 = p_2 = 0$ and increase with the strength of each preference with coefficients λ_1 and λ_2. Epistatic fitness interactions between the two preferences are measured by θ the joint cost of choice (Pomiankowski & Iwasa 1993; Iwasa & Pomiankowski 1994). If $\theta = 0.5$ then there is no interaction and the cost of each preference combines multiplicatively. As $\theta \rightarrow 0$ the overall cost is no more than the maximum when either preference is considered alone; whereas $\theta \rightarrow 1$ causes costs to combine in a greater than multiplicative manner and females using more than one preference face severe fitness loss.

Similar equations can be derived for the case of two preferences for two male handicaps, or one Fisher trait and one handicap (Iwasa & Pomiankowski 1994). In the multiple-handicap model we again assume that each male ornament has independent effects on female mate choice and male survival chances. We further assume that each ornament independently reveals male quality, so, by assessing two or more ornaments, females gain greater information about male quality.

When the joint cost of choice is small ($\theta \approx 0$), both Fisher's runaway and the handicap process lead to the exaggeration of both preferences (i.e. $\bar{p}_1 > 0, \bar{p}_2 > 0$). It is clearly beneficial for females to choose using two ornaments when there is little or no extra cost. Preference for a single male ornament is always invaded by a second preference for a different male ornament (Pomiankowski & Iwasa 1993; Iwasa & Pomiankowski 1994).

As the joint cost of choice rises ($\theta > 0.5$), the two processes give different outcomes. With Fisher's runaway (Pomiankowski & Iwasa 1993), females show strong preference for one ornament, with weak preferences for other male traits (i.e. $\bar{p}_1 > 0, \bar{p}_2 > 0$ and $\bar{p}_1 \gg \bar{p}_2$). The strong preference is for the male trait that gives the largest attractiveness benefit relative to the cost of choice. In contrast, with the handicap process (Iwasa & Pomiankowski 1994), females show strong preference for only one ornament. Preference for both ornaments is unstable and always degenerates to a single preference for one ornament (i.e. $\bar{p}_1 > 0, \bar{p}_2 = 0$). Either preference can be exaggerated, dependent on initial conditions. Once preference for a single male trait has evolved, other preferences cannot invade. The handicap process gives rise to local stability of existing preferences because the reliability of a signal increases with its cost. Hence as the size of an ornament increases, so does the benefit of choice. An established preference thus produces significant benefits that are greater than the benefits from choosing a novel, unexaggerated trait.

Another way of contrasting the two forms of sexual selection is by following the evolution of one preference for a handicap and a second preference for a Fisher trait (Iwasa & Pomiankowski 1994). With high joint cost of choice ($\theta > 0.5$) there is usually a mixture. The mixture contains strong preference for the handicap trait accompanied by weak preference for the Fisher trait. We expect preference for the handicap to show a much greater exaggeration because variance in direct benefits and mutation bias are likely to be much stronger on a trait with strong associations with quality (i.e. $(\sigma_v^2 h + w)\bar{t}' \gg u$). The strong handicap endpoint can be invaded by additional preferences for other Fisher traits but not by further handicap preferences.

Discussion

In this review, we have contrasted the contribution of Fisher's runaway and the handicap process in the evolution of sexual preference for male ornaments. These two hypotheses are really two extremes on a continuum. Fisher's runaway assumes that the male trait is purely attractive. So a female mating with a large ornamented male benefits only because her male offspring inherit the large ornament and thus are likely to have higher mating success in the following generation. To this the handicap process adds the idea that expression of the male ornament is condition-dependent. Given this, females gain an additional benefit when choosing males with larger ornaments, as these males have higher than average quality. This directly benefits the female when male quality affects her survival or fecundity (e.g. through male parental effort or male derived resources). In addition, when quality is heritable, the female benefits indirectly as her offspring inherit higher than average quality, and so have higher survival chances.

In the real world, male traits involved in mate choice simply do not fall into two types, Fisher and handicap traits. A better perspective is to view each ornament as having some degree of condition-dependent expression. The degree of this dependence will be determined by the condition-dependent cost function (k in Eq. (4a)). If the survival cost of bearing a larger ornament is very much greater for low quality than high quality individuals (large k), there will be strong condition-dependent expression. However, if quality has little impact on the survival chances of males with different ornament size ($k \approx 0$), there will be only weak condition-dependent expression.

Our goal has been to explain how exaggeration and diversity of sexual characters have arisen. Taking exaggeration first, our results suggest that stable exaggeration is more likely to be promoted by the handicap process (Iwasa & Pomiankowski 1994). We can combine the benefits of mate choice under Fisher's runaway and the handicap process (Eq. (3) and Eq. (6), setting $\gamma = 2$), to give an expression for the degree of exaggeration of female preference at a stable equilibrium,

$$\text{exaggeration} \propto \frac{a}{b}\left[u + (\sigma_v{}^2 h + w)\bar{t}\,'\right].$$

A similar expression governs the exaggeration of the male ornament.

The factors outside the brackets are common to both Fisher's runaway and the handicap processes. The coefficient a defines the effectiveness of the male ornament in causing increased mating success, and b defines the cost of female choice. The benefit of mate choice through Fisher's runaway depends on the degree of mutation bias (u). In the handicap process, the equivalent benefit term is $(\sigma_v{}^2 h + w)\bar{t}\,'$. There are three reasons why the latter is likely to be considerably larger. First, mutation bias is known to be strong on traits closely related to fitness (Iwasa *et al.* 1991, Burt 1995), so $w \gg u$. Second, we know that male behaviour can directly affect female reproductive success (e.g. parental care, infanticide, disease), leading to $\sigma_v{}^2 h > 0$. Finally, condition-dependence ($\bar{t}\,'$) is a common feature of exaggerated male sexual ornaments (Andersson 1994, David *et al.* 1998), so the handicap benefit term can potentially be very large. Though this comparison is an empirical question, we can tentatively conclude that the handicap process is likely to contribute more to equilibrium exaggeration than Fisher's runaway.

This conclusion needs to be placed in the light of our results concerning sexual trait diversity (Iwasa & Pomiankowski 1995; Pomiankowski & Iwasa 1998). Cyclic evolutionary change in sexual preferences and ornaments is a natural outcome of Fisher's runaway (Fig. 10.4). Two conditions are required for cyclic evolution. Selection on the male trait must be weak about the natural selection optimum but increase rapidly beyond a certain value, and female choice must be costly (Iwasa & Pomiankowski 1995). The male ornament and female preference undergo a series of repeated, rapid runaways interspersed with periods of semi-stable positive or negative exaggeration. If the model is expanded to multiple female preferences for different male traits (e.g. colours, songs, feathers), we find a complex switching between different sexual phenotypes through evolutionary time (Fig. 10.5, Pomiankowski & Iwasa 1998).

Fisher's runaway is likely to give rise to cyclic evolution because the benefit of choice is unlikely to be large, as mutation bias on traits is small (see above). Only when mutation bias is large will cyclic evolution be stopped and a stable equilibrium result (Iwasa & Pomiankowski 1995). However, if the male ornament has condition-dependent expression as predicted by the handicap process, a stable equilibrium is a far more likely outcome. If females benefit through good parent or good genes benefits, then cyclic evolution is less likely (Iwasa & Pomiankowski 1999).

Finally, we need to consider the evolution of multiple preferences for multiple sexual ornaments. We have shown that multiple ornaments are more likely to evolve through Fisher's runaway than the handicap process (Pomiankowski & Iwasa 1993; Iwasa & Pomiankowski 1994). The reason for this is easily stated. As a handicap trait becomes exaggerated, the cost of its production increases, and this increases the reliability of the trait to discriminate between males of different quality. So a greatly exaggerated (i.e. costly) ornament will reveal more about male quality than other less exaggerated traits. This means that the evolution of preference for one handicapping ornament will inhibit the establishment of further preferences for other handicaps. This restriction on the evolution of multiple preferences is not present when they evolve through Fisher's runaway (Pomiankowski & Iwasa 1993), as any trait is potentially attractive (i.e. preferred by females).

These results make predictions concerning the exaggeration and diversity of male sexual traits. We expect that the strongest preferences and greatest exaggeration will be seen in those ornaments with condition-dependent expression that act as handicaps which strongly reveal some aspects of male quality (e.g. goods genes or good parent). These traits should be relatively stable amongst closely related species. In contrast, ornaments with weakly condition-dependent expression, are likely to be subject to weaker preferences, be poor indicators of male quality and have evolved mainly through Fisher's runaway. We predict that these traits will be variable between closely related species.

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GEOFFREY A. PARKER *AND* MIKE A. BALL

11

Information about sperm competition and the economics of sperm allocation

11.1 Introduction

It is now almost three decades since sperm competition was defined in terms of competition between the ejaculates of two or more males for a given set of eggs (Parker 1970). That article reviewed the evidence in insects and suggested a variety of ways in which the selective pressure of sperm competition may shape a range of adaptations across behavioural, physiological and morphological levels. Sperm competition is now accepted as a discipline in its own right, and currently attracts considerable interest. In addition to a host of papers, there exist four books on the subject (Smith 1984; Birkhead & Møller 1992, 1998; Baker & Bellis 1995) and others are in preparation.

Interest has focused on both empirical and theoretical aspects of sperm competition, and our own contribution has mainly related to the formulation of a prospective theoretical basis. We wish in this chapter to summarise the current theoretical models and their predictions on one specific aspect of this work: the economics of sperm allocation by males in relation to the information available to them. We stress that our concept of 'information' is a broad one. We include information in the form of cues correlating with the risk or intensity of sperm competition, perceived by a given male at the time of mating, and also include 'information' in the sense of a 'self-knowledge' (an adaptive response in relation to a given male's personal circumstances or state). In order to do this we compare predicted sperm allocation patterns in the absence of information with those predicted under specific information regimes.

The theory underlying sperm competition has arisen mainly during the past decade or so. It derives from non-cooperative game theory, pioneered by Nash and others in the fifties and developed into evolutionary game theory by Maynard Smith (see review 1982). Sperm competition has game-like qualities because the sperm of a given male competes with the sperm of other males to fertilise a female's eggs. Thus the values of the characteristics of a male's ejaculate can be considered to be strategies. Usually the main characteristic under consideration is the number of sperm. The best number of sperm for a male to ejaculate depends on the numbers of sperm ejaculated by competing males. Fundamental to the analysis of sperm competition games is the notion that there is some fixed expenditure budget for a male, so that if more is expended on each ejaculate, less is available for other aspects of expenditure (such as finding new mates). In essence, there is a trade-off resembling (but not identical to) that for a bidder in an auction making decisions as to how much to expend in an individual auction relative to expenditure on finding and bidding in other auctions, when all bidders have a fixed amount of money to spend. Just as information about the risks from other bidders in the auctions will shape the optimal strategy in the economic case, so does information about risks from other males influence optimal sperm allocation strategy in sperm competition games. The females are analogous to the suppliers of the goods (i.e. the eggs) at the auctions: they want to get the best price (i.e. survival of their progeny) for their goods and to ensure that all the goods are sold.

Since the aim of the present chapter is to review the theory of sperm allocation under differing information conditions, the reader is referred to the original articles for details of the mathematical analyses. A broader review of sperm competition theory is given by Parker (1998), and some more recent developments are given by Mesterton-Gibbons (1999a,b), Fryer *et al.* (1999a,b) and Ball and Parker (2000).

11.2 Game theory models of sperm competition

A theoretical approach to sperm allocation (i.e. expenditure) under sperm competition was initiated by one of us (Parker 1982) and later extended as a series of 'sperm competition games' (reviewed by Parker 1998) to emphasise the link with evolutionary game theory. Sperm competition games are evolutionary games between rival males, whose ejaculates compete for the fertilisation of ova. Pay-offs depend on the ejaculation strategies played by other males in the population; analyses require an evolutionarily stable strategy (ESS; see Maynard Smith 1982) approach. The games have the following structure:

1 competing males have specified information and states;
2 males have a specified range of ejaculate strategies;
3 their ejaculates enter into competition; and
4 the sperm competition mechanism determines which sperm from each ejaculate are used randomly for fertilisation.

