

Chapter 11

The Ecology of Relationships

Anne E. Pusey & Craig Packer

11.1 Introduction

Whenever two individuals meet, their behavioural interaction may have consequences that will influence all of their subsequent interactions. Each animal may obtain information about its companion's competitive ability or its propensity to cooperate, or one animal may behave in a manner that raises or lowers its companion's chances of survival. As a result, behavioural ecologists have long realized that social behaviour must often be interpreted in the context of long-term social relationships (Hinde, 1983), and that these relationships are likely to be complex.

By living in groups, companions may benefit from reduced predation risk, improved defence of resources or communal rearing, but they also suffer from increased competition over critical resources. Relationships will therefore be structured both by cooperation and by competition, and, because self-interests will never entirely coincide, social relationships are expected to reflect a certain degree of coercion or compromise. Indeed, individuals can benefit by manipulating not only their own relationships, but also the relationships between their companions (de Waal, 1982; Cheney & Seyfarth, 1990).

What theory helps specify the general principles governing the form of social relationships? Most models of social behaviour have been restricted to assessing the net effect of isolated behavioural interactions. However, treatments of repeated interactions are becoming increasingly common. In this chapter, we first consider how competition structures relationships and then examine the long-term consequences of cooperation.

11.2 Competitive relationships

Animals generally compete for resources on an individual basis. However, the summation of competitive relationships within any given group can lead to complex patterns, and these have often been the subject of research in their own right. We start with the simplest pairwise interactions, discuss how pairwise relationships may lead to hierarchies, then discuss how these hierarchies vary in form and intensity across species.

11.2.1 Competition in pairwise contests

Single encounters

If opponents meet for only a single encounter, game-theoretical models predict that contestants will be more likely to engage in escalated fighting when the costs of injury are low relative to the value of the resource (Maynard Smith & Price, 1973). However, when fighting has significant costs, disputes are more likely to be settled according to certain asymmetries between the contestants (Parker, 1974a; Maynard Smith & Parker, 1976). These asymmetries may be based on differences in resource holding power (RHP) such as size, strength or fighting ability, or they may be uncorrelated with RHP (Hammerstein, 1981). Detectable differences in RHP are expected to lead to some form of assessment, where individuals 'size each other up' before committing themselves to an escalated fight, and the inferior competitor retreats before losing a costly battle. But, when assessment cannot provide a reliable prediction of the outcome and the costs of fighting are especially high, animals may settle their disputes according to an arbitrary cue. For example, individuals following the 'Bourgeois strategy' escalate if they are the first to reach the resource and retreat if they are a latecomer. Finally, if the value of the resource varies between individuals, the hungrier animal will be expected to tolerate greater costs and thus fight longer or harder (Parker, 1984; Houston & MacNamara, 1988).

Empirical studies have shown that all these factors influence fighting behaviour (assessment: Davies & Halliday, 1978; Clutton-Brock & Albon, 1979; Austad, 1983; bourgeois: Davies, 1978; Packer & Pusey, 1982; Waage, 1988; differences in resource value: Krebs, 1982; Rodriguez-Gironés *et al.*, 1996), and Maynard Smith and Riechert (1984) have demonstrated how these different asymmetries interact (e.g. large rival versus small owner, etc.).

Repeated encounters: dominance relationships and winner-loser effects

In stable social groups, the same two individuals are likely to compete repeatedly. If the difference in RHP between each opponent is consistent and detectable, the superior competitor should consistently win each contest and the inferior should defer to its opponent. The pair may then be said to have a dominance relationship. Dominance relationships pervade animal societies (reviewed in Wilson, 1975; Smuts *et al.*, 1987; Langen & Rabenold, 1994; Fournier & Festa-Bianchet, 1995), and they have been measured by the outcome of fights in dyadic encounters, the direction of approach-retreat interactions and the direction of threats and/or submissive gestures. These measures are generally correlated.

However, certain features of dominance relationships suggest that they involve more complicated processes than the simple summation of repeated

contests over resources. First, although dominance relationships are frequently correlated with some measure of competitive ability (Wilson, 1975; Fournier & Festa-Bianchi, 1995) (Fig. 11.1a), they often appear to be more clear-cut than expected from the individuals' relative RHP, and some are even based on traits that are uncorrelated with RHP (e.g. seniority or age). Second, the pattern of interactions between pairs often changes through time. Initially, fighting may occur even in the absence of a resource, and the subordinate subsequently defers to the dominant without a fight.

These observations suggest that individuals may compete for dominance per se and learn from the first few encounters with their opponent (see Huntingford & Turner, 1987; Clutton-Brock & Parker, 1995).

Both processes are well illustrated by the development of dominance relationships in blue-footed boobies (Drummond & Osorno, 1992). Two chicks hatch asynchronously in each nest. The older chick frequently pecks and jostles the younger for the first few weeks even in the absence of food and then maintains dominance by less frequent but daily aggression. The younger chick responds to aggression with submissive gestures and rarely challenges the older. Thus, the older chick establishes dominance and subsequently gains greater access to food. The younger chick usually behaves submissively even if it grows larger than the older (females grow more quickly and are eventually larger than males).

The importance of early experience is illustrated by a series of experiments that paired chicks with different backgrounds. When chicks that had been raised alone (and thus lacked any experience of dominance or subordination) were introduced to other singletons, the pairs established dominance relationships solely on the basis of size. But, when birds that had been raised in pairs were given new companions, dominant chicks maintained their dominance even when they were smaller than the new subordinate. Although large subordinates challenged the dominant chicks more often, they did not fight as tenaciously as the dominants and were more likely to adopt submissive postures.

Such winner-loser effects are common in species as diverse as crickets and mice (Huntingford & Turner, 1987) and may explain why dominance is sometimes determined solely by age or seniority rather than by differences in RHP. In some species, dominance changes with age according to a bell-shaped function which reflects the greater RHP of prime-aged animals (Fig. 11.1a). However, in other cases, dominance appears to increase continuously with age (e.g. dwarf mongooses: Creel *et al.*, 1992; cooperatively breeding birds: see Chapter 10), although this may still reflect rising RHP if very old individuals are not able to survive in the population. Among male hyenas (Smale *et al.*, 1996), dominance is determined by the length of time an individual has resided in the group (Fig. 11.1b).

Older or senior individuals presumably enjoy an initial competitive advantage so that the younger or newer individuals learn to defer and then continue

