

Punishment in animal societies

T. H. Clutton-Brock & G. A. Parker

Although positive reciprocity (reciprocal altruism) has been a focus of interest in evolutionary biology, negative reciprocity (retaliatory infliction of fitness reduction) has been largely ignored. In social animals, retaliatory aggression is common, individuals often punish other group members that infringe their interests, and punishment can cause subordinates to desist from behaviour likely to reduce the fitness of dominant animals. Punishing strategies are used to establish and maintain dominance relationships, to discourage parasites and cheats, to discipline offspring or prospective sexual partners and to maintain cooperative behaviour.

"Upon this a question arises: whether it be better to be loved than feared or feared than loved? It may be answered that one should wish to be both, but, because it is difficult to unite them in one person, it is much safer to be feared than loved, when of the two, either must be dispensed with. . . for love is preserved by the link of obligation which, owing to the baseness of men, is broken at every opportunity for their advantage; but fear preserves you by a dread of punishment which never fails."

Machiavelli, *The Prince*.

RECIPROCAL altruism or positive reciprocity has been a major focus of theoretical and empirical research in evolutionary biology¹ since Trivers first drew attention to its importance²⁻⁵. In contrast, negative reciprocity (retaliatory infliction of fitness reduction) has attracted little attention: theoretical research on aggression has mostly focused on questions concerning expected levels of expenditure in conflicts⁶⁻¹⁰, whereas empirical research has investigated the motivation, causation, development and distribution of aggressive behaviour^{11,12}. Yet individuals (or groups) commonly respond to actions likely to lower their fitness with behaviour that reduces the fitness of the instigator and discourages or prevents him or her from repeating the initial action. We refer to behavioural tactics of this kind as punishment, without implying either a conscious decision or a moral sense on the part of the punisher. Although (human) social scientists¹³ now commonly restrict the term to the imposition of penalties by those in authority, punishment is still widely used to refer to interactions between individuals in humans and our definition is similar to Grotius' "the infliction of an ill suffered for an ill done"¹⁴.

As all forms of animal punishment presumably involve some cost to the punisher and benefits may be deferred, punishment is temporarily spiteful¹⁵, in the same way that reciprocal altruism is temporarily altruistic¹ (Fig. 1). However, in the longer run, punishment is a form of selfish behaviour which benefits the punisher because it reduces the probability that the victim will repeat a damaging action or will refuse to perform a beneficial one. In most cases, punishers benefit because victims learn to avoid repeating damaging behaviour, although, in extreme cases, punishment may be beneficial because victims are eliminated or forced to emigrate. Punishing tactics may also be learned: as punishers will often receive reinforcement from their opponents' responses, they will be likely to repeat their behaviour.

Evolutionary game theory models developed for asymmetric animal contests confirm that punishing tactics will often be evolutionarily stable¹⁶⁻¹⁸. Box 1 considers the simplest situation where two individuals differ markedly in fighting ability so that one can punish the other without fear of retaliation, whereas Boxes 2, 3 and 4 consider the more complex situation where individuals can retaliate to punishment, incorporating retaliation as a variant of the simple hawks-doves game. We initially focus on situations where a subordinate can choose whether or not to transgress against a dominant while the dominant can choose whether or not to punish them, subsequently considering cases where the roles are reversed and subordinates can choose

whether or not to punish the transgressions of dominants. Box 3 shows that 'commonsense' evolutionarily stable strategies (ESSs), where dominant individuals punish subordinates who subsequently avoid transgressing, and where dominants transgress against subordinates without fear of punishment or retaliation, are the most likely states to develop.

Do animals punish each other?

Most theoretical investigations of animal conflict have focused on contests in which two individuals compete for a resource, but many aggressive interactions among social animals occur where resources are not immediately at stake^{12,19,20-22}. Individuals frequently respond to threats or attacks by threatening or attack-