In the models outlined here, the female is assumed to exert no preference over the strategy being considered. Current empirical interest centres on the role of the female in determining the outcome of sperm competition (e.g. Eberhard 1996; review of Birkhead 1998a), but so far no theoretical analysis of female influences has been published, though models of such processes are currently in progress.

Most sperm competition games seek ESSs from continuously variable ejaculation strategies. In a population in which males play the ESS ejaculation strategy, x^*, all mutants playing $x \neq x^*$ must do worse than x^*, so the plot of the mutant fitness $W(x, x^*)$ rises to a peak at which the 'mutant' plays the ESS. We can therefore solve for the ESS by setting

$$\left[\frac{\partial W(x,x^*)}{\partial x}\right]_{x=x^*} = 0; \tag{11.1a}$$

subject to

$$\left[\frac{\partial^2 W(x,x^*)}{\partial x^2}\right]_{x=x^*} < 0; \tag{11.1b}$$

to ensure that x^* is a maximum (e.g. see Maynard Smith 1982).

We assume that there is a trade-off between ejaculate expenditure and mating expenditure. Expenditure on matings determines the number of matings a male achieves, and his ejaculate expenditure determines the expected value of each mating. Increasing ejaculate expenditure increases the gain per mating, but reduces a male's number of matings. Fitness is simply the number of matings, $n(x,x^*)$, times expected value of each one, $v(x,x^*)$:

$$W(x,x^*) = n(x,x^*) \cdot v(x,x^*)\,. \tag{11.2}$$

Mesterton-Gibbons (1999a,b) has proposed as an alternative the use of an additive function for fitness in which net fitness is the gains from a given copulation minus the costs of that copulation in terms of future matings. This additive approach to fitness is compared with the multiplicative approach in (11.2) by Ball and Parker (2000). Fryer *et al.* (1999a,b) use a quite different concept, in which a male must expend his available sperm during two discrete 'rounds' of reproduction and fitness is the sum of the expected pay-offs across the two rounds.

The exact forms of n and v depend on the game under consideration. Assume that each male has a fixed total energy budget of R units, and the average cost of obtaining each mating (finding a female, etc.) is C units (which is invariant for all males, and assumed to be at the ESS value for C). The cost per unit mass of ejaculate is D, so an ejaculate containing x units of seminal fluid costs Dx . Let $<x>$and $<x^*>$be the average ejaculate expenditures by a mutant and by an ESS player respectively. The ESS number of matings per male is thus $R\,/(C+D<x^*>)$, whereas a mutant playing $x \neq x^*$ achieves $R\,/(C+D<x>)$ matings. Hence the number of matings gained by the mutant male, relative to the population average, is

$$n(x, x^*) = (C+D<x^*>)/(C+D<x>)\,. \tag{11.4}$$

Function $v(x, x^*)$ depends on the mechanism of sperm competition, and we have modelled exposure to sperm competition as two extremes:
(i) *Risk models* – sperm competition between two ejaculates occurs with low probability q and, on $(1-q)$ occasions, only one male fertilises the eggs. Thus proportion q of all females mate twice, and $(1-q)$ mate once. If sperm competition obeys the raffle principle (Parker 1982), i.e. a male's fertilisation gain is proportional to his relative contribution to the set of sperm competing for the G eggs. As a simple example, under the risk model, if we seek a single ESS value x^* for all matings

$$v(x, x^*) = G(1-q)\frac{x}{x} + 2qG\left(\frac{x}{x+x^*}\right). \tag{11.5a}$$

Note that for each of the $(1-q)$ matings with a female that will mate only once, a male encounters q females which will mate again in the future and q females which will have already mated. The mean number of matings per female is thus $(1+q)$.

Analyses prior to Parker *et al.* (1997) related to risk defined as the probability, p, that a given male, when ejaculating, will face sperm competition from another ejaculate (see Parker 1982, 1984a,b, 1993; Parker & Begon 1993; Ball & Parker 1996). This is not equivalent to q, defined as the probability of occurrence of sperm competition in the population. In fact $p = 2q\,/(1+q)$, since there are $2q$ matings facing sperm competition out of every $(1+q)$ matings (Parker *et al.* 1997).

Risk models are most appropriate for internal-fertilising animal groups where females relatively infrequently mate with more than one male at the same reproductive episode, e.g. many mammals, some birds, some insects, etc.

(ii) *Intensity models* – sperm competition typically involves N competing ejaculates; for example, groups of N male fish ejaculate at the moment the female releases her eggs. Though not restricted to externally fertilising species, intensity models have been applied mainly to such groups. As a simple example, under the intensity model, if again we seek a single ESS value x^* for all matings, where sperm competition obeys the raffle principle

$$v(x, x^*) = G\left[\frac{x}{x + (N-1)x^*}\right] \tag{11.5b}$$

c.f. Parker and Begon (1993).

To enable a 'dimensionless' comparison (Charnov 1993), ESS ejaculate effort is generally expressed as E, the expenditure on the ejaculate relative to the total effort expended per mating:

$$E = \left(\frac{Dx^*}{C + D\langle x^*\rangle}\right). \tag{11.6}$$

Having outlined the logic of sperm competition games we shall now abandon further mathematical detail and simply state ESS solutions for the following sperm competition models differing in the information available to males at the time of mating. All models assume that sperm competition obeys the raffle principle (Parker 1982).

11.3 Zero information

We need first to establish how sperm competition will generally affect sperm allocation when males have no information. Where $n(x, x^*)$ and $v(x, x^*)$ follow equations (11.5a, 11.5b) males of a given species have no information about sperm competition – their ejaculation strategy is tuned by natural selection to the population level of q or N. The ESS for the risk model is

$$E^* = \frac{q}{2}, \tag{11.7}$$

(Parker 1982; Parker *et al.* 1997). The proportion of mating effort which should be expended on the ejaculate equals half the proportion of females that engage in 'double mating' (Fig. 11.1a).

The ESS for the intensity model is

$$E^* = \left(\frac{N-1}{N}\right), \tag{11.8}$$

(Parker *et al.* 1996). Thus group spawning species should allocate virtually all of their reproductive resources to sperm when the group size is large (Fig. 11.1b).

This 'zero information' model illustrates expected trends across species (Fig. 11.1). The first evidence for a positive relationship between sperm production and sperm competition came from studies of relative testis size in fish (Robertson & Warner 1978; Warner & Robertson 1978; see also Robertson & Choat 1974) and primates (Clutton-Brock & Harvey 1977; Short 1979; Harcourt *et al.* 1981). There is much evidence that relative testis size increases with sperm competition in many animal groups (see Parker *et al.* 1997; Birkhead & Møller 1998). We can now proceed to ask more detailed questions about individual behaviour within a species.

11.4 Information and the risk model

A. Loaded raffles with perfect information

Suppose that the fertilisation raffle is not 'fair' – it is 'loaded' so that a male is favoured in a given 'role' (e.g. first or the second male to mate). Specifically, sperm from male 2 is devalued by factor r; if (say) $r = 0.5$, each of male 2's sperm count only half of each of male 1's sperm in the raffle. We (Parker 1990a; Parker *et al.* 1997) have investigated this possibility within the context of the risks model, assuming that males 'know' their roles perfectly.

There are two possibilities: roles could be occupied either randomly (each male is equally likely to be male 1 or male 2), or constant (e.g. a given male is likely always to be in a given role). This critically influences the predictions. The ESS for 'random roles' is for each male to spend equally on the ejaculate, despite having perfect information as to which role he occupies at any given time, and despite the fact that each male also 'knows' whether his sperm are favoured or disfavoured (more details of this situation are given later in section C). However, this is true only if there is sufficient sperm to guarantee that all eggs are fertilised. Mesterton-Gibbons (1999b) has shown that significant sperm limitation will tend to cause more sperm to be allocated by the favoured male; if sperm limitation is present but negligible, the difference between the ejaculates will also be

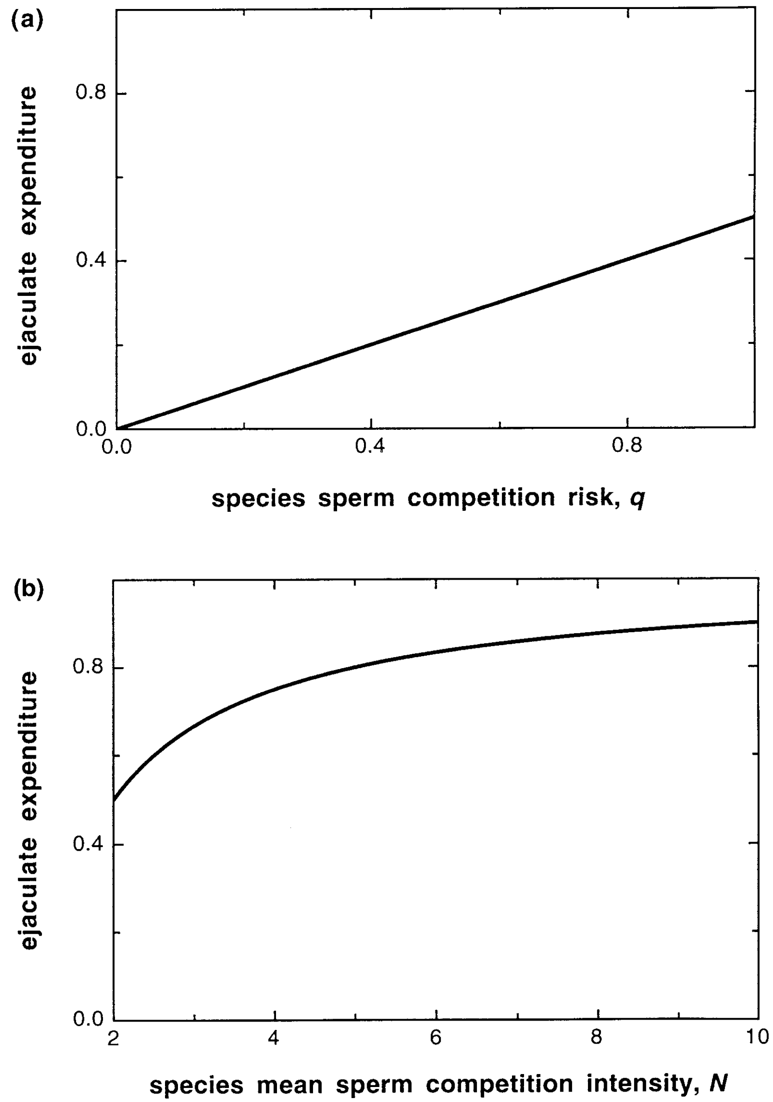

Fig. 11.1 Ejaculate expenditure with no information. (a) The risks model: ESS proportion of reproductive effort spent on the ejaculate plotted against the frequency of double mating in the species, q (from Eq. (11.7)). Modified from Parker *et al.* (1997). (b) The intensity model: ESS proportion of reproductive effort spent on the ejaculate plotted against the mean number, N, of males that are competing for a given set of eggs, for a given species (from Eq. (11.8)). (Modified from Parker *et al.* 1996.)

negligible (Ball & Parker 2000). In contrast, the ESS for constant roles is for the male in the favoured role to spend less on the ejaculate than the male in the disfavoured role (Parker 1990a): the greater the raffle's loading, the greater the disparity in ejaculate expenditures. This applies strictly only when given males are always in one or other role at the time of mating; when a given male may occasionally occupy the alternative role, he may or may not allocate more of less sperm in the disfavoured role (Mesterton-Gibbons 1999a; Ball & Parker 2000).