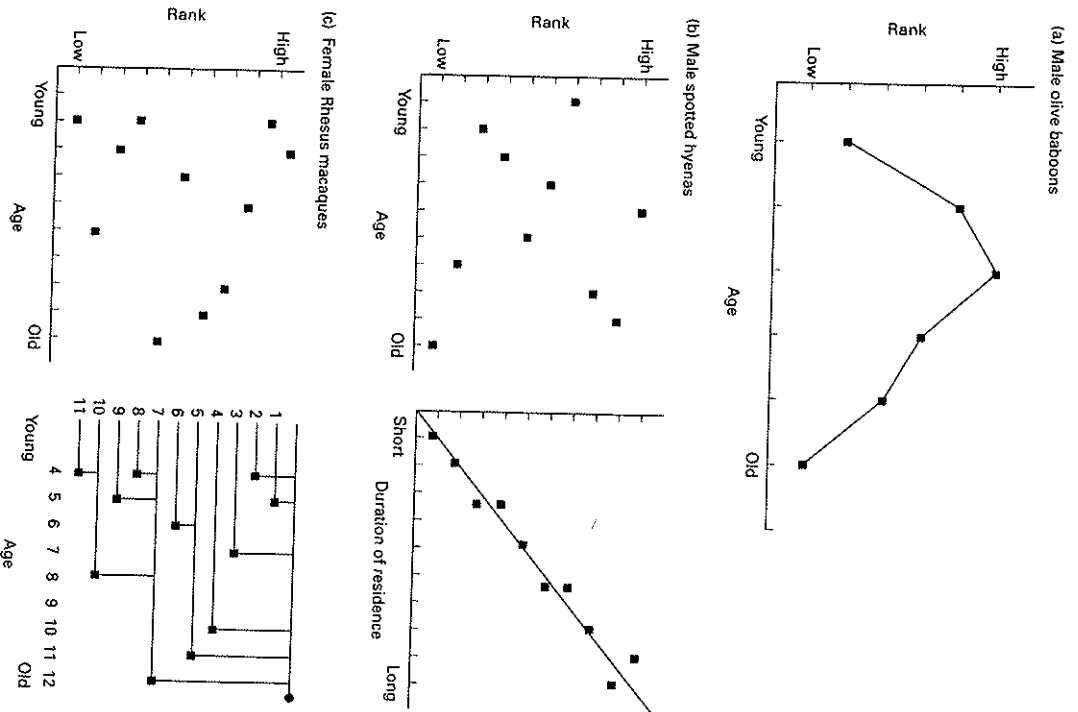


Fig. 11.1 The relationship between age and dominance in three different mammalian species. (a) In immigrant male baboons, dominance shows a bell-shaped relationship because prime-aged males have the highest RHP. (Modified from Packer, 1979.) (b) In immigrant male hyenas, dominance is not correlated with age, but instead increases with the length of residence in the clan. (Left-hand graph provided by K. Holekamp & L. Smale, personal communication; right-hand graph modified from Smale *et al.*, 1997.) (c) In female rhesus macaques, dominance is unrelated to age except as revealed by birth order, and her maternity is indicated by a circle in the top-right corner. Note that each daughter outranks all of her older sisters with the exception of the second-ranking female. Also note that each daughter ranks beneath her mother but above every adult that ranks lower than her mother. (Both graphs modified from Hinde, 1983.)

to do so. However, there are currently no theoretical models to explain why some species show such persistent deference and thereby form breeding 'queues'. Specifically, we need to know why RHP provides the basis of pairwise dominance relationships in some species whereas other species form long-term queues that are uncorrelated with RHP (see Ens *et al.*, 1995). Indeed, persistent respect of an arbitrary asymmetry is unexpected unless latecomers gain some incentive from waiting their turn (see Grafen, 1987; Schwagmeyer & Parker, 1987), although there may be some insights into this pattern from the study of alliances (see Section 11.2.2).

11.2.2 Dominance hierarchies

Hierarchies as the outcome of pairwise interactions

Dyadic dominance relationships can often be arranged in a linear hierarchy in which individual A is dominant to the rest of the group, B dominates all but A, C dominates all but A and B, and so on (Schjelderup-Ebbe, 1935; Walters & Seyfarth, 1987). This strict linearity is difficult to explain on the basis of pairwise contests. Unless individual differences in RHP are extreme, the outcome of a dyadic fight will sometimes differ from the direction of RHP differences, especially between animals with near-average abilities. Consequently, the correlation between dominance and RHP will be imperfect, and, since the probability that a hierarchy will be perfectly linear depends on the product of all these dyadic probabilities, linearity should decline rapidly with increasing group size (Landau, 1951; Chase, 1974).

Using a game-theoretical model, Mesterton-Gibbons and Dugatkin (1995) show that the probability of linearity is increased where individuals assess their relative RHP in each dyad and fight only if this exceeds an evolutionarily stable threshold. This threshold increases with the magnitude of variation in RHP, the reliability with which RHP predicts the outcome of a fight and the ratio of the cost of fighting to the value of winning. Such assessment reduces the number of fights and their associated uncertainty of outcome. Nevertheless, their model still predicts that linearity should decrease with group size, becoming highly unlikely in groups larger than about nine individuals. When the observed degree of linearity is greater than predicted by these models, dyadic dominance relationships are likely to be ordered by additional factors besides differences in RHP. These may include psychological reinforcement of 'losing status' through winner-loser effects (see Section 11.2.1) as well as the ordering of relationships through alliances.

Alliances

Some animals (e.g. female Old World monkeys and spotted hyenas) form stable linear hierarchies in groups much larger than 10 (reviewed in Chapais, 1992;

Frank *et al.*, 1995a). In most cases, these hierarchies are not based on individual RHP. Instead, daughters rank directly below their mother in reverse order of age, and the whole matriline ranks above the next most dominant matriline (Fig. 11.1c). Rank inheritance is achieved by mothers supporting their daughters against females from lower-ranking families and by supporting their youngest daughter against her older sisters (Kawai, 1958; Cheney, 1977; Datta, 1983). Females also intervene in disputes between non-matriline members, allying against individuals that rank lower than themselves (Chapais, 1983; Hunt & Horrocks, 1986; Netto & van Hooff, 1986). The consequences of female alliances on rank inheritance and maintenance is demonstrated by a recent series of experiments with Japanese macaques (Chapais, 1988a,b; Chapais *et al.*, 1991) (Box 11.1).

Box 11.1 Experiments on rank determination in Japanese macaques

Chapais and his colleagues performed experiments with a captive group of Japanese macaques consisting of three unrelated matriline.

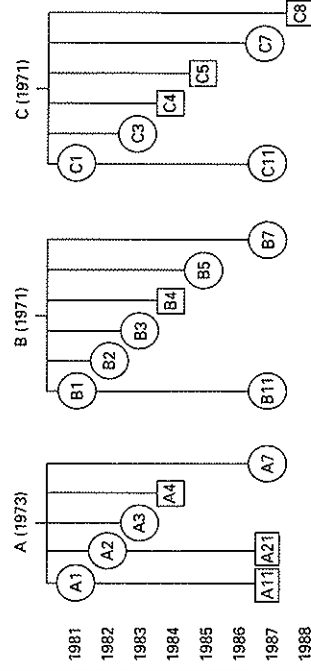


Fig. B.11.1 Composition of the group at the end of the study period (summer of 1989). Circles, females; squares, males. The alpha male is not represented. (From Chapais *et al.*, 1991.)

In the intact group, members of the A matriline ranked above the B and C matriline, and B ranked above C.

Chapais created a variety of experimental groups to examine how alliances influenced the inheritance and maintenance of dominance rank.

Inheritance of maternal rank

Lone females from high-ranking matriline were placed with several females from lower-ranking matriline, and an ally of the high-born female was later added. For example, female A1 was placed with the C matriline. She dropped

Continued on p. 260

Box 11.1 Cont'd.

in rank until she ranked below all the members of the C matriline. When her mother (A) was added to the group, A maintained her rank above the C matriline, and defended her daughter against members of the C matriline, so that A1 eventually regained her rank above the C matriline. In all other cases, mothers or adult daughters were also able to help their daughters or younger sisters to regain their rank (Chapais, 1988b).

Maintenance of rank

In a series of 58 experiments, a female from a high-ranking matriline was deprived of her allies and placed with:

- 1 a single but older/larger low-born female;
- 2 two or three low-born sisters;
- 3 a complete subordinate matriline.

Out of 148 dyads of high- and low-ranking females, dominance reversals occurred in 56%. The likelihood that the female lost her rank depended on two factors: (i) her absolute age; and (ii) the number of lower-ranking females. Females were most likely to maintain their rank when they were older and were placed with few rivals.

For example, when a 3-year-old member of the A matriline (A3) was placed with a B female that was 1 year older, A3 maintained her rank, and she was also able to maintain her rank above a pair of B sisters. But, when she was placed with two C sisters, one of whom was 2 years older, she did not maintain her rank. When a female aged 4 years or older from the A or B matriline was placed with an entire lower-ranking matriline, the female only managed to maintain her rank in five of 12 cases. For example, the matriarch A, maintained her rank over the entire B matriline, but B was not able to maintain her rank above the C matriline (Chapais, 1988a).

Chapais concludes the following.

- 1 Competition for rank is ubiquitous in matrilineal hierarchies, with low-ranking females constituting a potential and constant threat for any high-ranking female.
- 2 Kin can form revolutionary alliances.
- 3 Rank maintenance is conditional on the high-ranking female having enough alliance power to counter revolutionary alliances.
- 4 Competition for rank is somewhat constrained. In cases where the high-ranking female was outnumbered, rank reversals only occurred when the power asymmetry (relative size/age or relative alliance power) was pronounced. Chapais refers to this as a 'minimal risk strategy' of competition for dominance.