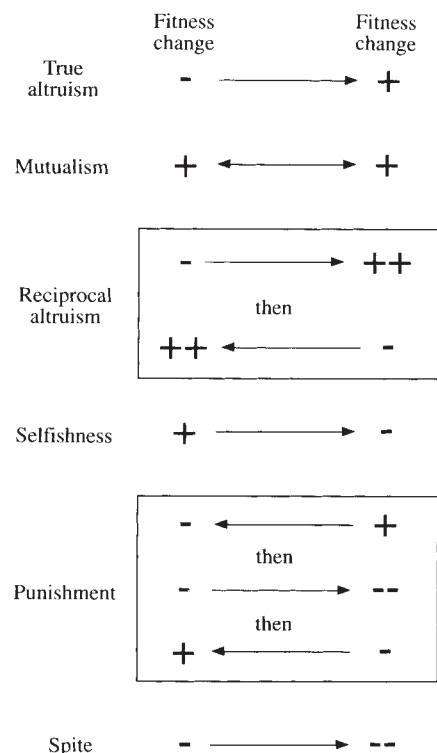


FIG. 1 The figure shows six categories of interactions between non-kin. A minus sign represents a loss of fitness, a plus sign a fitness gain. Arrows indicate the original initiator and recipient. In punishing interactions, a selfish action by the first player is followed by the first player being punished by the second. Subsequently, the first player modifies his/her behaviour so that it increases the fitness of the punisher at some cost to itself. Punishing tactics may also be used to coerce or augment altruistic behaviour in subordinates (see text). All six categories of interaction also occur between kin, though indirect benefits may alter the magnitude of fitness gains and losses.

BOX 1 Simple punishment games with a strong asymmetry in fighting ability

a

		Dominant (Player 1)	
		P	NP
Subordinate (Player 2)	D	$-jd_1 - jc_1$	$-Nc_1$
	T	$-jd_2 + jg_2$	$+Ng_2$
		$-Nd_1 - Nc_1$	$-Nc_1$
		$-Nd_2 + Ng_2$	$+Ng_2$

b

		Dominant (Player 1)	
		P	NP
Subordinate (Player 2)	C	$-jd_1 + kg_1$	0
	NC	$-jd_2 - kc_2$	0
		$-Nd_1$	0
		$-Nd_2$	0

c

		Player 1 = Potential PUNISHER	Player 2 = Potential PUNISHER	
Dominant (Player 1)	Subordinate (Player 2)	P	D, C	1 Mutual punishment
		D, C	P	
Dominant (Player 1)	Subordinate (Player 2)	NP	T, NC	2 Mutual non-punishment
		T, NC	NP	

3

Dominant (Player 1)	P	T, NC	3 Common sense punishment
Subordinate (Player 2)	D, C	NP	

4

Dominant (Player 1)	NP	D, C	4 Paradoxical punishment
Subordinate (Player 2)	T, NC	P	

To demonstrate the simplest punishment game (modified from ref. 16), assume initially that subordinate individuals cannot offer effective retaliation to dominants. Consider a repeated game between two animals, a dominant (player 1) and subordinate (player 2). **a**, Payoff matrix for a situation in which punishment can prevent a subordinate from committing an action against the dominant's interests. A 'strategy' prescribes how an individual behaves over N 'rounds', and an 'action' prescribes what happens in a given round. Payoffs over N rounds to the dominant are shown in the top right of each square, and payoffs to the subordinate on the lower left. At each round, an opportunity arises for the subordinate to increase its fitness at the dominant's expense. It may either transgress (T) by acting selfishly, or may desist (D), favouring the dominant's interests. If it plays T, it gains $+g_2$ units and the dominant loses $-c_1$ fitness units. However, the dominant may punish (P) the subordinate if it plays T, or may simply never punish (NP) whatever the subordinate does. Punish is never played if the subordinate desists. It has a significant damage cost to the subordinate of $-d_2$, and a small cost of $-d_1$ to the dominant. The subordinate must learn to desist: learning takes j rounds out of a total of N rounds ($k=N-j$). Thus against a P strategist, the payoff of a D strategist (which switches to D after j rounds) is $+jg_2 - jd_2$. Against an NP strategist, a D strategist continues to transgress and never switches to D, and hence receives $+Ng_2$ whereas the NP strategist loses $-Nc_1$. Payoffs are therefore the same as between T and NP strategists. Punishment occurs on each round between T and P strategists, so T's payoff is $+Ng_2 - Nd_2$ and P loses $-Nd_1 - Nc_1$. Note that T and NP strategies translate directly into actions, whereas D and P strategies prescribe actions that are conditional on opponents' actions. **b**, Parallel payoff matrix where punishment can prevent a subordinate from omitting to act in the dominant's best interests. Logic same as for **a**, but here the dominant gains if the subordinate cooperates. In practice, such circumstances are probably rarer than **a** but, in theory, they are identical. The subordinate may either act selfishly and fail to cooperate (non-cooperate, NC), or it may cooperate (C), giving the dominant $+g_1$ at a cost of $-c_2$ to itself. The rules about punishment, and learning to cooperate remain as in **a**. When the dominant plays NP, the payoff is zero to each player. When the dominant plays P and the subordinate C, the dominant gets $-jd_1 + kg_1$ and the subordinate gets $-jd_2 - kc_2$. But if the subordinate plays NC, it receives $-Nd_2$, and the dominant $-Nd_1$.