Simmons and Siva-Jothy (1998) review insect evidence relating to the predictions of the loaded raffle model, and find some support, though direct tests are not readily available. Circumstantial evidence is also found in mammals (Stockley & Purvis 1993). The random roles model may apply in 13–lined ground squirrels, *Spermophilus tridecemlineatus* (Schwagmeyer & Parker 1994). In the short reproductive season, oestrous females emerge from their burrows in early morning and a male usually arrives quickly, followed later by another and possibly a third: the modal number is two. The biology fits quite well with the assumptions of the random roles model that males typically overlap in time and can therefore have information about roles 1 and 2. The raffle is loaded: the value of mating second declines with time after the first mating (Schwagmeyer & Foltz 1990). Though arrival order is dependent on information about the female on the day before oestrus (Schwagmeyer *et al.* 1998), over the season a given male is equally likely to be first or second (Schwagmeyer & Parker 1994). No difference was detectable between first and second males in any behavioural measure which might correlate with the total sperm transferred, suggesting that the total ejaculate expenditure is equal, as predicted if roles are random.

B. Asymmetric information in raffles

What happens if one male has more information about the probability of sperm competition than his opponent? The previous game showed that loading a fertilisation raffle may or may not lead to unequal sperm expenditures, depending on role occupancy. We now examine what happens in the risk model under a fair raffle, but with one male having information that the probability of sperm competition is higher than that expected by his opponent (for details see Parker 1990b). This asymmetry of information can also lead to unequal sperm expenditures.

Consider the following situation (Parker 1990b). Males perform extra-pair copulations (EPCs) or sneak matings with a low probability per clutch of progeny. Sperm competition obeys a fair raffle, but one male (labelled male 1) has no information about sperm competition, so that his ejaculation strategy is shaped by the mean risk. The other (labelled male 2) 'knows' that when he mates he will always face sperm competition.

There are again random and non-random role versions. The 'EPC model' has random roles in that all reproductive males are paired to females, but all may perform extra-pair copulations (EPCs, Birkhead 1988) opportunistically with low probability (e.g. socially monogamous birds; see Birkhead & Møller 1992). The 'sneak–guarder' model is a non-random roles version in which given males are either sneaks (typically smaller, younger males) or guarders (typically larger, older males). Such dual-mating strategies are common (e.g. Dunbar 1982; Taborsky 1994). We again assume that each male 'knows' his role (EPC male or paired male; sneak or guarder).

Unlike the loaded raffle, ESSs are here very similar whatever the form of role occupancy. In both versions, male 1 with perfect information should spend more than male 2 with imperfect information (Parker 1990b). This disparity between males in roles 1 and 2 increases as sperm competition risk decreases. If the relative cost of sperm is the same in each role, then higher sperm expenditure in role 1 (EPC or sneak male) generates the further prediction that such matings should yield higher paternity. The average expenditure on ejaculates again increases with the average sperm competition risk across species.

Some evidence exists for these predictions. Male fish acting as sneaks have a higher relative testis mass (and sometimes higher absolute testis mass despite their smaller size, Petersen & Warner 1998) than guarding males of the same species. Sometimes the fertilisation success of EPCs in socially monogamous birds is much greater than expected from the relative number of matings, especially at low risk (Birkhead & Møller 1995). Zebra finch, *Taeniopygia guttata*, appear to generate greater sperm numbers when EPCs are most likely (Birkhead 1998b).

A difficulty can arise over deciding whether a sperm allocation difference derives from unequal information with unequal risk (present model) or from loaded raffle with non-random roles (previous model). As Stockley and Purvis (1993) note, their results on mammals could relate either to sneak–guarder effects or to non-random roles in a loaded raffle. It seems plausible that both effects could anyhow operate simultaneously.

C. Assessments of female risk status

Recent models have examined the possibility that, on encountering a female, a male may assess the risk that she is likely to present. Such models can become complex analytically; we give a brief summary here (for further details, see Parker *et al.* 1997; Ball & Parker 1998).

In its simplest form, the risk model allows a male, on meeting a given female, to make three possible decisions corresponding to the actual female states which can occur. He can therefore estimate that the female is in one of the following states:

(i) state 0 or 'no risk' (with probability $(1 - q)$ a female mates only once),
(ii) state 1 or 'future risk' (with probability q a female will mate now, and again in the future),
(iii) state 2 or 'past risk' (with probability q a female has already mated and will mate again now).

We can ask what a male should do when he assesses that one of these particular contingencies is more likely than the baseline expectation. We seek ESS sperm allocations that relate to each female state (0, 1, 2). In summary, the ESS at any given q is for a male to increase his ejaculate expenditure on assessing states 1 or 2. The more accurate his information, the more ejaculate he should expend with such females, and the less on 'no risk' females. This result is concordant with intuitive expectations that the more likely a male is to face sperm competition, the more he should ejaculate.

To dissect further, we outline three special cases.

(i) Perfect information

The opposite extreme from zero information (see equation 11.7; Fig. 11.1a) occurs when males have perfect information (see Parker *et al.* 1997). If able to discriminate accurately between females which will mate only once and those which will mate twice, males should expend an arbitrary minimum amount of sperm on meeting state 0 ('no risk') females, i.e.

$$E_0^* -> 0, \tag{11.9a}$$

and should expend an ESS effort of

$$E_1^* = E_2^* = \frac{(1+q)r}{(1+r)^2} \tag{11.9b}$$

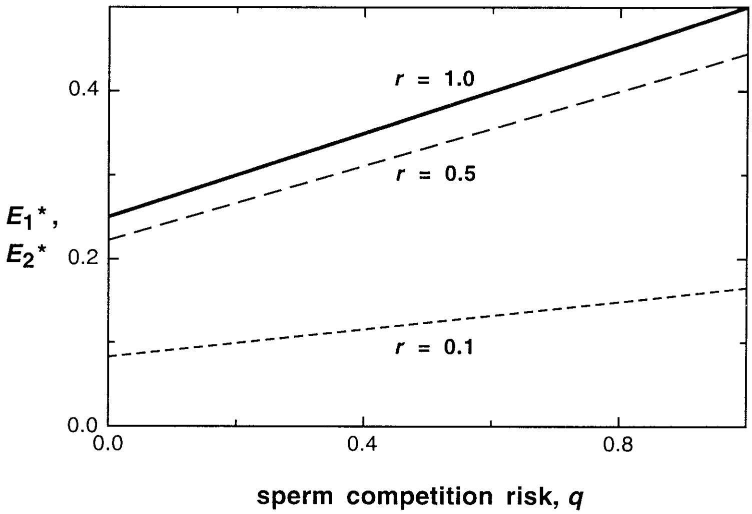

Fig. 11.2 Relation between ESS ejaculate expenditures, $E_1^* = E_2^*$, and the frequency of double mating in the population (risk q) when males have perfect information about the three female states, 0, 1, 2. The lines are for three levels of loading in the fertilisation raffle: $r = 1.0$ (bold line, fair raffle), 0.5 (each of male 2's sperm count as only half those of male 1), and 0.1 (each of male 2's sperm count as only one tenth those of male 1). The ESS expenditure for state 0 females (where there will be no sperm competition) is some arbitrary minimum expenditure $E_0^* - > 0$. (After Parker *et al.* (1997.)

on meeting state 1 or state 2 females (Fig. 11.2). The average expenditure is here equal to that of a population in which males have no information and is

$$E^* = \left[\frac{2qr}{(1+r)^2}\right]. \tag{11.10}$$

So relative testis size in the two populations should be the same whether males have perfect or zero information about females. Increased loading of the fertilisation raffle decreases the average expenditure, though the 'direction' of the loading (whether the first male or the second male is favoured) does not affect it if only the loading is altered.

(ii) Restricted recognition of states: partial information

Parker *et al.* (1997) analysed cases of 'partial information' where males can identify certain female states but cannot discriminate at all between others. Figure 11.3a represents a situation in which a male can recognise mated (state 2) females, but cannot distinguish between virgins (states 0,

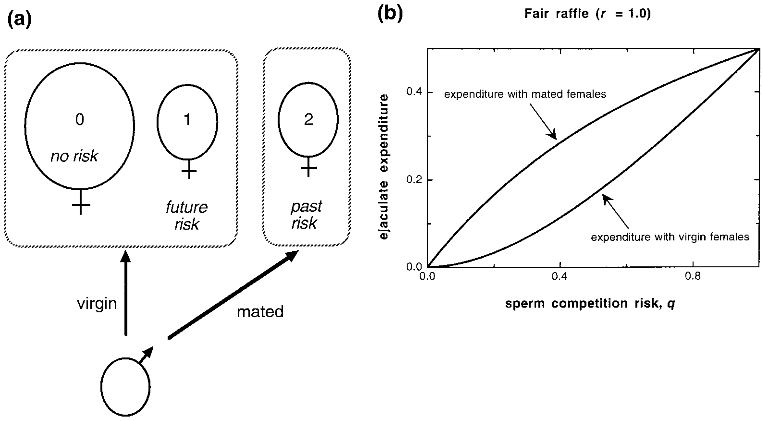

Fig. 11.3 (a) Schematic representation of the partial information model, in which a male can identify certain female states but cannot distinguish between others. In this example, a male can identify mated (state 2) females, but cannot discriminate between virgins that will not mate again (state 0 females) and those that will mate again in the future (state 1 females). (b) Ejaculate expenditures in relation to sperm competition risk in a species for the case of partial information shown in a, under the assumptions of a fair raffle. Males expend more with mated (state 2) females than they do with virgins (states 0, 1 females), following Eq. (11.11a) and (11.11b). (Modified from Parker 1998.)

1 females) which will (state 1) or will not re-mate (state 0). We obtained the following results. On meeting a virgin, a male should expend

$$E_{0,1}{}^* = \frac{q^2(1+q)r}{(q+r)^2}, = \frac{q^2}{(1+q)} \text{if } r = 1.0; \tag{11.11a}$$

and when he meets a mated female, he should expend

$$E_2{}^* = \frac{q(1+q)r}{(q+r)^2}, = \frac{q}{(1+q)} \text{if } r = 1.0; \tag{11.11b}$$

see Figure 11.3b. Where the risks are intermediate between the two extremes ($0 < q < 1$), males spend more on ejaculates with mated females, as intuition would suggest. If all females mate twice, on meeting a virgin a male should expend the same as if he meets a mated female. If q approaches 0, virtually no females mate twice, so, if a male meets a virgin, he should expend almost zero. This means that, on the vary rare occasion that a male meets a mated female, he need only deliver a tiny ejaculate to ensure high fertilisation success – hence both effort with mated females and effort with virgins converge to zero as risk, q, approaches zero.

A less plausible case of partial information occurs when a male cannot distinguish between state 0 and 2 females, but can recognise 'future risk' (state 1) females. For a fair raffle, we find that this model gives parallel results to one above: $E_{0,2}^*$ becomes equal to $E_{0,1}^*$, and E_1^* becomes equal to E_2^*. But, if the raffle is loaded, these equivalences remain only with the direction of the competitive loading reversed. To explain – the two equations for this 'future risk recognition' model equal the corresponding two above for the 'past risk recognition' model only if we replace r with $1/r$ (see Parker *et al.* 1997).

Some evidence exists for assessments of sperm competition risk available in a few internally fertilising species. For example, Baker and Bellis (1989) found that the number of sperm ejaculated by men increases with the proportion of time that they had been separated from their partner during the interval between copulations. The authors interpreted this as an adaptive response in the assessment of 'past risk' sense. Males may ejaculate more sperm in matings when a second male is present (rats, Bellis *et al.* 1990; the beetle *Tenebrio molitor*, Gage & Baker 1991; medflies *Ceratitis capitata* Gage 1991; a bushcricket *Requena verticalis*, Simmons *et al.* 1993), which can be interpreted as assessment of either past or future risk, or a combination of both. The Indian meal moth, *Plodia*, shows no reaction to the presence of a second male, but males transfer more sperm to females that have been mated previously, an effect which increases with the ejaculate size of the first male to mate (Cook & Gage 1995).

(iii) Mistakes

The essence of the 'mistakes in identification' models (Ball & Parker 1998) is that a male has imperfect information and so may misidentify the risk state of the female. For example, if he meets a mated (state 2) female, he has a certain chance of perceiving this as a state 0 or state 1 female (Figure 11.4a). Assuming that he has some information, he identifies the female state correctly more often than expected by chance.