Continued on p. 261

Box 11.1 Cont'd.

Non-kin alliances

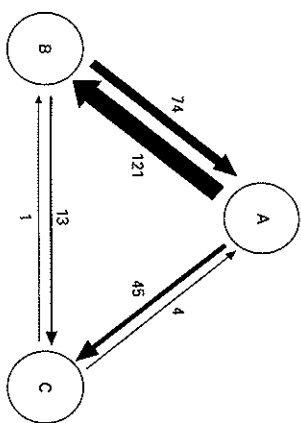


Fig. B. 11.2 Distribution of non-kin interventions among the three matrilines. The thickness of the arrows is proportional to the frequencies of interventions (numbers). Support given to a matriline (direction of arrow) is necessarily against the third matriline. (From Chapais *et al.*, 1991.)

Figure B. 11.2 shows the pattern of support between matrilines in the intact group. Members of A and B matrilines consistently supported each other against C, and rarely supported members of the C matriline against the other matriline.

In a series of experiments, a single female from the A or B matrilines was placed with the two other matrilines. In each case, the higher-ranking matriline supported the lone female against the C matriline rather than vice versa. For example, B was placed with the A and C matrilines. When B was alone with the C matriline she lost her rank (see p. 260). However, when the A matriline was also present, they supported her against the C matriline so that she maintained her rank above the Cs.

When A1 was placed with the B and C matrilines, the B matriline outranked A1, but supported her against the C matriline, rather than supporting the C matriline against her. Thus, she maintained her rank above the C matriline (Chapais *et al.*, 1991).

Chapais (1992) suggests that matrilineal hierarchies evolved from an initial state in which females were ranked by age or individual RHP. Females protected their daughters when they were most vulnerable and helped them side-step the lowest rungs of an age-graded hierarchy. Because mothers would be expected to support their daughters against more distant relatives, females eventually banded together with their daughters and granddaughters to overpower any high-ranking female that attempted to act on her own.

A linear hierarchy, however, would be unstable if females only supported members of their own matriline because a large low-ranking family could

overthrow a small high-ranking family. However, upheavals in rank (e.g. Erhardt & Bernstein, 1986; Samuels *et al.*, 1987) are rare, and stability apparently results from the pattern of non-kin support. Consider a descending hierarchy of three matriline: A, B, C. If females supported members of any non-matriline, matriline B could be threatened by 'bridging' alliances between A and C. Also, matriline A could be threatened by 'revolutionary alliances' between B and C. However, non-kin generally only aid each other against matriline that rank lower than either of them (i.e. A and B against C) (Box 11.1). By assisting higher-ranking matriline against lower-ranking families, midranking females may prevent the formation of bridging alliances, and, by supporting the most dominant of lower-ranking opponents, the highest-ranking females create a state of dependency that forestalls the formation of revolutionary alliances and maintains the status quo (Chapais, 1992).

In other cases, alliances can destabilize hierarchies and prevent them from being linear. Male chimpanzees live in a fission-fusion society in which males spend considerable periods apart. Male rank depends heavily on alliances, and if male A relies on the support of male C to dominate male B, he may be defeated by B when C is absent (Bygott, 1979). In addition, subordinate males are sometimes fickle in their alliances, with C sometimes supporting A against B and sometimes supporting B against A, thereby inducing a state of dependence in each and gaining greater access to resources (de Waal, 1982; Nishida, 1983). Again, however, there are no satisfactory explanations for why alliances act to stabilize the status quo in some species whereas they are destabilizing in others.

11.2.3 Benefits and costs of dominance

Stable dominance relationships may benefit both dominants and subordinates by minimizing the incidence of serious fighting. A classic study in chickens showed that hens in groups with stable hierarchies fought less and laid more eggs than those with unstable hierarchies (Guhl *et al.*, 1945). Also, damaging fights in a colony of chimpanzees were five times more frequent when male ranks were unstable (de Waal, 1982). Nevertheless, dominance relationships are generally expected to result in inequitable access to resources, and thus high-ranking individuals should enjoy greater reproductive success than subordinates. Although there is considerable evidence that dominant individuals do gain greater access to scarce or monopolizable resources, such as mates, food or safe refuges (reviewed in Huntingford & Turner, 1987; Langen & Rabenold, 1994; Fournier & Festa-Bianchet, 1995), high rank is not always associated with higher reproductive success. This sometimes results from the existence of equally successful alternative strategies, such as satellites or sneaks (Gross, 1996), which opt out of the competition altogether, or because there are also costs associated with maintaining high rank or high RHP. We consider two examples where high rank confers costs as well as benefits.

Spotted hyenas live in clans of up to 80 individuals in which all adult females rank above the adult males, and females form a stable matrilineal hierarchy (Frank *et al.*, 1995a). Hyenas feed on medium-sized antelope, and clan members compete intensely for carcasses with the result that high-ranking animals gain greater access to food (Frank, 1986). High-ranking females reach sexual maturity earlier, have slightly shorter interbirth intervals and recruit more offspring of each sex (Frank *et al.*, 1995a). However, female aggressiveness is associated with a syndrome that includes large body size, elevated levels of androgens and dramatic masculinization of the external genitalia. Female masculinization is suggested to have evolved because of the advantages of aggressive competition (Frank, 1986), but the syndrome carries considerable costs. Females give birth through a penis, and primate mothers suffer a high incidence of birth complications that may reduce their lifetime reproductive success by as much as 25% (Frank *et al.*, 1995b).

Female savanna baboons also form matrilineal dominance hierarchies (Cheney, 1977; Hausfater *et al.*, 1982; Johnson, 1987), although a small number of females are able to rise in rank above their matriline (Samuels *et al.*, 1987; Packer *et al.*, 1995). High-ranking females enjoy higher infant survival, shorter interbirth intervals and younger ages at sexual maturity (Packer *et al.*, 1995). However, rank is not significantly correlated with lifetime reproductive success in some populations because high-ranking females suffer more miscarriages and occasionally suffer from reduced fertility (Wasser, 1995; Packer *et al.*, 1995; but, see Altmann *et al.*, 1995). The source of these costs is unknown, but high-ranking female baboons show an imbalance in their ratio of oestrogen and progesterone (Wasser, 1995), high-ranking juvenile females have higher levels of androgens (Altmann *et al.*, 1995) and, in social carnivores, high-ranking animals show elevated levels of stress hormones (Creel *et al.*, 1996).

Packer *et al.* (1995) suggest that traits conferring high rank in females are subject to strong stabilizing selection because of their potentially negative effects on reproductive physiology. Although individuals that invest too much in aggressive competition suffer these costs, those that opt out of direct competition would suffer reduced feeding success. Thus, dominance behaviour will be expected to persist even if high rank does not confer significantly higher reproductive success.

11.2.4 Alternatives to dominance: ownership

When contestants are evenly matched and the costs of fighting are high compared to the value of the resource, animals may settle contests on the basis of asymmetries that are not correlated with RHP, including prior ownership of the resource (the bourgeois strategy: Hammerstein, 1981; Maynard Smith, 1982), provided that the contest does not approximate a war of attrition (Hammerstein & Parker, 1982). In social groups, this convention would translate into a state-dependent dominance that lasted only as long as one animal

retained ownership of the resource, and no persistent dominance relationships would be expected. African lions provide an apparent example.

Female lions compete with their pridemates for access to meat but respect each others' ownership of specific feeding sites at each carcass (Packer & Pusey, 1985). Their prey have tough hides, and meat can be extracted most readily from certain parts of the carcass. The first female to feed from each site refuses to yield to any other female in her pride, lunging and snarling if another ventures too close. Females 'respect' each pridemate's ownership, and roles are reversed as active feeders become temporarily satiated and move away from the kill. Breeding appears to be egalitarian, and dominance hierarchies have never been reported in female lions (Packer *et al.*, 1988) — in marked contrast to every other species of social carnivore (e.g. hyenas: Frank *et al.*, 1995a; mongooses: Creel *et al.*, 1992; wild dogs: Malcolm & Marten, 1982).