We now seek evolutionarily stable strategies (ESSs¹⁷) for **a** and **b**. I is an ESS if the payoff of I against itself exceeds that of I against any rare mutant strategy J: that is, $E(I, I) > E(I, J)$. 'Desist when 2, punish when 1' in **a**, and its analogue 'cooperate when 2, punish when 1' in **b**, is an ESS provided that (1) summed benefits exceed total punishment effort ($kc_1 > jd_1$ in **a**; $kg_1 > jd_1$ in **b**) to prevent player 1 from playing NP, and that (2) damage inflicted per punishment exceeds the cost per desist or cooperate ($d_2 > g_2$ in **a**; $d_2 > c_2$ in **b**) to prevent player 2 from playing T (a) or NC (b). But the strategy 'Transgress when 2, never punish when 1' in **a**, and its analogue 'non-cooperate when 2, never punish when 1' in **b** may also have some stability, because (1) player 1 is prevented from playing P, as $0 > -Nd_1$ and (2) any tendencies to show D (a) or C (b) unconditionally (that is, against NP) may prevent D or C spreading by drift, and so maintain T or NC. Thus strategies of altruism maintained by punishment, (D, P), (C, P), and probably also strategies of unpunished selfishness (T, NP), (NC, NP), can be ESSs. But the other possibilities (D, NP), (C, NP) or (T, P), (NC, P) cannot be ESSs: it can never pay to show altruism if there is no chance of punishment, or to punish without chance of eventual benefit.

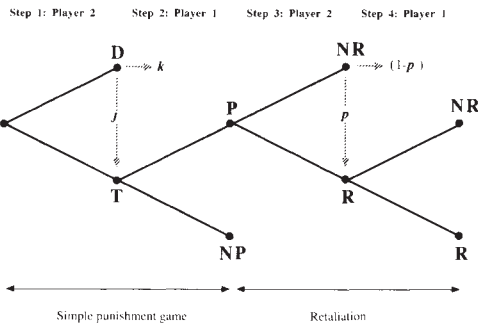
This game is characterized by two asymmetries: (1) the difference in dominance or fighting ability between players 1 and 2; and (2) the arbitrarily assigned role difference that gives player 2, the subordinate, the opportunity to transgress (or cooperate), and player 1 to punish. If we relax our assumption that only player 2 can transgress (or cooperate) so that roles can be reversed, this represents a separate game. It is possible for one ESS to apply when the subordinate has opportunity to transgress (or cooperate) and for the other to apply when the dominant occupies this role. **c**, Possible ESSs are shown as shaded pairs. Shading indicates the role that each player occupies: shaded, opportunity to transgress or cooperate (D/C, T/NC); unshaded, opportunity to choose punish or never punish (P, NP). It is possible for both players to play desist-punish reciprocally ('mutual punishment') as the opportunities occur (c_1), or for both players to play transgress-never punish ('mutual non-punishment'; c_2). A 'common sense punishment' ESS (c_3), *sensu*¹³, occurs if the dominant makes the subordinate desist or cooperate by punishing, but, when roles reverse, it acts selfishly, playing transgress or non-cooperate without risk of reprisal. Finally, a 'paradoxical punishment ESS' could exist (c_4) in which subordinates extort gains by punishment, yet transgress against dominants without risk of reprisal. In nature, state c_4 seems not to occur, and punishment is often common sense as in c_3 , or non-existent as in c_2 . Cases where both individuals punish, c_1 are probably also common¹⁶, but the magnitude and effect of punishment is generally asymmetric so that dominants modify subordinates' behaviour to a greater extent than vice-versa. Reasons for the prevalence of certain states are explored in Boxes 2, 3 and 4.

Note that in the models (this Box and Boxes 2, 3 and 4) desist (or cooperate) is learned as a result of punishment following initial transgressions. An alternative (potentially cheaper) strategy would be an innate response to desist immediately, without requiring to learn by punishment. We envisage that the nature of asymmetries in fighting ability and resource value, and the multiple contexts for punishment are generally so complex that a complete set of innate rules would be difficult to achieve. Learning to desist is a simple general way of coping with this complexity, albeit at some expense¹⁶. For punishments to be seen in nature, learning in repeated encounters of the same dyad appears to be necessary. The formal conditions in all models would be modified by kinship.

BOX 2 Punishment games with retaliation: a prospective model

THIS Box and Boxes 3 and 4 examine situations in which individuals that are punished are able to retaliate: the four ESSs outlined in Box 1, figure c are then not equally probable. Player 1 is defined as the opponent in the role of potential punisher. We first outline a prospective model (this Box), then (Box 3) examine ESSs in which player 1 punishes player 2, who then learns to desist or behave altruistically ('punishment ESSs'), and later (Box 4) analyse 'non-punishment ESSs'.