The analysis is complex, but some general conclusions emerge. A male allocates more sperm when he assesses greater risk, and (unless risk is high) typically allocates more sperm when he can perceive this risk more accurately. Each strategic expenditure typically, but not invariably, increases with risk, and the average expenditure for the species always does. An interesting finding is that very small increases in perceived risk can result in large differences in sperm allocaton.

The model can at present be solved only for two special cases, representing zones towards the two limits of the range between zero and perfect

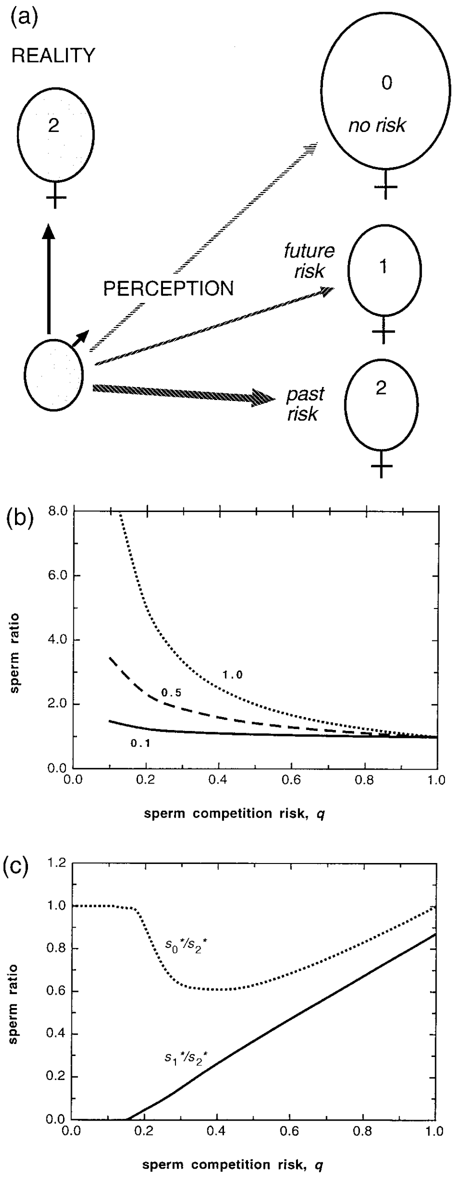

Fig. 11.4 (a) Schematic representation of the mistakes in identification model, in which a male may misidentify the state of a female. In this example, a male meets a mated (state 2) female (labelled 'REALITY'). His perception is imperfect, and, although he has a higher probability of identifying her correctly than expected by random chance, he sometimes makes mistakes and identifies her incorrectly as a state 0 or state 1 female. (b) Case where male cannot distinguish at all between virgins (states 0, 1), but has some ability (increasing with γ, from $\gamma = 0.1$ to perfect identification, $\gamma = 1.0$) to recognise state 2 (mated) females. Plot is the ratio of sperm delivered to females assessed as state 2 relative to that for females identified as virgin (states 0, 1). (c) Case where male can identify mated (state 2) females perfectly, and has limited ability ($\gamma = 0.1$) to distinguish between states 0 and 1 females, in a raffle with $r = 1.5$. Plot is the ratio of sperm delivered to females assessed as state 0 or 1 relative to that for females identified as mated (state 2). (Modified from Ball & Parker 1997, where further details are given.)

information. Specifically, towards the zero information limit, we have analysed the case where males have no ability to distinguish between two of the three female states, but have some ability to identify the third. Towards the perfect information limit, we have examined the situation where males can identify one female state perfectly, and also have some ability to distinguish between the other two states.

To demonstrate, first consider the case where males have no information at all about virgins (states 0 or 1), but have some ability to recognise state 2 (prior mating). We seek two strategies, s_2^* and $s_{0,1}^*$, corresponding to the sperm numbers ejaculated to females perceived to be 2 and 0,1 respectively. For example, in Figure 11.4b we plot the sperm ratio ($s_2^*/s_{0,1}^*$) in relation to the species level risk, q, at three different levels of assessment ability (increasing with parameter $\gamma = 0.1$, 0.5, 0.9), for a fair raffle ($r = 1.0$). We find that males expend more sperm on females perceived to be in state 2, and increasingly so as their assessment ability increases. The difference in relative sperm numbers decreases with q, but expenditures increase with q, and the absolute expenditure difference is greatest at intermediate q.

Now consider the case where males can identify state 2 (mated) females, and have some ability to discriminate between the two forms of virgin (states 0 and 1). We now seek the three sperm number strategies, s_0^*, s_1^*, and s_2^*, corresponding to the sperm ejaculated on estimating states 0 or 1, or identifying state 2. Figure 11.4c plots the two sperm ratios, (s_0^*/s_2^* and s_1^*/s_2^*) in relation to risk, q. The ability to discriminate between 0 and 1 female states is relatively poor (parameter $\gamma = 0.1$), and the raffle is loaded against the first male to mate ($r = 1.5$). The results are not intuitively obvious. At low levels of risk, q, males spend an arbitrary minimum amount of sperm on females perceived to be in state 0, and (perhaps oddly) equal amounts on females perceived (often incorrectly) to be state 1 as those identified with certainty as state 2. This effect prevails for all risk levels up to that at which s_0^* increases from its arbitrary minimum, at higher risk levels sperm number s_1^* is always below s_2^*, and s_0^* increases from zero but is always less than s_1^* and s_2^*. The absolute sperm expenditures increase with q (see Ball & Parker 1998).

It is difficult to find evidence for these models because of the problem of knowing how likely males are to make mistakes in perception of female states. We offer but one prospective candidate. It seems rather unlikely in species often living in dense aggregations that the cue ‘presence of a second male at the time of mating’ could increase information about risk very significantly. However, a large increase in sperm numbers can sometimes be detected (e.g. more than doubling of sperm numbers in medflies, Gage 1991, and *Trilobium* beetles, Gage & Baker 1991); it is tempting to suggest that this could relate to the finding that small increases in perceived risk can result in large differences in sperm allocation (Figure 11.4c).

11.5 Information and the intensity model

When sperm competition is intense with several competing ejaculates, the risk approach is inappropriate; we must turn to an alternative such as the intensity model, which is usually couched in terms of group spawning fish, with each of N competing males ejaculating simultaneously at the moment the female releases her eggs. It applies equally to internally fertilising species where N males mate with a female at about the same time.

There have been two approaches to intensity models, depending on whether fertilisation approximates to an instant process (all eggs fertilised simultaneously), or whether fertilisation occurs continuously over a longer time period during which some of the sperm may die before fertilising eggs.

A. Instant fertilisation

The ESS for zero information, in which males cannot estimate the number of competitors and sperm allocation is shaped only by the mean N for the species, has already been given in Eq. (11.8); ESS ejaculate expenditure increases asymptotically with sperm competition intensity across species (see Fig. 11.1b).

Parker *et al.* (1996) also examined two cases where males can assess the number of competing ejaculates. In the first, males have very limited information and are able only to estimate whether the number of competitors is greater or less than the species-level average number, N. When, on average, N_H males are present in conditions perceived as 'high competition', and N_L males in 'low competition', and $s_H{}^*$ and $s_L{}^*$ are the ESS sperm numbers allocated under the two conditions ('high' and 'low' respectively), the ESS sperm ratio is

$$\frac{s_H{}^*}{s_L{}^*} = \left(\frac{N_H - 1}{N_L - 1}\right)\left(\frac{N_L}{N_H}\right)^2. \qquad (11.12)$$

Note that if N_H and N_L are large, the sperm ratio approximates to N_L/N_H: counterintuitively, and, for a wide range, more sperm should be shed under low than under high competition.

This unexpected result was confirmed in a parallel model of perfect information (males can respond to the exact number of competitors present; Parker *et al.* 1996). To construct such a model requires an assumption about the distribution of males at spawnings. If the number of males, N_i, present at spawning i follows a Poisson process, the ESS expenditure for a male assessing N_i is:

$$E_1{}^* = \left[\frac{(N_i - 1)}{N_i{}^2}\right]N, \tag{11.13}$$

where N is the species average number of males present (i.e. across all spawnings). Fig. 11.5a plots $E_i{}^*$ against N_i, for three species differing in N. Despite the fact that ejaculate expenditure *increases* with the average intensity of sperm competition in a species, for all $N_i > 2$, males *decrease* their expenditure within a species as the local intensity, N_i, increases. Maximum expenditure occurs at $N_i = 2$. If $N_i = 1$, there is no sperm competition, and an arbitrary minimum sperm number is released, as in the risk model with perfect information.

Parker *et al.* (1996) found that the *average* ejaculate expenditure in this model with perfect information is identical to one with zero information, paralleling the similar conclusion above for the risk models. Thus average expenditure across species rises asymptotically, conforming to Eq. (11.8). Why does average expenditure increase across species – but local expenditure decrease within a species – with sperm competition intensity? The first effect is a general one found in all models and is anticipated intuitively. The second (within species) effect is perhaps best explained in terms of a human analogy: the value of buying extra tickets in a raffle for a fixed prize becomes greater the fewer the competitors. Note that the risk models deal with the range from only one mating (i.e. no sperm competition, $N_i = 1$) to just two matings (i.e. $N_i = 2$); across this range the present model also shows increased expenditure (Fig. 11.5a). Following the raffle analogy, it pays to buy a single ticket (the arbitrary minimum) if there are no competitors, and many tickets if there is just one competitor. There is no contradiction between the two sorts of model; they analyse different parts of the sperm competition spectrum.

Thomaz *et al.* (1997) found that the relative success of each salmon parr (in spawnings where several parr and one anadromous male compete) declines with the number of parr, a result which may be interpreted in terms of the predictions in Fig. 11.5a.

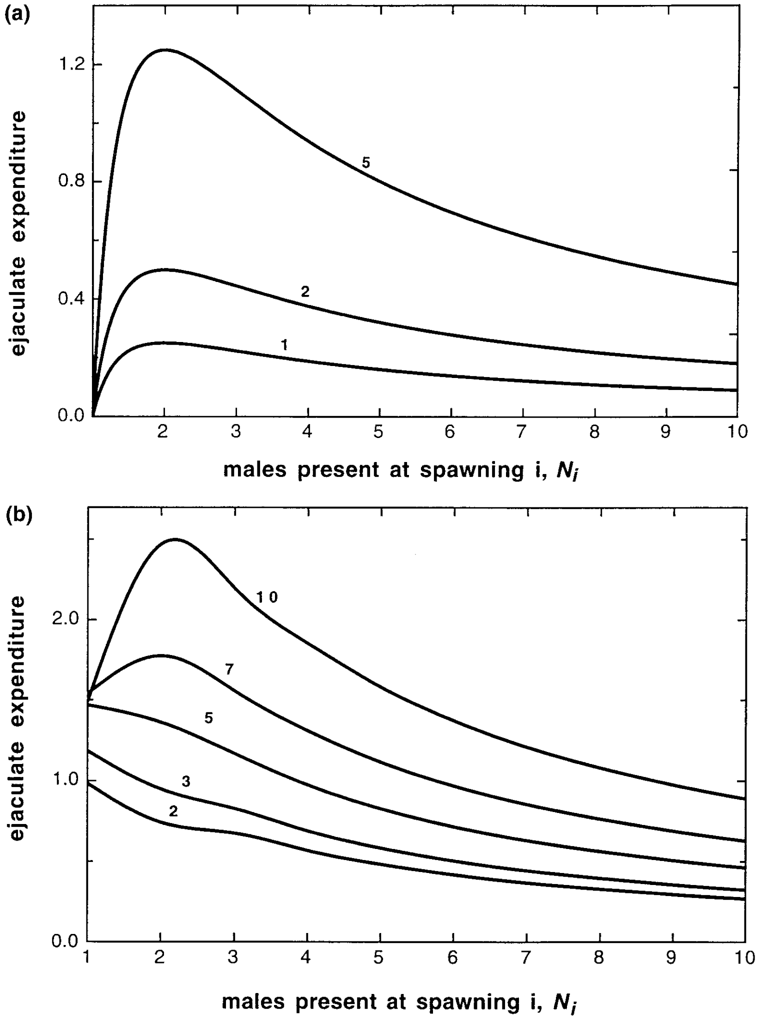

Fig. 11.5 Ejaculate expenditure (relative to the average total reproductive effort per spawning) plotted against the number, *Ni*, of males competing at spawning of type i for perfect information under the intensity model. (a) Expenditures under the instant fertilisation assumption, following Eq. (11.13). The curves are for three different species which are identical except for the mean number of males present at a spawning: $N = 1, 2$ and 5 (after Parker *et al.* (1996). (b) Expenditures under the continuous fertilisation model, assuming that the propensity for fusion of gametes is low (see Ball & Parker 1997 for parameter values and further details). The curves are for three different species which are identical except for the mean number of males present at a spawning: $N = 2, 3,$ 5, 7, and 10. (Modified from Ball &Parker 1997.)