Male lions form coalitions that compete intensively against other coalitions for access to female prides, but coalition partners also compete for access to individual oestrous females (Packer & Pusey, 1982). When one male forms a consortship with an oestrous female, his coalition partners respect his 'ownership' of the female, avoiding the pair and retreating from the threats of the consorting male. Again, dominance is temporary and state dependent, with an owner on one occasion becoming a rival on another. Individual mating success is unequal in coalitions where companions vary in age or size but is equivalent in coalitions where companions are evenly matched. However, paternity tests revealed a considerable skew in reproductive success in larger coalitions (Packer *et al.*, 1991), even in groups that showed no obvious dominance hierarchy. We do not know whether ownership rules are ignored by those few males who do enjoy high reproductive success, or if reproductive skew results from some other form of male–male competition or from the preferences of the females.

We have argued that lions respect ownership both because contestants are usually evenly matched in age and size and because of the high costs of fighting. Besides having sharp teeth and strong jaws, lions can easily blind an opponent with their claws. However, hyenas are also formidable fighters yet show strict dominance (see Section 11.2.3). An additional cost of fighting to lions is that companions are vital alliance partners for territorial defence and damaging or killing a companion would be highly detrimental (see Section 11.3.3).

11.2.5 Dominance and models of reproductive skew

Models of reproductive skew (see Chapter 10) may help explain the occurrence, strength and intensity of dominance hierarchies. Assuming that the dominant can control the subordinate's reproduction, these models predict that four parameters will affect the extent to which reproduction will be skewed:

- 1 the probability a subordinate can breed successfully on its own elsewhere;
- 2 the extent to which the subordinate can increase the dominant's productivity;
- 3 the genetic relatedness of the pair;
- 4 their relative fighting abilities.

Under certain circumstances, dominants are expected to cede reproductive opportunities to subordinates to induce them to stay (staying incentives), or to induce them to cooperate without fighting (peace incentives). In general, these incentives will increase with increasing prospects for breeding alone (since leaving becomes more advantageous for the subordinate), increasing productivity by the dominant (since the dominant can afford to surrender more to the subordinate), and decreasing kinship (since the subordinate gains fewer inclusive fitness effects from assisting the dominant). Peace incentives will increase as fighting ability becomes more similar.

How do these incentives influence dominance behaviour? If dominants cede more reproduction to subordinates, do they merely permit subordinates more access to food or mates, while continuing to enforce strict dominance, or do dominance relationships themselves become less clear-cut? Keller and Reeve (1994) suggest that as the incentives increase, the frequency and intensity of dominance interactions should decrease, not only because subordinates gain a lower payoff from 'testing' the fighting ability of the dominant but also because dominants have less to lose from such challenges. Dominance should therefore be most pronounced when skew is high, but this does not appear to be the case in several mammalian species. Male lions generally exhibit high skew but inconspicuous dominance, while female baboons exhibit relatively low skew but pronounced dominance. However, much more research is necessary to quantify the severity of dominance interactions across species and to measure their associated skew.

11.3 Cooperation

Although kinship plays an essential role in the evolution of cooperative behaviour (as reviewed in Chapters 9 and 10), the formation of cooperative relationships between non-relatives has also generated considerable theoretical interest and extensive empirical research. Cooperative behaviour is often assumed to involve a short-term cost (if only through an 'opportunity cost' from failing to behave selfishly), but the long-term consequences of repeated cooperation may be fundamental to understanding social relationships. In fact, most theoretical work explicitly recognizes that cooperation involves repeated interactions between the same pair of individuals.

11.3.1 Reciprocity

The basic paradigm for most evolutionary models has been the 'Prisoner's

dilemma' (Box 11.2) where individuals have only two alternatives: to cooperate or to defect. By definition, mutual cooperation gives a higher payoff than mutual defection. However, in the prisoner's dilemma, a defector gains an even higher payoff when paired with a cooperator. Thus, although everyone would do best if everyone cooperated, a selfish mutant could always invade a cooperative population.

Box 11.2 Reciprocity: the basic problem

Considerable theory has been developed to specify the conditions when individuals might form long-term cooperative relationships despite short-term advantages from selfish behaviour. Most models specifically deal with interactions between two unrelated individuals where each individual only has two options, either to cooperate or to defect.

	Against	
	Cooperate	Defect
Cooperate	R	S
Defect	T	P

Models of reciprocity are based on a specific set of payoffs called the 'prisoner's dilemma'. If both players cooperate, they both receive the reward (R) from mutual cooperation, but if both defect they receive the punishment (P) from mutual defection. If the opponent cooperates, there is a temptation (T) to cheat which causes the lone cooperator to receive the sucker's payoff (S). Because $T > R > P > S$, defection confers the highest short-term benefits. However, repeated interactions theoretically permit the evolution of cooperation through some form of reciprocity. Such strategies cooperate in the first encounter but only continue to cooperate if their opponent also cooperated and to defect if their opponent defected.

The simplest strategy involving reciprocity is called 'tit-for-tat' (TFT). TFT initially cooperates then behaves according to its opponent's behaviour during the prior move. In an iterated game between two individuals playing TFT, both contestants start out cooperatively and both continue to cooperate in all subsequent interactions:

1's payoff RRRRRRRRRRRR...
 Player 1: TFT CCCCCCCCCCCC...
 Player 2: TFT CCCCCCCCCCCC...
 2's payoff RRRRRRRRRRRR...

Continued on p. 267

Box 11.2 Cont'd.

In an iterated game of N encounters, each individual therefore receives a cumulative payoff of RN .

If TFT meets a pure defector (ALL-D), TFT suffers in the initial encounter, but then gains the same payoff as ALL-D in all subsequent interactions:

1's payoff SPPPPPPPPPPPP...
 Player 1: TFT CDDDDDDDDDDDD...
 Player 2: ALL-D DDDDDDDDDDDDD...
 2's payoff TTPPPPPPPPPPPPP...

An iterated prisoner's dilemma gives a cumulative payoff matrix of:

	Against	
	TFT	ALL-D
TFT	RN	$S + P(N-1)$
ALL-D	$T + P(N-1)$	PN

In a population of TFT, ALL-D cannot invade if $RN > T + P(N-1)$, which is most likely when N is very large. Although TFT can never invade ALL-D, as $N \rightarrow \infty$, $PN \approx S + P(N-1)$, and TFT may persist long enough to gain a foothold in the population, then spread if it can primarily interact with other TFT strategists (i.e. if the population is spatially structured).

Although selfish behaviour is expected to dominate whenever individuals meet for only a single encounter, repeated interactions allow the evolution of cooperation through some form of reciprocity (Trivers, 1971). By basing its own behaviour on the prior behaviour of its opponent, an individual can benefit from mutual cooperation while preventing cheats from prospering.

Following Axelrod and Hamilton (1981), numerous authors have investigated the conditions where reciprocity can evolve. Their original analysis suggested that animals might follow a simple strategy called 'tit-for-tat' (TFT) which shows an initial bias towards cooperation then copies each of its opponent's moves. Box 11.2 presents a simplified version of the iterated prisoner's dilemma and outlines the major features of the game. We seek a strategy that is not only able to withstand invasion by a selfish strategy ('all defect' or ALL-D) but that can also invade a purely selfish population. This latter point is important since selfishness is generally assumed to be the ancestral condition.

Although TFT has often been considered an evolutionarily stable strategy (ESS: *sensu* Maynard Smith, 1982), there is no ESS in the iterated prisoner's dilemma. This partly results from the mathematical pathologies of the repeated game: in a population of TFT, an unconditionally cooperative strategist (ALL-C) would gain the same overall payoff and thus be able to persist by drift. Once enough ALL-C have appeared, the population could be invaded by ALL-D. In addition, certain strategy combinations can replace TFT. A population playing TFT can be invaded by a pair of mutant strategies called tit-for-two-tats (TF2T), which waits for its opponent to defect twice in a row before retaliating, and suspicious TFT (STFT), which has an initial bias to defect before playing TFT (Boyd & Lorberbaum, 1987).