Opponents differ in fighting ability, and may make occasional 'tests' of (or occasional mistakes about) their relative fighting ability or dominance. Incorporating these features (retaliation; mistakes) makes it likely that an ESS is attained in which strong individuals punish weaker subordinates; the reverse is less likely. If the asymmetry in fighting



ability is strong, punishment can flow only from a dominant to a subordinate, and not vice versa.

It is easiest to consider this extended game as a sequence of successive steps or moves between players 1 and 2 (see figure). At step 1, player 2 has the opportunity to transgress (T), or to learn to desist (D) towards player 1, but j training rounds of punishment are required before player 2 switches from T to D for the remaining k rounds ($j+k=N$). At step 2, player 1 may punish (P) if 2 played T, or never-punish (NP). Thus steps 1 and 2 are identical in strategies and payoffs to the simple game (Box 1, figure a or, by analogy, Box 1 figure b).

Step 3 occurs only if player 1 punishes at step 2: player 2 may then retaliate (R) by making an escalated attack on player 1, or may non-retaliate (NR). If he chooses NR, he nevertheless escalates (that is, plays R) with a low probability, $p \rightarrow 0$. One interpretation is that p represents rare deviations such as may be advantageous for testing relative fighting ability; another relates to mistakes about roles¹⁰. If player 2 plays non-retaliate at step 3, the game stops and payoffs remain unaltered. If retaliate is chosen, then (step 4) player 1 may also choose to retaliate, or to non-retaliate. In steps 3 and 4, R always beats NR without escalation or injury, whatever the relative fighting abilities of the two contestants. But if both choose R, fighting results in an injury costing either $-D_1$ fitness units to player 1, or $-D_2$ to 2, after which the round ceases. The probability that player 1 is injured, and hence loses, is x ; player 2 thus loses with probability $(1-x)$. If player 1 is stronger than player 2, $x < (1-x)$. Steps 3, 4 resemble the asymmetric 'hawks-doves' game^{9,18}.

ing the initiator of the attack and quantitative analyses of aggressive interactions confirm that reciprocal aggression is common (though individuals will also attack each other without obvious initial provocation). In addition, dominant animals often respond aggressively to individuals that have failed to react in an appropriate fashion. For example, rhesus macaques that find sources of preferred food and do not give food calls announcing their find are more likely to be the target of aggression than individuals that give food calls^{23,24}. Subordinates that gain priority of access to preferred food sources are also likely to be attacked by dominants: in small groups of domestic horses, subordinates that are separated and fed within sight of dominants are likely to be attacked on their return to the group. (C. Feh, unpublished data). Though experimental evidence is lacking, many studies suggest that individuals gain from retaliatory aggression because it reduces the probability of recipients repeating potentially injurious actions^{16,19}. Sequences of reciprocal aggression may span hours, days, or even weeks, and are commonly associated with displays likely to attract the attention of other group members to the interaction^{19,21}. Punishers are typically dominant to the individuals they punish, though subordinates sometimes punish dominants at times when they cannot retaliate^{19,25}. The intensity of attacks appears to be related to the extent to which individuals have infringed each other's interests and to be modified by kinship, age and sex.

In social primates, aggressive exchanges often involve kin of the principal protagonists. In vervet monkeys, adult females who have been displaced from food sources may seek out and attack their displacer's relatives²⁶⁻²⁸. In macaques, members of different matrilineal groups ally with each other and individuals that have been displaced or attacked by members of another matriline commonly respond by attacking a vulnerable member of their aggressor's matriline²⁹⁻³¹. Attacks on a member of one matriline are commonly followed by retaliation against members of the aggressor's matriline by relatives of the victim²⁹.

Retaliatory aggression may also involve unrelated allies. In savannah baboons, males commonly develop close 'friendships' with particular females, and individuals that have been involved in fights may seek out and threaten or chase their attacker's 'friend'^{32,33}; and vice versa, males may threaten or attack other males or females that attack or harass their 'friends' or may

attack the friends of their aggressors^{19,33}. Where individuals respond to attacks on their allies with retaliatory aggression, aggressors sometimes show affiliative behaviour to their victim's kin immediately after an attack. For example, in pigtail macaques, aggressors are more likely to show affiliative behaviour to their victim's kin in the minutes following an attack than at other times³¹. Similarly, in vervet monkeys, aggressive interactions are commonly followed by affiliative interactions with members of the opponent's matriline^{27,28}.