B. Continuous fertilisation

This version of the intensity model has exactly similar assumptions, except that the sperm of N_i males compete continuously until all eggs are fertilised, or all the sperm have died. It has been employed mainly towards understanding the simultaneous evolution of optimal size (mass) of individual sperm and number of sperm in an ejaculate (Ball & Parker 1996, 1997). A sperm's longevity is assumed to be affected by its mass. In a model exactly analogous to the one above, Ball & Parker (1997) examined the case where males at a given spawning can regulate the number of sperm they ejaculate, but not the sperm mass. Sperm mass can change through evolutionary time but cannot be altered in response to local conditions in the way that sperm numbers can. Males have perfect information about the number of competitors, N_i, at spawning i, and their strategy is also influenced by the species-average number of males at spawnings.

The results are again that (i) ejaculate expenditure should increase with the average level of sperm competition viewed across species, and that (ii) within a species ejaculate expenditure always decreases as N_i increases above 2 (as before). But we now find that within a species, ejaculate expenditure can decrease as the number of competing ejaculates increases from just 1. This can occur only if fertility (measured as the number of eggs fertilised by the time that all sperm have died) is sufficiently low, which requires a relatively low intrinsic propensity for fusion of the gametes, and low average numbers of competitors, N. An example is shown in Figure 11.5b, in which expenditures decrease from $N_i = 1$ even up to $N = 5$. This difference from the instant fertilisation model arises because, under continuous fertilisation, optimal ejaculate characteristics can be defined for the case where there is no sperm competition (Ball & Parker 1996, 1997; see also Shapiro & Giraldeau 1996). The ESS for zero competition ($N_i = 1$) maximises the total distance travelled by the entire ejaculate in its lifetime; this contrasts with the instant fertilisation model above, in which males are assumed to ejaculate an undefined arbitrary minimum sperm number in the absence of competition. Thus, where fertilisation is so slow as to result in high infertility, it can be best to expend most if there are no competitors at all, a result which is impossible to generate under the assumption that all eggs are fertilised instantly in all conditions.

Despite the fact that males are predicted to decrease sperm numbers when spawning in large groups, fertility nevertheless increases with increasing group size, favouring female choice of high male numbers at spawning. This generates sexual conflict, since males do better when there are no competitors.

11.6 Concluding remarks

This review demonstrates how careful one must be when making predictions within and across species. The results of the last model are radically different depending on whether the model relates to the view across species, or to the view within a species. There is little doubt that the sperm expenditure should increase across species with increases in sperm competition risk or intensity. All models so far investigated have generated this result. But this across-species prediction clearly cannot be generalised to interpret within-species cases; in the last model expenditure declines with sperm competition intensity, at least for the range $N_i \geq 2$ (Parker *et al.* 1996).

The present review has covered only those systems in which the mechanism of sperm competition follows some form of raffle, fair or loaded. Systems not obeying the raffle principle are known to occur; an example concerns sperm displacement which is common in insects. Much remains to be investigated through the application of the approaches reviewed here to sperm displacement systems. Possibly the most studied example, both theoretically and empirically, of how a male's phenotype should influence his sperm allocation pattern, comes from studies of optimal copula duration in the dung fly, *Scatophaga stercoraria*. This has been omitted because it has been featured in two previous reviews (Birkhead & Parker 1997; Parker 1998); it gives good evidence that sperm allocation is tuned to a male's phenotypic state in quite a precise manner.

The search for female influences on sperm competition outcomes has dominated the empirical studies over the past several years. Despite enthusiastic marshalling of the evidence for female control and sperm preference by females (e.g. Eberhard 1996), much of it is flawed, and some effects can be explained by purely male differences (see Simmons & Siva-Jothy 1998). Nevertheless, plausible mechanisms have been proposed which could, in principle, allow females to influence sperm competition and hence influence paternity (see papers in Birkhead & Møller 1998). It is clear that there will often be sexual conflict in the sense that the mating or ejaculatory strategy which is best for a male need not be best for the female (Parker 1984a; Stockley 1997).

It is currently an exciting phase in the study of sperm competition and sperm allocation. One of the real problems concerns measuring natural ejaculates, either in the female (which typically means killing the female after mating), or for external fertilisers, in the external medium. It is especially difficult to measure ejaculates from more than one male, but some progress can be made by radio-labelling with different isotopes (e.g. Simmons *et al.* 1999). There is a continuing need for theoretical development, and for empirical support, and this is a field where progress is being achieved by the synergistic interplay of theoretical and empirical approaches. Data without theory is meaningless, but sometimes theory can proceed into realms of fantasy beyond the data. Very often, theoretical development is much hampered by lack of hard evidence: without some factual basis, it is impossible to begin modelling, or even to ask the appropriate theoretical questions. It is possible that we have been at this stage for some time with female influences on sperm allocation, though perhaps a picture is now gradually beginning to emerge.

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ROBIN I. M. DUNBAR

12

The economics of male mating strategies

The mammalian strategy of internal gestation followed by lactation imposes severe constraints on what males can do in terms of parental investment. This asymmetry in the processes of reproduction results in male mammals placing disproportionate emphasis on mating strategies and less on parental care than is typical of most other taxa. Although male mammals can contribute indirectly to parental care (e.g. by defending a feeding territory for the females(s) or acting as an anti-predator defence), this only remains an option where females can gain a net benefit from associating with males relative to the foraging costs that additional animals must inevitably impose on them.

This asymmetry in reproductive biology has one important implication for mammalian social systems. In birds, it is not uncommon for males to arrive first on the breeding ground. Having partitioned the available space among themselves, they settle on their territories to await the arrival of the females who then choose among them. While a similar pattern can be observed in those mammals that adopt a lek mating system (notably some deer, antelope and pinnipeds), the reverse is probably more typical of many mammals (and most primates). In a classic experiment, Charles-Dominique (1977) released a number of dwarf galago (*Galago demidorvii*) into a forest in Gabon. He found that the population developed its own natural structure in a surprisingly ordered manner. First, the females established their ranges; once they had decided how to distribute themselves, the males then mapped themselves onto the female distribution. This pattern is largely a reflection of the fact that, in general, male mammals can make only a limited contribution to a female's rearing effort; as a result, coalitions with other females may have more impact on a female's fitness, thus making female grouping patterns of greater interest to females than their relationships with males.

In effect, male mammals are left with what is essentially an optimal foraging problem: the females form a set of patches of varying size (number of females) and richness (likelihood of females being in oestrus) scattered around the environment and the males have to decide how to distribute their time among these patches. Optimal foraging theory suggests that this will depend on the return rate (measured here in terms of number of fertilisations per unit time), which in turn depends on the search costs (here, the travel time between female groups) and the handling time (here, the delay until the next female with whom the male can mate comes into oestrus, including time required for both fighting with other males in order to gain access to those females and mate-guarding after copulation). Both these key variables are influenced by female grouping patterns (i.e. patch size) and female reproductive patterns (i.e. patch richness).

Emlen and Oring (1977) pointed out that male mating strategies can often be understood in terms of males' abilities to monopolise access to oestrous females. Where females live in groups, it may pay individual males to monopolise them (female-defence polygamy); alternatively, it may pay males to defend areas which females frequent (resource-defence polygamy) since excluding rivals from an area may ensure that the territory-holder has exclusive mating access to all the females on his territory if and when they come into oestrus. Dunbar (1988) showed that whether a male could defend a group of females (or a territory) should depend on both the number of females in the group (territory) and their reproductive synchrony. Individual males could defend large groups of females only if the females' reproductive cycles were unsynchronised: a significant degree of synchrony resulted in there being too many females in oestrus at any one time for the male to be able to prevent rivals from gaining access to them.

In this chapter, I explore the implications of these ideas for the mating strategies of male mammals. For convenience, however, I shall focus on specific primate and ungulate examples. I shall try to show that, even in those cases that are characterised by a significant degree of male parental care, a great deal of male behaviour can be understood in terms of a choice between staying in the current patch (female group) or leaving to search for another patch (a roving male strategy). I use a number of relatively simple economic models to assess the costs and benefits of alternative strategies for different strategies that males might opt for. My strategy is to begin with the simplest possible situation (where females live solitarily) and then progressively add additional variables in order to explore more complicated social arrangements.

It is important to note that I have made no attempt to consider the females' interests in any of these analyses. This is not because I consider them to be unimportant, but rather for purely heuristic reasons so that we can see the males' decisions shorn of all considerations other than the bare minimum. This provides us with a kind of testbed against which to evaluate the actual behaviour of the animals. As with all modelling approaches, I thus begin by making the fewest possible assumptions about the situation. If my simple model is enough to explain most of the variance in behaviour that we see, then we know all there is to know. If the models do not account adequately for the observed patterns of behaviour, then the unexplained variance becomes the issue of crucial interest: what else do we need to add into the model in order to account for the rest of the variance in the animals' behaviour? In many cases, the roles and interests of the females will turn out to be crucial, but it is essential to begin with the simplest possible situation which assumes that females play no immediate role and are simply passive recipients of the males' decision choices. The assumption here is not that females have no interests in their own reproductive success, but rather that the mating decisions of the males have no effect on the females' performance and hence that the females can ignore them.

Dispersed females

If the costs of group living are high relative to the benefits that derive from it, then females will forage solitarily and distribute themselves around the habitat in a more or less even fashion. The problem that males then face is whether it is more profitable to pursue a roving male strategy that will allow them to mate with many females or to be 'social' and stay with one female. The latter strategy (in effect, monogamy) has the merit of ensuring that the male will have mating access to the female if and when she does come into oestrus. The problem for slowly reproducing species like primates is that a male may have to wait a very long time for a female to come into oestrus. In apes, this could be as long as 4–5 years. Would the male still do better to rove or should he stay with his female?

Two key factors need to be considered here. One is the male's ability to gain access to females. Since this is largely a consequence of his ability to defend a territory that encompasses the ranges of several females, this reduces to the simpler question of how large an area a male can actually defend. The second consideration is the number of females within that territory that a male can expect to encounter if he adopts a roving male strategy.

A roving male's ability to monopolise access to the females in a population depends on his ability to keep rivals away. He can do this either by dominating individual males in the immediate vicinity of oestrous females (as male goats do, for example) or he can do it by defending a territory in which he keeps rivals away from all the females. Since territorial behaviour provides a simpler bounded solution to the problem of access, I will consider the question only in these terms for the moment. However, it is worth pointing out that a male could pursue a nomadic roving strategy in which he searched aimlessly throughout the continental landmass he lived on without altering the basic form of the decision he has to make. Territories may be useful in that (a) they confine the males' ranging to a familiar area and (b) they enable the male to reduce the amount of fighting he has to do to keep rivals away from his females.