The most important weakness of TFT, however, is that any mistakes can lead to a permanent breakdown in cooperation (Box 11.3). Thus, if both

Box 11.3 The problem of mistakes

As originally formulated, the iterated prisoner's dilemma assumed that animals never made any mistakes in judging their opponent's behaviour, but TFT is so responsive that a single mistake leads to a long series of mutual retaliation:

```

1's payoff  RRRRRRSTSTST...
Player 1: TFT  CCCCCCDDDDDC..
Player 2: TFT  CCCCCCDDDDDC..
2's payoff  RRRRRRSTSTST..
    
```

By the convention of these models ($T + S/2 < R$, so these over-reactive responses confer lower fitness than a strategy that can recover from such mistakes and resume mutual cooperation. The simplest of these is TF2T which only stops cooperating after two successive defections by its opponent:

```

1's payoff  SSPPPPPPPPPP...
Player 1: TF2T  CCDDDDDDDDDDDD..
Player 2: ALL-D  DDDDDDDDDDDDDDD..
2's payoff  TTPPPPPPPPPPP...
    
```

TF2T is not provoked into defecting by a single mistake:

```

1's payoff  RRRRRRTPRRRR..
Player 1: TF2T  CCCCCCDDCCCC..
Player 2: TF2T  CCCCCCDDCCCC..
2's payoff  RRRRRRRRRRRR...
    
```

Continued on p. 269

Box 11.3 Cont'd.

The most robust of these mistake-correcting strategies is called 'Pavlov' because it changes its behaviour after receiving a poor payoff (P or S), but repeats its behaviour after receiving T or R . Pavlov also has an initial bias to cooperate:

```

1's payoff  RRRRRRPPRRRR..
Player 1: Pavlov  CCCCCCDDCCCC..
Player 2: Pavlov  CCCCCCDDCCCC..
2's payoff  RRRRRRSPRRRR..
    
```

Note that the individual receiving T defected again in the following move whereas the individual receiving S changed its behaviour to defect. But once both received P , both changed their behaviour to cooperate, and mutual cooperation was thereby restored.

Pavlov can also exploit an unconditional cooperator (ALL-C). Whereas TFT or TF2T would quickly return to mutual cooperation after a single round of exploiting ALL-C, Pavlov continues to defect and therefore 'never gives a sucker an even break':

```

1's payoff  RRRRRRRTTTT...
Player 1: Pavlov  CCCCCCDDDDDD..
Player 2: ALL-C  CCCCCCDDCCCC..
2's payoff  RRRRRRSPSSSS..
    
```

Although Pavlov performs better than TFT in an imperfect world, it fares poorly in a population of ALL-D (only receiving SPSPSP...).

Against	Pavlov	ALL-D
Payoff to Pavlov		
Pavlov	RN	$N(S + P)/2$
ALL-D	$N(T + P)/2$	PN

Thus, Nowak and Sigmund's (1993) analysis suggests that Pavlov is most likely to appear in a population after TFT has replaced ALL-D and can only persist if $R > (T + P)/2$.

opponents play TFT, a single mistake sets up an alternating pattern of retaliation with each animal changing its behaviour in response to its partner until a second mistake either restores mutual cooperation or leads to mutual

defection. Box 11.3 outlines the various strategies that might permit reciprocity in the face of mistakes. These include TFT which 'forgives' a single mistake and 'Pavlov' which repeats its prior move after receiving a good payoff (R or T), but changes its behaviour after a poor payoff (S or P). If cooperation breaks down, Pavlov results in mutual defection for just one move before cooperation is restored. Nowak and Sigmund's (1993) analysis suggests that while TFT may often be the first form of cooperation to appear in a selfish population, it will generally be replaced by Pavlov.

It is important to note, however, that all these analyses are based on quite restrictive assumptions. Pairs of animals are assumed to make simultaneous decisions without any information about the opponent's current move (for a rigorous examination of alternating decisions see Nowak & Sigmund, 1994). Contests are always between pairs of individuals; reciprocity based on communal resources is unlikely to evolve in groups larger than two (Boyd & Richerson, 1988). Payoffs are assumed to be perfectly symmetrical and to remain unchanged through evolutionary time. Asymmetrical payoffs may mean that one partner faces a prisoner's dilemma while the other does not (Facker & Ruttan, 1988), or that a dominant individual might have the option of manipulating its subordinate partner (Clutton-Brock & Parker, 1995; see also Section 11.3.2).

Even in games that allow mistakes (e.g. Nowak & Sigmund, 1993), the mistake rate is low, the game is assumed to be infinitely iterated and players can only remember the opponent's behaviour in the prior move (thus excluding tolerant strategies such as TFT). The assumption of an infinite iteration allows the outcome of the initial encounter to be ignored. Thus, TFT behaves the same as ALL-D in a population of ALL-D and so can persist until drift enables a critical mass of TFT cooperators to interact and reap the rewards of mutual cooperation; TFT then permits the coexistence of ALL-C or Pavlov, but ALL-C is prone to invasion by ALL-D, whereas Pavlov is less so. Infinite iteration also assumes that animals will not 'discount' future payoffs, and thus that they will forego immediate payoffs for higher future rewards, whereas empirical studies show that animals have strong preferences for immediate gain (Stephens *et al.*, 1995).

The theoretical literature on the iterated prisoner's dilemma may therefore be summarized as supporting a general tendency toward some form of cooperation in very long-term relationships. The conditions where cooperation is actually expected, however, are extremely limited — provided that animals are only allowed two options in each interaction: either to cooperate or to behave selfishly.

11.3.2 Other routes to cooperation

Given the substantial difficulties facing the evolution of reciprocity, it is important to consider alternative explanations for cooperation, especially when evaluating empirical data. We outline three of these in Box 11.4.

Box 11.4 Other routes to cooperation

A: Short-term mutualism

Cooperative interactions do not necessarily involve a prisoner's dilemma. Two heads may be better than one (with both individuals receiving the largest award from mutual cooperation), and there may be no advantage from exploiting a companion's behaviour.

		Against	
Payoff to		Cooperate	Defect
Cooperate	$R = 6$	$S = 3$	P
Defect	$T = 2$		

In this case, cooperation is expected even when opponents meet for only a single encounter. By definition, $R > P$, but if $P > S$, defection is also an ESS, and cooperation is most likely to evolve in a structured population (where families of cooperators typically receive R , while families of defectors mostly receive P).

B: Long-term models of mutualism

Payoffs may conform to the prisoner's dilemma in the short term but become mutualistic in the long term. This transition, however, does not result from following complex behavioural strategies (as is the case for reciprocity), but from the rebounding consequences of selfishness.

Consider a daily game where the payoffs depend not only on the behaviour of each contestant, but on the number of animals playing the game each day, and each animal receives a higher payoff as a member of a pair than as a solitary. Let the pairwise payoffs follow the prisoner's dilemma, but assume that defection increases the partner's risk of mortality. The survivor subsequently becomes a solitary who receives a daily payoff of X , where $X < S$. In the extreme case, a single defection kills the partner, and the partner cannot be replaced. Thus, the payoffs are accumulated as follows:

1's payoff	S
Player 1: ALL-C	C
Player 2: ALL-D	DDDDDDDDDDDDDD...
2's payoff	XXXXXXXXXXXXXX...

When both defect, one or both is killed. Payoffs are either:

1's payoff	P
Player 1: ALL-D	D
Player 2: ALL-D	DDDDDDDDDDDDDD...
2's payoff	PXXXXXXXXXXXXXX...

Box 11.4 Cont'd.

Or:

1's payoff P
 Player 1: ALL-D D
 Player 2: ALL-D D
 2's payoff P

But when both cooperate:

1's payoff RRRRRRRRRRRR...
 Player 1: ALL-C CCCCCCCCCCCCCC...
 Player 2: ALL-C CCCCCCCCCCCCCC...
 2's payoff RRRRRRRRRRRR...