Punishment appears to be particularly common in five social contexts where pronounced conflicts of interest occur:

■ **The establishment and maintenance of dominance relationships.** During the establishment of dyadic dominance relationships, two individuals frequently trade attacks or threats until one of them establishes a superior position. This is often followed by a period of consolidation when most attacks or threats are directed by the dominant at the subordinate. Subsequently, subordinates usually avoid contests, and mild threats by dominant individuals are sufficient to constrain their behaviour. However, from time to time, subordinates test dominants, probably because this allows them to check for changes in the dominant's fighting ability, which would permit them to reverse the relationship. Unsuccessful challenges commonly elicit attacks by the dominant, followed by a period of heightened sensitivity to any failure by subordinates to respond to mild threats^{19,34,37}.

An example of the role of punishment in the establishment of dominance relations comes from studies of the development of aggressive interactions between chicks of the blue-footed booby, a species in which females are larger than males³⁷. Parents typically lay two eggs which hatch asynchronously. Older chicks establish their dominance by pecking and jostling younger chicks. Any serious challenge by the younger chick elicits fierce and determined escalation of these attacks by the older chick. Dominance relationships developed immediately after hatching commonly persist, even if relative sizes change: for example, though female chicks are substantially larger than males, first hatched males retain their dominance rank (and feeding priority) over later-hatched sisters.

In social primates where a male's competitive ability depends partly on supportive coalitions with other group members, individuals are most likely to join coalitions against individuals that

BOX 3 Punishment ESSs

In a punishment ESS, player 1 will be punishing and, later, benefiting because player 2 desists from injurious activities, or acts 'altruistically'. But if player 1 loses when player 2 retaliates against punishment, there will be social consequences. Player 1 loses status (costing $-V$ units) and player 2 gains status (gaining $+U$ units). The logic here is that for a small number, l , of rounds after losing, player 2 transgresses and player 1 plays not-punish. For this case, $-V=lc_1$, and $+U=lg_2$ (though we retain the symbols V, U for generality). If player 1 wins, there are no additional payoffs, and the next round proceeds normally.

We now examine how relative fighting ability influences ESS conditions through the term x . We therefore derive the conditions required to prevent unilateral deviations (J_1 by player 1, or J_2 by player 2) from each candidate ESS, l . Strategies are categorized by actions at successive steps: for example, P/R, D/R is 'if player 1, punish at step 2, retaliate at step 4; if player 2, desist at step 1, non-retaliate at step 3'.

The table gives stability conditions for all possible punishment ESSs. As punish, transgress cannot coexist (Box 1), an ESS must involve punish, desist. The four candidates are P/R, D/NR;

Candidate ESS = l ; general conclusion	Mutant strategy, J_1 or J_2	Stability condition for $E(l, l) > E(J, l)$	Comments
A $l = P/R, D/NR$ Punish/retaliate; Desist/non-retaliate Very likely: if player 1 is stronger than player 2	1. $J_1 = P/NR$	$\mu_1 > 0$	Favoured if player 1 is stronger than player 2
	2. $J_1 = NP/R$ or NP/NR	$kc_1 > j[d_1 + px(V + D_1)]$	Only marginally harder to satisfy than in the simple game if player 1 is stronger than player 2
	3. $J_2 = T/NR$	$d_2 > g_2 + p\mu_2$	Marginally easier to satisfy than in the simple game if player 1 is stronger than player 2; marginally harder if player 1 is weaker
	4. $J_2 = T/R$	$d_2 > g_2 + [(N_0 - pj)/(N_0 - j)]\mu_2$	Much easier to satisfy than in the simple game if player 1 is stronger than player 2; much harder if player 1 is weaker
	5. $J_2 = D/R$	$\mu_2 < 0$	Favoured if player 1 is stronger than player 2
B $l = P/NR, D/NR$ Punish/non-retaliate; Desist/non-retaliate Impossible: always pays 2 to retaliate	6. $J_1 = P/R$	$0 > \mu_1$	Favoured if player 2 is stronger than player 1
	7. $J_1 = NP/R$ or NP/NR	$kc_1 > j[d_1 + pV]$	Marginally more difficult to satisfy than in the simple game
	8. $J_2 = T/NR$	$d_2 > g_2 + pU$	Marginally more difficult to satisfy than in the simple game
	9. $J_2 = T/R$	$d_2 > g_2 + [(N_0 - pj)/(N_0 - j)]U$	Much more difficult to satisfy than in the simple game
C $l = P/R, D/R$ Punish/retaliate; Desist/retaliate Unlikely because of contradictions between conditions. Pays weaker opponent to play NR if stronger plays R	11. $J_1 = P/NR$	$\mu_1 > 0$	Favoured if player 1 is stronger than player 2
	12. $J_1 = NP/R$ or NP/NR	$kc_1 > j[d_1 + x(V + D_1)]$	Much harder to satisfy than in the simple game especially if player 2 is stronger than player 1
	13. $J_2 = T/NR$	$d_2 > g_2 + [(pN_c - j)/(N_c - j)]\mu_2$	As $p \rightarrow 0$, easier to satisfy than in the simple game if $\mu_2 > 0$, i.e. player 2 stronger than player 1
	14. $J_2 = T/R$	$d_2 > g_2 + \mu_2$	Easier to satisfy than in the simple game if player 1 is stronger than player 2; harder if player 2 is strong than player 1
	15. $J_2 = D/NR$	$\mu_2 > 0$	Favoured if player 1 is stronger than player 2
D $l = P/NR, D/R$ Punish/non-retaliate; Desist/retaliate Unlikely because of conditions 17, 19 and implausibility (a weak punisher always loses a fight each time it punishes opponent)	16. $J_1 = P/R$	$0 > \mu_1$	Favoured if player 2 is stronger than player 1
	17. $J_1 = NP/R$ or NP/NR	$kc_1 > j(d_1 + V)$	Much harder to satisfy than in the simple game
	18. $J_2 = T/NR$	$d_2 > g_2 + [(pN_d - j)/(N_d - j)]U$	As $p \rightarrow 0$, easier to satisfy than in the simple game
	19. $J_2 = T/R$	$d_2 > g_2 + U$	Much harder to satisfy than in the simple game
	20. $J_2 = D/NR$	$U > pU$	Always satisfied: can never pay player 2 not to retaliate if player 1 will not escalate