We can answer the first of the two questions we posed above relatively easily by exploiting a result originally obtained by Mitani and Rodman (1979). They argued that the ability to defend a territory was largely a function of the extent to which animals could patrol their territories in order to detect and drive out intruders (see Box 12.1). We can use their result to estimate the largest area that a male can successfully defend, and then use this in turn to determine the number of females he can expect to find on his territory, given the typical ranging area required by a female to provide her year-round foraging needs.

Van Schaik and Dunbar (1990) used this approach to assess the functional significance of obligate monogamy in gibbons (*Hylobates* spp.). Using data from 11 gibbon populations, they found that, in principle, males could defend territories that were typically 2–8 times larger than those they actually did defend. The only exceptions were two populations of the more folivorous large gibbon, the siamang (*H. syndactylus*). If we assume that females and their dependent young require two-thirds of a normal gibbon territory to provide the resources they need for successful survival and reproduction, then we can calculate the number of extra females occupying the territory that a male would be able to monopolise while providing a defended resource area for each female. The number of females that a male currently associates with (one in monogamous mating systems) provides the baseline for comparison: in the course of a normal reproductive cycle (i.e. the average interbirth interval), a social (i.e. monogamous) male would obtain just one fertilisation. How many more fertilisations would a roving male expect to obtain during the same time interval?

Box 12.1 The Mitani–Rodman territoriality index

Arguing from basic geometric principles, Mitani and Rodman (1979) suggested that a group's ability to defend its territory was likely to be a function of its ability to patrol the area so as to detect and eject intruders. They suggested that the ratio of range size to day journey length might be a reasonable measure of defendability and proposed the following index:

$$D = d/(4A/\pi)^{0.5}. \tag{1}$$

where D is their defendability index, d is the day journey length and A is the size of the ranging area, with A and d measured in the same units. They were able to show that territorial species of primates can be distinguished from non-territorial species by a function $D \approx 1$. Very crudely, territories appear to be defendable providing an animal (or group) can cover enough of its range area during the course of the average day's ranging to be able to travel from one side to the other at least once.

Mitani and Rodman (1979) have been criticised on a number of grounds, both theoretical and empirical, but most of these criticisms have been based on misunderstandings. One misunderstanding has been the assumption that the value $D = 1$ has some biological meaning. In fact it does not: it was an empirical finding that resulted from their use of range area as the basis for calculating an index of the animals' ability to patrol the territory. Had Mitani and Rodman conceived their analysis in terms of territory perimeters, the equivalent criterion for successful territorial defence would have been $D = 1/\pi$. The Mitani–Rodman finding simply observes that an animal's ability to defend its territory is related to the length of its typical day journey relative to the size of the territory. This should not necessarily be taken to imply that animals defend their territories by literally shuttling backwards and forwards across them, as some have assumed; rather, it is simply an index of the mobility of the animals (and thus the proportion of their territory area that they are likely to monitor during a given time interval).

None the less, it might be argued that animals in fact defend their territories by checking the perimeter zone for intruders, and not the

Box 12.1 (*cont.*)

interior. The effectiveness with which they can do this will depend on the frequency of visits to the perimeter zone as they wander about the territory during the course of feeding. Lowen and Dunbar (1994) considered this biologically more realistic model and derived equations from those for gas dynamics to estimate the frequencies with which a randomly moving group (or animal) might be expected to encounter segments of boundary. Although the Lowen–Dunbar index of defendability afforded a significant improvement over the Mitani–Rodman index in its ability to discriminate between territorial and non-territorial species (it accounted for about half the unexplained variance in the original Mitani–Rodman analysis), the conclusion from this analysis is that Mitani and Rodman were basically right.

One factor that neither model considers, however, is the density of rivals. The defendability of an area will depend not just on its size relative to the animals' ability to visit and monitor the perimeter, but also on the rate at which intrusions occur. When the number of intruders is low, animals may be able to defend a larger area than when the rate of intruders is high. It would be easy to factor this into these models of territoriality, though no one has yet done so.

The important conclusion is that Mitani and Rodman (1979) were sufficiently correct for their formulation to be used to estimate the maximum area that a male can defend, all other things equal. We can do this simply by setting $D = 1$ (the minimum required for successful defence of a territory) and then inverting Eq. (1) to express the defendable area in terms of the observed day journey length:

$$A_{max} = 0.25\ \pi d^2.$$

where A_{max} is the maximum area that a male can defend.

According to the van Schaik–Dunbar analysis, by staying in a monogamous relationship with one female, most male gibbons are incurring an opportunity cost of between 0.4 and 6 *extra* females (and hence the equivalent number of additional offspring *per reproductive cycle*). Dunbar (1995a) obtained similar results from an analysis of callitrichids, a group of small South American monkeys with a largely monogamous mating system.

The fact that males prefer monogamy over roving male polygamy in these cases implies a significant selection pressure in favour of investing in a pairbond of at least equivalent magnitude. Males must be contributing something quite substantial to the female's ability to produce and rear offspring successfully. In other words, even though a polygamous male could expect to sire between 1.4 and 7 offspring per reproductive cycle in the gibbon case, he will lose so many of these that his *net* reproductive output measured in terms of surviving offspring will be less than one (the number he gets by being monogamous). On the basis of a detailed analysis of predictions from a set of four alternative hypotheses, van Schaik and Dunbar (1990) argued that the empirical evidence points towards the risk of infanticide as the key factor, with predation as the most plausible alternative.

Notice that, in this analysis, the model provides us with a null hypothesis against which to evaluate the actual performance of an individual male. In effect, the model gives us the worst case condition, namely the payoff that would accrue to the male if he simply ranged at random around his territory. If the male uses other strategies for increasing the rate at which he locates females (e.g. by targetting areas where females are known to congregate, such as fruiting trees) or if females behave in such a way as to provide the male with information on their receptiveness, he may do better than the model predicts. If the model predicts a higher payoff than the social strategy, then the claim that the male does better by roving is all the stronger; in the case where a male does better by being social, then the payoff to the targetted roving strategy will have its limit at the mean female group size (i.e. the payoffs for the social and roving strategies will converge).

One counter-argument to this analysis might be that it ignores the fact that males who opt for polygamy will encounter resistance from other males in the population: monogamy may thus be the default strategy when males are unable to keep rivals out of larger territories. I shall have more to say about the male's behaviour in the presence of rivals in a later section. For present purposes, however, it is enough to note that polygamy (and especially roving male polygamy) is usually associated with sexual dimorphism in mammals, and especially so in primates and ungulates (Alexander *et al.* 1979). Any marginal differences in RHP (resource holding potential) that allow one male to hold a slightly larger territory than the other males in the population will very quickly spread through the population as this male's descendents come to dominate the gene pool in future generations. Since body size is the principal factor influencing RHP in most of these species, this will lead to a correlated increase in both sexual dimorphism and polygamy. In other words, this problem does not need to be taken seriously.

Females in groups

In the previous section, we considered only the case where females live and forage on their own (i.e. female group size is one). If females choose to live in groups (the equivalent in conventional optimal foraging models of an increase in patch size), what effect does this have on the male's decisions?

We can examine this by asking whether males would do better by associating with the female groups (i.e. being social) or by pursuing a roving male strategy in which they searched at random for female groups and stayed with each only so long as there was some chance of a female being in oestrus (or at least of coming into oestrus within some specified time period). We can use the 'gas model' (so called because it is based on the equations for gas dynamics from physics) to estimate the number of females that a randomly searching male could expect to meet (and fertilise) within a given period of time, given the density and distribution of females in the habitat, the area of the search path he carves out (determined by the distance he travels during the day and the width of his search distance either side of that path) and the likelihood that an individual female will be in oestrus (see Box 12.2). In effect, it asks: how many females in oestrus will he encounter if he searches a given proportion of his total range area (or territory) per day during the course of an average interbirth interval?

Once again, the reproductive cycle (defined as the mean interbirth interval) provides a convenient time unit for analysis, since each female will produce one (and only one) litter during this period: a social male who stays with a group of females throughout the reproductive cycle will gain exactly one conception for each female in the group during that time interval. The expected number of females fertilised by a social male will therefore be identical to F, the number of females in the group. If the

Box 12.2 The gas model of male mating strategies

The gas model uses the equations from the physics of gas dynamics to model the behaviour of randomly searching males. It provides a baseline against which the behaviour of males pursuing more structured mating strategies (targetted searching, social males) can be evaluated. In effect, the model provides the worst-case situation of what a male who has no information about the location and density of receptive females can expect to achieve in terms of mating success if he simply searches at random through his home range. The payoff for a randomly searching male (measured in terms of the numbers of females fertilised) is given by:

$$E(f) = F_g N_f (K2rd/A_{max}),$$

where $E(f)$ is the number of females a male can expect to fertilise in a typical reproductive cycle (defined by the mean interbirth interval), $K2rd/A_{\mathrm{max}}$ is the probability that a male will find a group of females when searching at random (from the gas model, with a day journey length [or *velocity*] of d km, a detection distance either side of the line of travel of r km and a range size of A_{max} km^2) in a reproductive cycle of length K days, N_f is the number of female groups in the male's ranging area and F_g is the expected number of females in each group who will be in oestrus when he locates the group. F_g is the expectation of a Poisson variable with a parameter g (the probability that any one female will be at risk of conception on any given day) and a sample (or group) size of F females (where F is the mean female group size in the population). The detection distance r is the mean distance at which females can be detected, whether this is done visually or vocally; it may, of course, be habitat- as well as species-specific. (Note that this formulation differs from the original given by Dunbar (1988), which instead used the density of female groups rather than their number.)

The use of the standard reproductive cycle as the time base for the analysis allows us to compare the roving male's payoff with the payoff to a social male: a social male's payoff will simply be the number of females in his group, since each one will be receptive just once during the same time interval (the average interbirth interval).

Fig. 12.1 shows that it pays males to go roving whenever F is low or r and d are large.

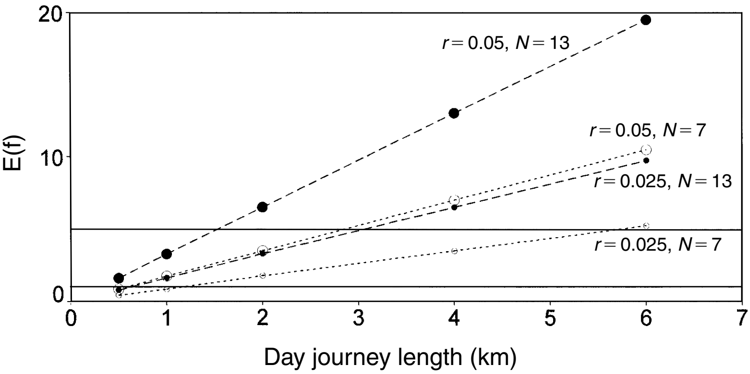

Fig. 12.1 Number of fertilisations predicted by the gas model for males pursuing social or roving male strategies for different male day journey lengths in a population with a male ranging area of 12 km^2. The horizontal lines show the payoffs to social males who join a single female (lower line) or a group of five females (upper line). Payoffs to roving male strategists are shown for alternative detection distances (large vs. small symbols) and female densities (broken vs. dotted lines). Female densities are equivalent to 13 and 7 females occupying non-overlapping territories within the 12 km^2 territory of the male community.

payoff to a roving male, calculated as above, is $E(f)$, then the male's decision rule will be:

Be social whenever $F > E(f)$, else be a roving male.

Fig. 12.1 shows the number of fertilisations that a male can expect to gain as a function of the length of his day journey calculated from the gas model. The example I use here is based on the parameter values typical of the Gombe chimpanzees: $A_{\max} = 12$ km^2, with a mean female group size of $F = 1.1$, and g is taken to be 15/1825 days (assuming that females are fertilisable for a total of 5 days in each of 3 menstrual cycles during any given reproductive cycle of 5 years duration: see Goodall 1986). (Note that this is not necessarily the same as the period of 'full oestrus' for those species that exhibit external signs of fecundability. Dunbar (1988) provides data suggesting that female baboons are 'at risk' of being fertilised for about 5 days around the mean date of ovulation, and this figure is probably typical of most anthropoid primates.)