Thus, the cumulative payoffs are:

Against

Payoff to	ALL-C	ALL-D
-----------	-------	-------

ALL-C	RN	S
ALL-D	$T + X(N-1)$	$P \text{ or } P + X(N-1)/2$

If $N > 1$ and $R > (T + X)/2$, the most likely outcome would be unconditional cooperation. However, the population would have to be structured for cooperation to invade a population of pure defectors. Note that in this case, pure cooperation clearly fares better than any conditional strategy (such as TFT) if animals risk mistaking their companion's behaviour.

Group-living often confers advantages strong enough to counter the short-term advantages of selfish behaviour. A good example is Lima's (1989) model of cooperative vigilance. Each individual must trade-off vigilance for foraging. A more vigilant individual protects itself and its companion from predation, but spends less time foraging. The short-term selfish optimum should therefore involve relatively little vigilance. However, because the predator is assumed to capture only one prey at a time, an animal's survival greatly reduces its companion's risk of predation (due to the dilution effect). Thus, in a repeated-encounter game, animals will have to improve their companion's chances of survival so as to minimize their own long-term risk of predation.

C. Producers versus scroungers

Obtaining resources can often entail an inherent cost, but no resources will be

*Continued on p. 273***Box 11.4 Cont'd.**

available unless someone works to extract them. In this case, there may be a temptation to defect ($T > R$), but cooperators are at an advantage when they are rare.

Against

Payoff to	Cooperate	Defect
-----------	-----------	--------

Cooperate	$V/2 - C/2$	$V/2 - C$
Defect	$V/2$	0

Two individuals compete for a resource of value, V , extracting the resource incurs some cost, C . As long as someone works to extract the resource, it is divided between both contestants. If both work together, each pays 50% of the costs. As long as $V/2 - C > 0$ cooperators (producers) can invade defectors (scroungers), but if defectors gain equal access to the resource without paying any costs, scroungers can always invade producers.

In this case cooperation will be frequency dependent, and in large groups subsets of cooperators may coexist with a proportion of defectors.

D. Coerced cooperation

Most models of cooperation assume that animals have only two options, either to cooperate or to defect. In addition, these models assume that both players possess exactly the same skills and RHP. However, most animals live in groups with definite dominance hierarchies and their relationships will generally be asymmetrical (see Section 11.2). Thus, a difference in RHP or dominance rank may permit one animal to coerce its companion into behaving cooperatively (Clutton-Brock & Parker, 1995). Note that the following analysis now describes phenotype-limited strategies:

Consider a two-person game with the same basic structure as the prisoner's dilemma. However, now allow a dominant animal to punish any subordinate that fails to behave cooperatively. Let d be the costs to the dominant of punishing the subordinate, and i the costs to the subordinate of being punished. If $S > P - i$, then a defecting subordinate will do better to change its behaviour to cooperate than to risk further punishment. If the subordinate subsequently starts to cooperate and $T - d > P$, the dominant benefits by punishing the subordinate every time it defects:

Continued on p. 274

Box 11.4 *Cont'd.*

Punishment

↓
 1's payoff $P - i$ SSSSSSSSSSSS...
 Player 1: subordinate D CCCCCCCCCCCC...
 Player 2: dominant D DDDDDDDDDDDD...
 2's payoff $P - d$ TTTTTTTTTTTT...

However, if $S < P - i$, the subordinate would be better off incurring repeated punishment rather than submitting to the demands of a tyrannical despot. In which case, the dominant might be expected to behave as a benevolent despot, habitually cooperating and forcing the subordinate to cooperate as well:

Punishment

↓
 1's payoff $T - i$ RRRRRRRRRRRR...
 Player 1: subordinate D CCCCCCCCCCCC...
 Player 2: dominant C CCCCCCCCCCCC...
 2's payoff $S - d$ RRRRRRRRRRRR...

Here the subordinate will cooperate if $R > T - i$, and the dominant will be expected to punish each defection if $R - d > S$.

The most obvious explanation for cooperation is that when an individual meets a cooperative partner, it gains a higher payoff from cooperating than from defecting. In the absence of any temptation to cheat, cooperation is clearly an ESS even in a single-encounter game and no elaborate safeguards against cheating will be expected. The set of payoffs described in Box 11.4A are often described as 'byproduct' mutualism (West-Eberhard, 1989) because cooperation is the best strategy regardless of the opponent's behaviour, and thus cooperation is merely a byproduct of following the optimal strategy.

Mutualistic advantages can also arise in long-term interactions, even if the payoffs from any single encounter are consistent with the prisoner's dilemma. In Box 11.4B, we present a simplified example in which individuals gain a short-term advantage from cheating, but this selfish behaviour results in the loss of their companion with the consequence that they must subsequently live alone. With strong enough advantages of grouping, unconditional cooperation will be favoured in an iterated game (Lima, 1989). Again, in such situations, no elaborate cooperative strategies are necessary: the well-being of one's companions has an important effect on personal fitness. However, the outcome of more realistic games will depend on the ease with which partners can be replaced.

Cooperation may not always be two-sided or ubiquitous. 'Producers' may extract more resources per capita than 'scroungers', yet a population of producers will often be prone to invasion by scrounging and vice versa (see Barnard, 1984). In pairwise interactions, this may result in one individual cooperating while the other defects (Box 11.4C), but in larger groups a subset of individuals would be expected to cooperate while the remainder defect (see Section 11.3.3). Thus, a majority of individuals may cooperate unconditionally.

Finally, several recent models have examined the possibility that cooperation may be imposed by coercion (e.g. Boyd & Richerson, 1992; Clutton-Brock & Parker, 1995). This approach is especially relevant here, since dominance relationships are explicitly incorporated into the structure of the payoffs — and dominance relationships are nearly universal in animal societies. The important addition of these models, however, is that individuals can physically punish defectors whereas earlier models only permit TFT or Pavlov to withhold further cooperation.

As outlined in Box 11.4D, dominant animals may often be expected to coerce subordinates to behave cooperatively. For simplicity, we have assumed that a single punishment induces the subordinate into cooperating in all subsequent encounters. In reality, of course, the evolution of 'enforced cooperation' will depend on the speed with which the subordinate 'learns' to cooperate in response to the dominant's behaviour (Clutton-Brock & Parker, 1995) as well as on the rate of recidivism. If dominants can impose sufficiently heavy costs they may be able to exploit the subordinate and maintain a highly one-sided relationship. However, in other circumstances the dominant would be forced to settle for a mutually cooperative relationship (also see Section 11.2.5 and Chapter 10).

In summary, none of these routes to cooperation requires strategies as elaborate as TFT or Pavlov, and in many cases such 'reactive' strategies would be highly disadvantageous compared to a simple strategy of 'all cooperate'. Coercion may be reactive (i.e. the subordinate is punished if it does not cooperate), but only leads to mutual cooperation when the dominant cannot maintain a purely exploitative relationship with the subordinate.

11.3.3 Empirical studies

Several recent reviews (e.g. Packer & Rutan, 1988; Emlen, 1991; Clements & Stephens, 1995) have concluded that reciprocity is rare to non-existent in nature, while others suggest that reciprocity is widespread (e.g. Dugatkin *et al.*, 1992). Reciprocity remains one of the most beguiling concepts in behavioural ecology, but the most formidable obstacle to proving its existence stems from the difficulty of measuring short-term payoffs. Does a particular example of cooperation really follow a prisoner's dilemma or is it mutualistic?

Here we outline three different studies of cooperative behaviour that highlight the difficulties in disentangling the alternatives.

Cooperation in African lions

Field studies confirm that African lions are highly cooperative. Lions hunt in groups (Scheel & Packer, 1991; Stander, 1992), females raise their young in a communal crèche (Pusey & Packer, 1994) and both sexes defend joint territories against like-sexed individuals (McComb *et al.*, 1994; Heinsolin & Packer, 1995; Grinnell *et al.*, 1995). Lions of each sex gain higher reproductive success by living in groups (Packer *et al.*, 1988): males in larger coalitions gain higher per capita reproductive success than those in smaller coalitions, and females in moderate-sized prides have higher fitness than those in very small prides. These advantages, however, are the summed outcome of a variety of behaviours, and we discuss the evolutionary basis of each in turn.