$\mu_1 = [V(1-x) - xD_1]$; the expected value of escalation to player 1.

$\mu_2 = [xU - (1-x)D_2]$; the expected value of escalation to player 2.

N_i = the number of interactive rounds after correcting for the l rounds that ensue each time a punisher loses during retaliation: $N_a = N/[x(l+1) + (1-x)]$; $N_b = N/(l+1)$;

$N_c = N/[1-P] + Px(l+1) + P(1-x)$; $N_d = N/[1-P] + P(l+1)$.

frequently join coalitions against them^{38,39}. In some primates, dominant males not only punish rivals for challenging their position but also punish their rival's supporters as well. For example, in chimpanzees, dominant males depend partly on the support of mature females to maintain their position. In a captive group of chimpanzees, de Waal¹⁹ describes how a younger male challenging an established dominant regularly threatened or attacked his rival's female supporters. His declining rival was unable to intervene and, eventually, the females transferred their support to the challenger. The frequency with which the new alpha male directed aggression at females then declined rapidly.

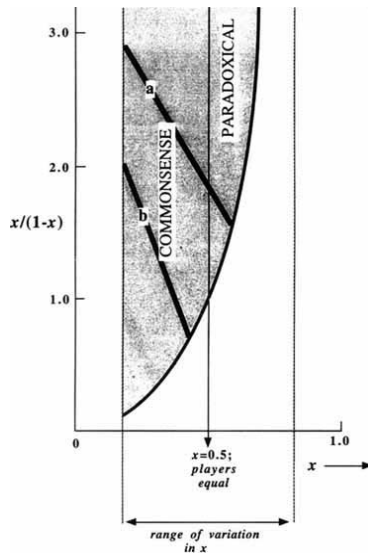
■ **Theft, parasitism and predation.** In many animals, individuals surreptitiously remove resources from their neighbours or

parasitize their investment in their progeny. In birds, neighbours commonly attempt to steal nesting material or food from each other⁴⁰ or to dump eggs in their neighbours' nests⁴¹. In some mammals, juveniles will try to sneak milk from lactating females other than their mother⁴², whereas young males may persistently attempt to sneak copulations with females that are being guarded by mature males^{43,44}.