The payoffs to the male are shown for social and roving males under different conditions in Fig. 12.1. The two horizontal lines represent the payoff to social males living in groups that contain, respectively, 1 and 5 females. The sloping lines show the payoffs to roving males for different male day journey lengths under conditions of high versus low female density ($FN_f = 13$ females as at Gombe and $FN_f = 7$ females as at Bossou) and small ($r = 0.025$ km) versus moderate ($r = 0.05$ km) detection distances (the distance either side of the path of travel in which a male is statistically certain to locate a female group if there is one there). In summary, it pays males to be social whenever female density is low, detection distances are small and day journey length is low. The latter two variables are equivalent to search time in classical optimal foraging models; the first is equivalent to patch richness and density. Conversely, when females are solitary, it only pays males to be social if their day journey lengths are extremely short (below about 1 km).

We can test this model by comparing the actual behaviour of great ape populations against the predictions of the model. Table 12.1 gives the relevant parameter values for all great ape populations for which the relevant data are available. Table 12.1 also gives the mean female party size for each population, which provides the baseline gain rate for social males. The final column shows the percentage of males recorded in parties that also contain adult females.

The ratio of the two payoffs (payoff for social males divided by payoff for rovers) is a measure of the selection pressure favouring each strategy and the percentage of males opting for one strategy rather than the other should be a function of this variable. Fig. 12.2 shows how males' preferences for associating with females is influenced by the selection ratio for the great apes. The best fit regression line for the data is clearly non-linear: with the X-axis log-transformed, there is a significant linear regression for percentage of males associating with females on payoff ratio ($r^2 = 0.75$, $F_{1,7} = 9.48$, $P = 0.018$). Thus the males seem to behave in such a way that switches from one state to the other as the payoff ratio changes. More importantly, perhaps, the data points rise very rapidly from zero association with females (below a payoff ratio of about 1.0) to 80% association (at a payoff ratio of 2.0). Within this narrow range, we can expect the males' preferences to match the payoff ratios in a quantitative fashion: this will partly reflect the natural variance in mean party size within a population, but it will also partly reflect the males' own ambivalence on the exact trade-off when they encounter a party of a given size (some males will choose one option and others the other option when the call is close, but they will tend to converge more closely on the 'right' option as the cost:benefit ratio gets larger and more 'visible' to them).

Table 12.1: *Population parameters and expected payoffs for social and roving males in various great ape populations*

Population	d^a (km)	A (km^2)	F	Mean female party *size*	$E(f)^b$	Males in female parties (%)	Sources
Chimpanzee populations							
Mahale (Tanzania)	6.0	15.0	10.0	2.9	6.0	10.9	Nishida (1968)
Kibale (Uganda)	5.0	14.9	14.0	$<$5.0	7.1	46.0	Ghiglieri (1984), Chapman & Wrangham (1993)
Taï (Ivory Coast)	3.0	27.0	9.0	*c.*3–5	1.5	74.0	Boesch & Boesch (1989), Boesch (1996), Doran (1997)
Wamba (Zaire)	2.4	58.0	*c.*17.0	11.5	1.1	86.0	Kuroda (1979), Kano (1992)
Lomako (Zaire)	7.6	22.0	12.0	4.5	6.5	86.2	White (1989)
Gorilla populations							
Virunga (Rwanda)	0.4	8.0	2.0	2.0	0.1	100.0	Fossey & Harcourt (1977)
Lopé (Gabon)	1.1	21.7	2.5	2.5	0.2	100.0	Tutin (1996)
Orang utan populations							
Kutai (Borneo)	0.7	5.0	4.0	1.1[c]	1.0	8.2[c]	van Schaik & van Hooff (1996)
Tanjung Puting (Indonesia)	0.9	5.0?	4.0	1.0	1.1	16.6[d]	van Schaik & van Hooff (1996)

Notes:

[a] Day journey length data from Bean (1998).

[b] Detection distance of $r = 0.05$ km is assumed for all sites.

[c] Estimated from Rodman (1973), where 5.3% of all parties encountered consisted of two or more adults.

[d] From Galdikas (1985).

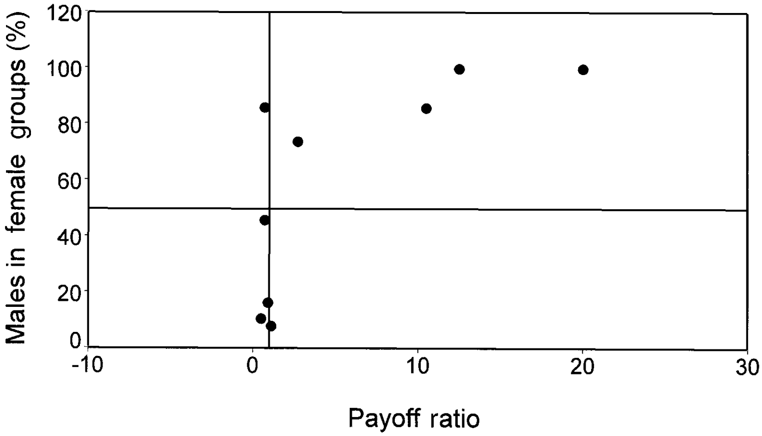

Fig. 12.2 Percentage of males associated with adult females plotted against the ratio of the payoffs for the two strategies (social divided by roving) for various great ape populations. The vertical line marks the point at which the payoffs for the two strategies are equal; at this point males would be ambivalent about which strategy to opt for and should choose the two strategies with equal frequency (i.e. about 50% of males should be social). (From Table 12.1.)

The only real exception to this relationship seems to be the bonobo population at Lomako: this is listed as having a suspiciously long day journey length (7.6 km for both sexes) in the data source I have used (Bean 1998). This value could be either a transcription or a sampling error. (I have been unable to identify the original source for the Lomako day journey length.) The observed level of male sociality (86%) would suggest a day journey length closer to that for Wamba (2.0 km). It is possible, however, that the data for party composition and day journey length derive from different time periods. Alternatively, the Lomako data can be interpreted at face value as implying that the switch from one strategy to the other is very sharp, producing a step-transition at a payoff ratio of one. Excluding Lomako significantly improves the linear fit to the log-transformed data ($r^2 = 0.84, F_{1,6} = 31.7, P = 0.001$), adding further weight to the suggestion that either this population is deviant in some way or the data are in error.

If males are ambivalent about which strategy to opt for when the payoffs are equal, half the males should opt for one strategy and half for the other. The point of equilibrium is marked by the cross-hairs in Fig. 12.2. The equation produced by the distribution in Fig. 12.2 gives a value for the proportion of males in female groups (41.9%) at a payoff ratio of 1.0

that does not differ significantly from the expected value of 50% [$t_6(y = 50\%) = 0.53, P > 0.95$].

It is particularly noteworthy that not only do the chimpanzees seem to fit the model well (the model was, after all, developed to explain their behaviour), but so too do both the orang utan and the gorilla. This latter finding gives added confidence in the model since these two species differ dramatically in their ranging and grouping patterns and most people would not have expected this outcome.

Male group size

So far, we have assumed that males live solitarily and do not attempt to interfere with each other's mating activities. A male's ability to monopolise a group of females will depend on his ability to defeat rivals whenever males are forced into competition with each other. Males will often be forced into competition with each other either when the size of female groups is such that individual males cannot monopolise a group of females, or when it pays males to form a coalition so as to defend a larger territory (or group: e.g. lions: Bygott *et al.* 1979) or retain control over a territory (or group) for longer (e.g. oribi: Arcese 1999). The next question to ask, then, is how male group size might affect males' mating strategies.

When males compete directly with each other for access to individual females as these come into oestrus, the choice a male has is between staying with a female group (and competing with the males present in the group) or adopting a roving strategy that will at least offer the opportunity of bringing him into contact with other groups that may contain fewer more dominant males. In either case, the male's access to females within a given group is constrained by his ability to defeat rival males in that group.

A model that incorporates dominance effects was developed by Dunbar *et al.* (1990) to examine the mate searching strategies of male feral goats. Male goats compete directly with each other for access to individual oestrous females in a fiercely competitive polygamous mating system. Females are typically distributed around the habitat in small heft groups of 3–15 females and, during the rut, males move from one female group to another over a wide area in search of females in oestrus. Females are in oestrus for only about 36 hours, so that the probability of there being more than one female in oestrus on any given day is small. Once a male has located a group, he will join it and compete with any other males present (or who join later) to monopolise any oestrous female that happens to be in the group. Success in this venture depends on the male's rank (and this, in turn, depends largely on his age and therefore size). A male's ability to mate thus depends on whether or not the number of females in oestrus at any one time is equal to or greater than his rank among the males currently in the group (a classic priority-of-access model: see Altmann 1962).

A male can choose to stay with a group once located in the hope that a female he can monopolise will come into oestrus, or he can leave and continue searching in the hope that the next group he locates will contain fewer higher-ranking males (or more oestrous females). Which option is the better for a male depends on the size of the female group, his age, his rank among the males currently in the group (i.e. his chances of winning a fight), the likelihood that a more dominant male will join the group if he stays for a given length of time, the mean size of female groups in the population as a whole and, finally, the time it will take him to find another group of females. The model (which is summarised in Box 12.3) suggests that low-ranking males (i.e. the youngest and oldest males) ought to leave large female groups since these are statistically more likely to contain larger numbers of more dominant males than are smaller groups, but males in their prime should stay because they are better able to compete successfully.

Data on the behaviour of male feral goats on the Isle of Rhum (northwest Scotland) show that most males do follow the optimal strategy. The only exceptions are very young males who persist in staying on in groups to compete with higher-ranking males when it would, in fact, pay them to leave. Since old males follow the optimal strategy (and indeed pursue a number of strategies designed to minimise competition with prime males), it seems likely that male goats learn the optimal strategy as a result of experience.

Surprisingly, male goats appear not to use the number of females in the group as a cue for joining (except for very young males whose joining rates rise exponentially with female group size). This may be because the males cannot predict the number of oestrous females in the group on the basis of group size alone, even though the likelihood of the group containing an oestrous female *must* increase with the number of females in the group. One reason this might be so is that, when they first locate a group from a distance, it is difficult for them to distinguish between adult females (who might be in oestrus) and young adult males (who certainly will not be): only once they have actually joined the group are they able to determine who is who. In contrast, male joining rates are related to the number of

Box 12.3 Male strategies in a mating free-for-all

When males compete with rivals for access to individual females (as in the priority-of-access model), the payoff to a male is a function of his ability to defeat opponents, in addition to those variables that influence his chances of finding a female in oestrus. The following model is developed in more detail in Dunbar *et al.* (1990).

A male's chances of mating with an oestrous female in the group he has just joined is:

$$r_{xf} = sf/[1 + (1 - w_x)(m_f - 1)],$$

where r_{xf} is the number of fertilisations the male can hope to achieve, s is the probability that any one female will be in oestrus on that day, f is the number of adult females in the group, m_f is the number of males in the group before he joins (or alternatively, the expected number of males in groups of f females) and w_x is the male's chances of winning a fight against any male chosen at random from the group. In contrast, the expected number of fertilisations achieved by a male who decides to rove rather than stay with the group is:

$$E_x(r) = \Sigma\, r_{xf} p_f,$$

where p_f is the proportion of female groups that contain f females.

The male's decision rule should be:

Stay whenever $r_{xy} > E_x(r)$, else go roving.

Clearly, everything hinges around the size of the current group relative to the mean for the population, because the expected number of females in the next group the male locates will be the mean female group size.

males already in the group, probably because mature males are conspicuous by their body and horn sizes from a considerable distance. Males' joining rates show a hump-shaped distribution against the number of males in the group with a peak at around 2–4 males. More importantly, males vary in their expressed preferences: old males exhibit a marked preference for small groups with two males, whereas very young males are willing to enter groups with more males even though these are less profitable for them. As we would expect, prime-age males who are most likely to win fights against all-comers are willing to enter groups with the broadest range of males compared to other age classes of males.