Group hunting. By hunting together, individuals can increase their joint hunting success so that $R > P$. However, an individual joining a hunt is likely to incur costs, whether from the energetic effort required to capture the prey or from the risk of injury while subduing the prey. When the prey is large enough to feed an entire group, the decision to join a group hunt may follow a prisoner's dilemma (Packer & Rutan, 1988). If the success rate of a lone hunter is already high, a second hunter may not be able to improve the group's success rate sufficiently to overcome its own costs of hunting, in which case $T > R$. However, if individual success rate is very low, two heads may be so much better than one that the improved chances of prey capture can overcome the personal costs of joining the hunt, in which case $R > T$.

Lions, like most other group hunters (Packer & Rutan, 1988), show the clearest evidence of cooperation when R is likely to be greater than T , and thus when cooperation is mutualistic. Scheel and Packer (1991) found that individual behaviour during group hunts could be classified into several discrete strategies, one of which, 'refraining', involves almost no participation in the hunt. 'Refrainers' remain stationary or move only a few paces towards a distant prey animal and do not join in the final charge. Other lions clearly cooperate, actively stalking the prey and participating in the final charge. Consistent with predictions of mutualism, the probability that Serengeti lions cooperated during a group hunt depended on two factors relating to hunting success.

1 Lions were most likely to cooperate when the prey was difficult to capture, and showed higher levels of 'refraining' when their companions pursued prey that was more easily captured.

2 Since male lions are less skillful hunters than females, they are less able to improve the females' success rate, and they 'refrained' more than females.

Perhaps the most impressive data on cooperative hunting in lions comes from Stander's (1992) studies in Namibia. These animals demonstrated a clear

division of labour, with certain individuals habitually stalking to the left, others habitually stalking to the right and the remainder moving directly towards the prey. However, they hunted fleet-footed prey in open habitat, and individual hunting success was close to zero. Thus, their cooperative hunting was highly likely to have been mutualistic.

Across a variety of species, cooperative hunting appears to be restricted to circumstances of simple mutualism (see Caro, 1994; Creel & Creel, 1995), even though cooperation might theoretically evolve by reciprocity. However, it might often be impossible to detect whether a hunt has failed due to the elusiveness of the prey or to the detection of another hunter (Packer & Rutan, 1988). Strategies such as TFT and Pavlov are sensitive to the mistake rate (see Box 11.3), and thus reciprocity may not evolve in situations where failure is the most likely outcome of a cooperative interaction.

Although cooperative hunting appears to be largely mutualistic, this conclusion must be considered provisional until experimental tests of reciprocity can be devised. All published studies are strictly correlative; no field study has ever measured T , R , S and P .

Communal cub-rearing. Female lions pool their cubs in a 'crèche' and raise them communally, even nursing each other's cubs. In the short term, communal nursing may involve a prisoner's dilemma (see Caraco & Brown, 1986). A defector directs all her investment to her own cubs while a cooperator allows all cubs to nurse equally. Thus, the defector pays some small costs of vigilance to ensure that only her cubs nurse from her, but her cubs gain exclusive access to her milk. A pair of cooperative females avoid the costs of excluding other cubs ($R > P$), but when a defector is paired with a cooperator, the defector's cubs gain all their mother's milk plus a portion of the cooperator's (T), while the cooperator's cubs only gain a portion of their mother's milk (S). With trivial costs of enforcement, $T > R > P > S$.

However, females do not form crèches in order to engage in communal nursing. Crèches are protective coalitions against infanticidal males, and groups of mothers are more effective than solitary ones (Packer *et al.*, 1990). Once together, though, the mothers have to balance a number of different activities, and cubs often try to nurse when their mothers are resting or sleeping. Thus, mothers are constrained to be gregarious and communal nursing is largely a consequence of their cubs' parasitic behaviour (Pusey & Packer, 1994). It is therefore misleading to view communal nursing in isolation. Instead, losing milk to non-offspring appears to be a cost of forming the crèche, with individual females adjusting their milk distribution according to their personal costs.

Field observations revealed that female lions nursed indiscriminately only when paired with their closest female kin. When their companions were distant relatives, mothers directed most milk to their own offspring. Lion litter size varies from one to four, and milk production appears to be independent of litter size. Females with small litters were more generous than mothers

of larger litters, presumably because of the lower costs of milk loss (Pusey & Packer, 1994). Although the precise payoffs are impossible to measure, there is no evidence that communal nursing in lions involves any form of reciprocity; after kinship and litter size were controlled for, females did not nurse their companions' cubs according to the extent to which their own cubs were nursed by their companions.

Group territoriality. Lions maintain joint territories that persist over generations, and successful reproduction requires a high-quality territory. The lion's roar is a territorial display, and both sexes respond cooperatively to the pre-recorded roar of a like-sexed stranger. Approaching the speaker and even attacking a stuffed lion hidden nearby. Playback experiments reveal that lions are most likely to respond when they outnumber their opponents and that they often monitor each other's behaviour while approaching the speaker (McComb *et al.*, 1994; Grinnell *et al.*, 1995). Territorial defence is likely to involve a short-term prisoner's dilemma, with joint defence being more effective than non-defence ($R > P$) and a defector suffering fewer risks of injury than a cooperator during an intergroup encounter ($T > S$). A single defender can repel a lone intruder, so $T > R$.

However, several studies suggest that lions cooperate unconditionally, rather than basing their responses on their companions' behaviour. Grinnell *et al.* (1995) found that males would approach the speaker when their companions were absent, thus cooperating even when their companions' response could not be monitored. Even more strikingly, Heinsohn and Packer (1995) found that certain females habitually lagged behind their companions during the approach to the speaker. 'Leaders' could recognize whether their companions were also leaders or if they were 'laggards'. However, when paired with a laggard, a leader would continue toward the speaker, arriving considerably earlier than the laggard. Thus, the leaders cooperated rather than 'defected' in response to their partner's defection, nor did they physically punish a laggard for failing to cooperate.

As in communal nursing, a focus on short-term payoffs is probably inadequate: male lions enjoy only a brief tenure within a pride and they need their companions for future interactions (Grinnell *et al.*, 1995). Males must therefore behave cooperatively at every opportunity to enjoy long-term mutualistic advantages (see Box 11.4B). For females, the territory is a long-term resource that must be defended habitually and any failure to defend the territory today will result in fewer resources tomorrow (Heinsohn & Packer, 1995). However, as long as enough females maintain effective defence of the territory, a proportion of laggards can take advantage of their companions' behaviour, resulting in a mixture of producers and scroungers (see Box 11.4C).

In summary, the precise evolutionary basis of the lions' cooperative behaviour is difficult to determine because of their complex social system and the long-term consequences of their short-term decisions. Furthermore,

behaviour in one context may well rebound on another, with foraging success influencing territorial defence, and so on. Nevertheless, it is striking that one of the most cooperative of all mammalian species shows no obvious adherence to the rules of reciprocity.

Predator approach behaviour

Many species of fish approach and orientate towards a novel predator, and this behaviour has been dubbed 'predator inspection' whereby individuals obtain information about the predator's hunger and aggressiveness (Pitcher *et al.*, 1986; Milinski, 1987). Repeated tests have shown that experimental groupings of sticklebacks, guppies and mosquito fish will move into close proximity of the predator, and they often do so in pairs (Milinski, 1992; Turner & Robinson, 1992). Milinski (1987) was the first to suggest that predator inspection involved a prisoner's dilemma, defining any move towards the predator as 'cooperation' and any movement away from the predator as 'defection'.

Cooperative pairs gain R because of the advantages of inspecting the predator from the comparative safety of a group. Defecting pairs only gain P because they learn nothing about the predator's state. Single defectors gain T by remaining at a safe distance and watching the predator's response to the cooperative companion. Finally, the lone cooperator gain S from incurring the risk of being selected by the predator. Thus, $T > R > P > S$. Milinski (1987, 1990) and others (Dugatkin, 1988, 1991; Masters & Waite, 1990; Huntingford *et al.*, 1994) have shown that sticklebacks typically copy each other's behaviour while approaching a predator, and most have interpreted this pattern as evidence of TFT.