With few exceptions, individuals respond aggressively to detected cheats or parasites. In birds, long chases occur though rapid escape is often possible. In mammals, attacks on detected parasites may be damaging or fatal: for example, elephant seal pups that are caught attempting to steal milk from unrelated females are often badly bitten and sometimes killed^{42,45}. Simi-

BOX 3 continued

P/NR, D/NR; P/R, D/R; and P/NR, DR. All unilateral deviations are considered in the table; that is, three mutant J strategies for each player. The number of training rounds, j , is unaffected by mutant strategy by wins or losses at steps 3, 4. To illustrate how conditions in the table are calculated, consider P/R, D/NR. Call this strategy I. For I to be an ESS against J_2 , in which player 2 deviates unilaterally by playing T/NR, we require $E(I_2, I) > E(J_2, I)$. Now, $E(I_2, I) = j[-d_2 + g_2 + p(1-x)D_2]$, as



punishment normally occurs only in j rounds, and player 2 retaliates only in pj rounds. For a mutant playing T/NR, there is punishment on all rounds, except each set of l rounds following wins, thus punishment occurs on $N' = N / [(1-p) + px(l+1) + (p(1-x))]$ rounds, where N' is the new number of 'active' rounds after correcting for the effects of l , thus $E(J_2, I) = N'[-d_2 + g_2 + p(xU - (1-x)D_2)]$. Whatever the correction, the number of 'active' rounds is assumed always to exceed the number of training

rounds ($N' > j$), and so the stability condition is that $d_2 > g_2 + \mu_2$, where $\mu_2 = xU - (1-x)D_2$, the expected value of escalation to player 2. Similarly, $\mu_1 = (1-x)V - xD_2$, the expected value to player 1. Note that in the table we assume that: $p \rightarrow 0$, $N' > j$, $pN' < j$, and that as player 1 becomes strong relative to player 2, the effect of x is to make $\mu_1 > 0$, $\mu_2 < 0$, and vice versa.

It is clear from the table that an ESS in which neither player

retaliates (B) is impossible, and that one in which both retaliate (C) is possible only if both players can gain by escalating¹⁸. Assuming that injury is sufficiently severe, only ESSs in which one opponent is prepared to retaliate can be stable, and by far the most likely ESS is to play P/R when player 1, and D/NR when 2(A). This has requirements similar to the simple game (that $kc_1 > jd_1$; $d_2 > g_2$), and that player 1 has a positive expectation from escalation, and player 2 a negative expectation. This implies punishment of a weak individual by a strong individual. The alternative (D), in which a weak player 1 is unlikely to punish a strong player 2 which subsequently retaliates and wins on every training round, is implausible, for player 2 is unlikely to learn to desist. It is also likely to be invaded by tendencies for player 1 to never punish and for player 2 to transgress (conditions 17 and 19).

Thus of the four candidates, only the strategy P/R, D/NR seems a plausible ESS (A). To satisfy conditions 1 and 5 in the table, we require that the ratios V/D_1 and D_2/U both exceed the value $x/(1-x)$. Thus in the figure, we plot $x/(1-x)$ (heavy curve) against x , the probability that player 2 wins an escalated contest. An arbitrary range for x is indicated by the two vertical broken lines, which are equidistant about the continuous vertical line for $x=0.5$ (where players have equal fighting abilities). For an ESS of type A in the table, ratios V/D_1 and D_2/U must both occur in the shaded area in the figure. There is clearly a much greater zone of attraction for commonsense punishment (stronger punishes weaker: shaded area left of the $x=0.5$ line) than for 'paradoxical' punishment (weaker punishes stronger: shaded area left of the $x=0.5$ line), though this cannot be dismissed. Now, suppose that $V=U$, and that D_1 is some decreasing function of x , whereas D_2 is an increasing function of x because the probable injury differences increase with the disparity in strength between players. Two possible relationships for $V/D_1 = D_2/U$ and x are shown as lines a and b in the figure. For line a, a commonsense ESS exists for all $x < 0.5$, but only a small range of $x > 0.5$ allows a paradoxical ESS. For line b, only a commonsense ESS is possible, across a range where player 1 is significantly stronger than player 2; if x is only a small amount less than 0.5; no ESS of type A can exist.

Thus punishment can flow in either direction with respect to dominance (see Box 1c), but it is much more likely to flow in a commonsense direction, reducing the probability of mutual or paradoxical punishment ESSs as outlined in Box 1c, 1 and 4.

larly, harem-holding fallow bucks will repeatedly chase persistent sneaks over long distances and attack them with their antlers if they can catch them⁴⁴. Here, too, sneaks are sometimes killed by harem holders.

Similar attacks or threats are often directed at heterospecific parasites or even at predators. Both brood parasites, such as cuckoos, and predators are commonly the target of persistent mobbing⁴⁰; for example, side-striped jackals will persistently mob leopards that hunt in their territory, preventing them from successfully stalking ungulates (personal observation). Lions not uncommonly attack jackals and spotted hyenas that parasitize their kills, sometimes killing individuals⁴⁶. In many of these species, hosts and their predators or parasites are territorial, so that the same individuals encounter each other repeatedly. Although aggression directed at parasites or predators may have other benefits, one likely advantage is that it teaches individual predators and parasites to avoid repeating attempts on the same individual or in the same location.