These results suggest that males respond in quite a fine-tuned way to the reproductive payoffs they can expect to gain from different strategies; they also suggest that this sensitivity may be learned as the animals gain experience in successive ruts. It seems that young males initially may be misled by attention to the wrong kinds of cues (e.g. the total number of females in the group), but they learn to identify the optimal strategy the hard way through losing contests with older more powerful males.

One consequence of this behaviour is that we should expect males to adopt an 'ideal free' distribution in which the number of males in a group is a function of the number of mating opportunities (which, in turn, will be a function of the number of females in the group and their reproductive characteristics). This is what we do observe among the goats: the number of males in a group at any one time increases linearly with the number of females (see Dunbar *et al.* 1990).

Similar considerations apply among primates. Although female primates have longer fertile periods (i.e. periods during the menstrual cycle when copulation is likely to result in conception), their long interbirth intervals mean that the number of females in oestrus on any given day is small. Building on arguments by Altmann (1962) and Emlen and Oring (1997), Dunbar (1988) showed that a male's ability to monopolise access to the females in the group by keeping rivals out ought to depend on both the number of females in the group and their degree of reproductive synchrony. So long as there is likely to be only one female in oestrus at any one time, the dominant male can easily monopolise her and keep rivals away. However, as the likelihood of two or more females being in oestrus simultaneously increases, so the male's chances of keeping rivals at bay declines. A number of primate taxa show just such a relationship between the number of males in a group and female group size. Examples include *Papio* baboons (Dunbar 1988), Hanuman langurs (*Presbytis entellus*: Newton & Dunbar 1994) and guenons (genus *Cercopithecus*: Andelman 1986).

The main reason why males follow an ideal free distribution is likely to be that dominant males become increasingly less able to prevent rivals gaining access to individual females in oestrus as the number of females in the group increases (see Dunbar 1982). The same effect can, in fact, even be demonstrated within groups: Cowlishaw and Dunbar (1991) found that, in polygamously mating primates, the dominant male's ability to monopolise all the matings in the group depends crucially on the operational sex ratio (the number of males per reproductively active female). They showed that the correlation between male rank and mating success declines as both male cohort size (effectively a measure of the operational sex ratio, since there tends to be only one female in oestrus on any given day) and female reproductive synchrony increase.

However, this model considers only the handling time costs of the conventional optimal foraging model. It does not consider the search time costs that males incur when deciding to leave a group and continue searching. If we add the search time costs (a function of population density or home range size), we would expect males to be less willing to leave a group (or alternatively they will fight harder to stay in it) when the intergroup distance is large (because they will take longer to find another group and incur higher risks from predation or starvation while searching) than when it is small.

Srivastava and Dunbar (1996) tested this prediction on Hanuman langurs (*Presbytis entellus*). This species is widely distributed across the Indian sub-continent and its mating system varies between one-male groups (where a single breeding male monopolises the females, while excluded rivals form all-male bachelor groups) and multimale groups (where breeding males share the females with their rivals). Approximately 70% of the variance in the percentage of one-male groups in the population was explained by a combination of female group size, reproductive seasonality (an index of female reproductive synchrony) and home range size (an index of interpatch distance). Multimale groups were significantly more common in those populations which (for other purely ecological reasons) had large home ranges where males had to travel long distances (or search large areas) in order to locate an alternative group. Since increased search costs make a roving strategy less profitable, males will opt to fight harder to stay in the current group even if the dominant male would prefer them to leave. An alternative explanation for this particular result might, of course, be that larger groups with larger home ranges become more dispersed during the day, making it more difficult for a dominant male to prevent rivals from associating with at least some of the females. Unfortunately, we do not have the data available to check on this possibility, though future studies might consider the question.

Male parental investment

The final case to consider is that where the male can offer the female some form of parental investment. I have already alluded to this in the context of gibbon mating strategies. There we found that, on face value, it would pay most male gibbons to opt for the roving male strategy, even though in practice they do not. The opportunity cost that these males incur by being social is very considerable (typically something in the order of up to four times as many fertilisations in a lifetime as they gain from being monogamous). Even allowing for the fact that the resulting rivalry between males might reduce tenure length (and life span), it is clear that successful males would do considerably better by opting for roving male polygyny. That they do not, implies that they must gain some equivalent benefit by staying with one female. The gas model suggests that the male's problem is not one of locating females during the limited time period when these are in oestrus, even given that males search completely at random. Consequently, the benefit can only be in terms of increased offspring survival. Van Schaik and Dunbar (1990) suggested that this gain comes principally through a reduction in the risk of infanticide (a problem that primates are peculiarly susceptible to because of their unusually long interbirth intervals: see also van Schaik & Kappeler 1997).

Assuming that male gibbons are indeed behaving optimally, we can use the fitness differential between the two strategies to determine the risk to infant survival that males would otherwise run if they opted for the roving male strategy. This is simply the inverse of the ratio of the payoffs. Since, for gibbons, this is typically 1 : 3.14 (assuming a maximum territory size of 1 km^2: see van Schaik & Dunbar 1990), this implies that infant mortality would otherwise be $1 - [1/(1 + 3.14)] = 0.758$ (in addition to existing mortality risk).

The male's contribution to rearing might, in fact, take a number of different forms, several of which may operate simultaneously. Protection from infanticide has been suggested by van Schaik and Dunbar (1990), but other possibilities include protection from predators, provision of an exclusive food source and direct care-giving. Cowlishaw (1992), for example, has shown that the patterns of female gibbon calling behaviour are consistent with the view that the female is using the male's territorial behaviour (itself geared to maintaining exclusive mating access to the female and/or minimising infanticide risk) to ensure an exclusive feeding territory for herself and her offspring. Thus, for the female, the male's behaviour has a double benefit: in addition to keeping infanticidal males at arms' length, he also inadvertently keeps (at least some) ecological competitors out of the territory.

When males take on a more direct form of paternal investment (such as responsibility for carrying and caring for infants), the male will inevitably be constrained into what amounts to monogamy: a male that simply defends a feeding territory for his female can do so as easily for several females as for one, but a male cannot distribute direct care-giving in the same way. Dunbar (1988, 1995a) showed that male care is particularly viable when the female can produce twin litters twice a year, otherwise polygamy is always the better option (see also Wright 1984; Goldizen 1987a). It is easy to show that when the effective female group size is one (i.e. only one female breeds in each group) the strategy set in which females twin and males are monogamous with paternal care is a stable solution for species like marmosets and tamarins where twinning is a biological possibility (Dunbar 1995a).

More interesting from the present point of view is what happens once males acquire helpers-at-the-nest who are willing to offer parental care to offspring that are not necessarily their own. Such behaviour is characteristic of callitrichids: young males in particular commonly act as helpers (Ingram 1977; Goldizen 1987b). Once a male has a helper, it may pay him to leave the rearing of his offspring to the helper (who then gains the opportunity to monopolise matings with the female when she next comes into oestrus) in order to search for more females with whom to mate. The payoff to the breeding male depends on his ability to become the breeding male for a new female relatively easily (both in terms of his ability to find a new female and his ability to take over as breeding male) (see Box 12.4).

The benefit to the satellite is that he gets to sire the female's next litter. Even if he risks being displaced back to satellite status by a new dominant male joining the group, he will benefit providing the rate at which more dominant males join groups is not too great (see Box 12.4). Eventually, of course, he will become a dominant male too, but a satellite strategy at least allows him to get started on reproduction earlier than he would otherwise have done. In addition, being a member of a social group during this stage of his life may be safer in terms of predation risk than wandering alone on the periphery of the population.

It is clear that the preconditions for roving male polygamy in these species are created by the fact that younger males are unable to acquire breeding territories of their own. These conditions appear to be created, in turn, by the fact that seasonal stress in higher-latitude habitats increases the levels of postnatal mortality in females, resulting in a positive relationship between latitude and male-biased sex ratios (Dunbar 1995b). Postnatal mortality in infants also increases with latitude (Dunbar 1995b),

Box 12.4 When does it pay to exploit a satellite?

In small-bodied primates like callitrichids, it may pay a breeding male to accept another male on to his territory to act as a satellite and helper-at-the-nest to assist with the rearing of the offspring. If the satellite is willing to take on the job of rearing, then it may pay the breeding male to leave the satellite with the female and go roving in search of other females he can impregnate (after first becoming the breeding male in the new group). The satellite gains by being able to fertilise the female's next litter. A detailed mathematical analysis suggests that it can pay the breeding male to trade-off some loss on infant survival by leaving them in the care of the satellite in order to acquire access to another female, especially if he is related to the satellite (and will thus gain in terms of inclusive fitness from some portion of the satellite's subsequent matings with the female). The critical condition for the breeding male to desert once a satellite has joined him is:

$$k_B > \{B[1 - r + (rt/12)] - Dt/12\}/B$$

where k_B is the probability that he will find another female in the remainder of the year, B is the number of offspring that male can expect to produce in a year if he stays and helps the female rear them, D is the number he will gain if he deserts the female after her first conception ($0 < D < B$), t is the population-specific mean length of interbirth intervals (in months) and r is the coefficient of relationship between the male and his satellite (Dunbar 1995b).

It will increasingly pay the male to desert as $r \to 1$, $D \to B$ and $t \to$ 12 months. Note that $D \to B$ only when there is a satellite to act as surrogate parent; moreover, the extent to which $D \to B$ will depend on how competent or conscientious the satellite is at rearing compared to the biological father. When $D \geq 0.5B$, roving is a viable strategy as long as $k_B > 0.70$ for all t, providing $r > 0.25$; alternatively, for $r = 0$, roving is only viable if $k_B \geq 0.5$ providing $t = 12$ or, for all values of t, providing $D \approx B$. These are relatively benign conditions. Indeed, for many of the populations for which data are available, the minimum value of k_B under which desertion would be viable for a male is below 0.5 when $r = 0.5$, and in at least two of these populations the minimum is $k_B = 0$. Estimates of the actual values of

Box 12.4 (*cont.*)

k_B for those populations for which the relevant data exist suggest that they are well in excess of these minimal requirements, assuming that satellites are either siblings of the breeding male or his offspring from a previous breeding relationship (Dunbar 1995b).

Similar considerations apply in the satellite's case: it pays males to become satellites if their chances of obtaining a breeding female of their own are poor. As in the case of the breeding males, a satellite gains if his host male is a relative, but satelliting may still pay even if the males are unrelated, providing the satellite's alternative opportunities of gaining access to breeding females are low. The critical conditions under which it pays a male to become a satellite are:

$$k_S < [m + d - rd - rm - (mt/12) - (dt/12) + mrk_B + D(mrt/12 + drt/12)/B]$$

where $\boldsymbol{k_s}$ is the probability that the satellite will acquire a breeding female (territory) of his own within the next 12 months and m and d are the probabilities that the breeding male will emigrate or die, respectively, within the next 12 months (Dunbar 1995b). The value of becoming a satellite declines as $k_S \rightarrow k_B$ (i.e. when the satellite can as easily acquire a breeding female of his own); when $k_S < k_B$, then satelliting becomes increasingly advantageous as $D \rightarrow 0$, $r \rightarrow 1$ and $t \rightarrow 6$ months.

making it increasingly advantageous for breeding pairs to accept satellite males as helpers in order to reduce the load on the parents.

Conclusions

These results suggest that a great deal of the behaviour of male mammals (and in particular, male primates) can be understood as mating strategies (sometimes with adjunct parenting strategies bolted on) set against a background of females distributed in a more or less fixed way in the environment. This does not mean to say that females are necessarily locked rigidly into particular groups; rather, it means only that female grouping patterns have a distinct and discrete character (at least in terms of mean and variance). It is largely the distribution of females and their reproductive characteristics that influence males' decisions on whether or not to pursue a roving male strategy. Roving male polygamy is preferable to the social option (which limits the number of females that a male can gain access to) whenever the search time for finding the next female(s) is low and female group sizes are small.

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