However, several other authors have viewed the same behaviour quite differently, interpreting it instead as 'pursuit deterrence' (e.g. Lazarus & Metcalfe, 1990), and one study has shown that non-approaching fish suffer higher risk of predation than the approaching partner (Godin & Davis, 1995a,b). This result is consistent with a broad literature suggesting that cryptic predators are less likely to attack once they have been detected (e.g. FitzGibbon & Fanshawe, 1988). If this is also generally true in predatory fish, the short-term payoffs from approaching the predator would be mutualistic, with $R > S > P > T$. Copying the partner's behaviour in this case can simply be explained by shoaling: individuals benefit from the dilution effect by staying as close together as possible, whether moving toward or away from the predator.

Despite nearly 10-years research in a highly tractable system, where straightforward manipulations can be performed with mirrors, models and trained fish, it is still not clear which of these alternative viewpoints is more nearly correct. While it seems intuitive that $R > P$ (the fish do typically approach the predator in pairs, so the behaviour must confer some benefit), it has proven remarkably difficult to measure S and T to everyone's satisfaction.

Godin and Davis's (1995a,b) data suggest that $S > T$, but their methods have been criticized by Milinski and Boltschauser (1995), and data collected by Dugatkin (1992) suggest that, in mixed groups, individuals that had previously been classified as inspectors suffered greater predation risk than non-inspectors.

In the absence of any consensus concerning the payoffs, it is still possible to test hypotheses that distinguish between TFT and shoaling. Assuming that the fish are in a prisoner's dilemma and that they are playing some form of reciprocity, they should copy each other's behaviour according to certain rules (Lazarus & Metcalfe, 1990; Reboreda & Kacelnik, 1990; Huntingford *et al.*, 1994; Stephens *et al.*, 1996). If both animals cooperate on one move they should continue to cooperate on the following move; if both defect, both should either defect again (if playing TFT) or cooperate (if playing Pavlov). If one cooperates and the other defects, then the behaviour of one or both will be expected to change depending on whether the animals are playing TFT or Pavlov.

The predicted transition matrices for these two strategies are given in Table 11.1, as well as empirical data collected by Stephens *et al.* (1996) who took as separate 'moves' the animals' net movement every 1.09 s. These data show that while mutual cooperation is followed by further cooperation 57% of the time, and that mutual defection is typically followed by further defection (consistent with TFT), the most important predictions of TFT and Pavlov are not met. Whenever a non-cooperator is paired with a cooperator, the fish were not reactive but instead tended to repeat their prior move (the most common response to CD was CD, etc.).

Consistent with shoaling, however, fish were most likely to copy each other's movements when they were in close proximity and to move towards each other when farther apart (even when this meant moving in opposite directions with respect to the predator). Thus, a major goal of their movements seems to be to maintain close proximity with their companion, rather than to maintain a close check on each other's cooperative tendencies.

Critics of the shoaling hypothesis counter that if there was an inherent, mutualistic advantage of grouping, then every fish in the tank should approach the predator together whereas they typically approach in pairs (Milinski *et al.*, 1990; Dugatkin, 1996). Pairwise approaches are also considered evidence of reciprocity since TFT is most likely to evolve in small groups (Boyd & Richerson, 1988). Proponents of shoaling counter that the advantages of predator deterrence are likely to be frequency dependent, so that the optimal group size for approaching the predator may only be one or two (Godin & Davis, 1995b; Stephens *et al.*, 1996).

The chief attraction of this system compared to most field studies has been that short-term payoffs are likely to be the sole determinant of the fishes' behaviour. However, it is disturbing to realize how inconclusive the predator inspection/deterrence controversy has been. Perhaps it is futile to study the

Table 11.1 Transition matrices for predator-approach behaviour predicted by TFT, Pavlov and empirical data collected by Stephens *et al.* (1996). The unique predictions of TFT are printed in **bold**, and of Pavlov in *italics*. By TFT, if both defect (DD) in the first move then both should continue to defect (DD) in the next move; if one defects when its partner cooperates in the first move (DC), the two should reverse their behaviour (CD) in the second, and vice versa (CD → DC), while a cooperative pair (CC) should continue to cooperate (CC). With Pavlov, mutual defection (DD) should provoke mutual cooperation (DD → CC), as should mutual cooperation, whereas defection by a single partner should lead to mutual defection (CD → DD and DC → DD).

From	To			
	DD	DC	CD	CC
<i>Tit-for-tat</i>				
DD	1	0	0	0
DC	0	0	1	0
CD	0	1	0	0
CC	0	0	0	1
<i>Pavlov</i>				
DD	0	0	0	1
DC	1	0	0	0
CD	1	0	0	0
CC	0	0	0	1
<i>Observed</i>				
DD	0.609	0.156	0.147	0.088
DC	0.266	0.362	0.117	0.256
CD	0.240	0.167	0.359	0.234
CC	0.090	0.135	0.204	0.571

evolutionary mechanism of cooperation when short-term payoffs cannot be experimentally controlled and manipulated.

Cooperative key-pecking in blue jays

In order to clarify the role of short-term payoffs in eliciting cooperative behaviour, Clements and Stephens (1995) conducted a series of operant feeding experiments where pairs of blue jays were each allowed to press one of two coloured keys. One key had the effect of being cooperative because if both cooperated, both received R , whereas if both pressed the opposite key, both received P , with $R > P$. The payoffs for these experiments (measured in numbers of food pellets) either conformed to a prisoner's dilemma or to simple mutualism (Fig. 11.2) and were held constant until the birds showed the same response more than 90% of the time for 4 consecutive days.

The birds typically completed 200 trials per day, and all three pairs showed the same result (Fig. 11.2): after a brief period of random pecking, they reacted to the prisoner's dilemma by settling into a pattern of mutual defection. Once the payoffs were changed to mutualism, the birds showed mutual cooperation.

Then, most intriguingly, when once again faced with the prisoner's dilemma, the birds quickly switched back to mutual defection, even though they entered the final phase playing mutual cooperation.

Although these results derive from a highly artificial experimental design, the study clearly shows that animals may not be as predisposed toward reciprocity as has often been claimed. Because the birds were separated by a partition, there was no scope for punishment (see Box 11.4C), and it would be interesting to test whether birds might enforce cooperation if they could physically punish non-cooperation by their partner. Future studies may seek to find a more naturalistic system but the first concern should be to have absolute control over the four possible payoffs from a pairwise game.

In summary, these studies emphasize the importance of carefully controlled experiments in determining whether cooperation results from mutualism or reciprocity. In practice, it may be impossible to provide definitive tests in naturalistic settings: animals do not behave in a vacuum and behaviour often has long-term as well as short-term consequences. There are many putative examples of reciprocity, but almost all suffer from the same general problem: does the behavioural exchange truly involve a prisoner's dilemma? For example, because of their greater cognitive abilities, non-human primates are widely believed to exchange altruistic acts (de Waal & Luttrell, 1988) and yet claims of reciprocity in these species have also been contested (see Bercovitch, 1988; Noë, 1990; Hemelrijk, 1996). One commonly cited context has been the exchange of altruistic behaviour for social grooming, yet there is no convincing evidence that grooming is itself costly (Dunbar, 1988; Hemelrijk, 1994). Without a clearly designed test where R , S , T and P are all known with certainty, any claims of reciprocity seem increasingly tenuous.

Fig. 11.2 Cooperative behaviour in three pairs of blue jays during operant feeding tests (Clements & Stephens, 1995). Black circles plot the percentage of trials each day in which the birds showed mutual cooperation (C), open circles show mutual defection (D), dotted lines show CD plus DC. When the payoffs followed a prisoner's dilemma, the number of food pellets received by each bird was $T = 5$, $R = 3$, $P = 1$, $S = 0$; when mutualistic, $R = 4$, $T = 5$, $P = 0$. The birds were separated by a glass partition in one treatment and by an opaque partition in the other, but the nature of the partition had no effect on the results.