■ **The establishment of mating bonds.** In polygynous or promiscuous species, males sometimes attack females that refuse to associate with them⁴⁷. Territorial male red and fallow deer will prod straying females with their antlers^{44,48}. Male hamadryas baboons initially threaten females that stray with an eyebrow flash but if they fail to return immediately, will bite them on the neck⁴⁹. In rhesus macaques, males are most likely to attack oestrous females when the female's nearest adult neighbour is either subordinate to the attacker or of a different social group from the female^{50,51}. In chimpanzees, Goodall⁵² describes how males repeatedly attack females in the early stages of consort

formation until they become more cooperative and follow the male closely. In all these cases, it seems likely that one of the principal benefits of aggression to males is that it reduces the risk of losing potential mating partners. Dominant males will also punish members of either sex that interfere with female consorts. Smuts³³ describes two cases in which male baboons punished females dominant to their consort partner who attempted to interfere with their partners.

Males also punish females that refuse their mating attempts. In social primates living in multi-male groups (including savannah baboons, rhesus macaques and chimpanzees), males sometimes attack females that reject their attempts to mate, hitting or biting them^{47,52-55}. Dominant male primates may also punish females for approaching, courting or mating with subordinates or with males from other groups^{50,52,56,57}. Females are clearly aware of these risks: for example, female hamadryas baboons will hide from dominant males while being groomed by subordinates or non-group males⁴⁹. In a captive group of chimpanzees, de Waal¹⁹ describes how females sometimes consistently refused to mate with subordinate males when the dominant male was present, but immediately mated with them when the dominant male was confined for the night¹⁹. Attacks by males appear to increase the chance that females will subsequently mate with their aggressors^{47,55}. For example, male Japanese macaques that show aggression to females during the mating season were significantly more likely to mate than males that did not show aggression towards females⁵⁸. In captive lowland gorillas, females learn to present more frequently to more aggressive males whom they otherwise avoid⁵⁵.

BOX 4 Non-punishment ESSs

ESSs for non-punishment are again likely to be affected by fighting ability. Two plausible forms of transgression strategy might be chosen by player 2. Weak transgression (WT) is an opportunistic attempt to transgress against player 1, which is successful only if player 1 replies with non-retaliate (NR). If player 1 replies with retaliate (R), WT gives up immediately without gain or loss to either opponent. In contrast, if player 1 plays retaliate, strong transgression (ST) persists until one of the players is injured. As before, the probability that player 1 is injured and loses is x at a cost of $-D_1$, and the probability for player 2 is $(1-x)$ at a cost of $-D_2$. There are again N rounds and the resource is worth g_2 to player 2 and c_1 to player 1. A payoff matrix is given in the figure.

		Player 1	
		R	NR
Player 2	WT	0	$-Nc_1$
	ST	$-Nx D_1$	$-Nc_1$

		Player 1	
		R	NR
Player 2	WT	0	$+Ng_2$
	ST	$+Nxg_2$ $-N(1-x)D_2$	$+Ng_2$

There are four candidate ESSs: WT, R; WT, NR; ST, R; ST, NR. We can immediately discount WT, NR: it always pays player 1 to retaliate if player 2 will give up. ST, R requires that both players have a positive expectation from escalation ($c_1 - xD_1 > 0$ to prevent 1 from choosing NR, and $xg_2 - (1-x)D_2 > 0$ to prevent 2 from choosing WT). This is unlikely if damage

costs are high, or the contest is sufficiently asymmetric. The remaining two ESSs are 'common sense': WT, R is stable if player 1 has a positive expectation from escalation (favoured if player 1 is stronger), and ST, NR is stable if player 2 has a positive expectation (favoured if player 2 is stronger). Thus, although the possibility exists for a weak player to show ST or R against a strong player, it is much more likely that the dominant will keep his resource (WT, R), or take resources from the subordinate (ST, NR), depending on which role he is in.

Finally, we evaluate the ESS types outlined in Box 1c in the light of retaliation (Boxes 2, 3 and this Box). Mutual Punishment (1) is unlikely, but cannot be discounted if opponents have rather similar fighting ability. Mutual non-punishment (2) is feasible; usually, the dominant player will maintain his resources by force, and the subordinate give his up without retaliation. A form of common sense punishment (3), in which the dominant punishes the weaker subordinate and takes resources by force from it when roles are reversed, is also entirely feasible. Paradoxical Punishment (4) is unlikely but cannot be discounted. The range of possibilities is now wider than that suggested by Box 1c. Less likely states include: 'common sense punishment, paradoxical transgression' (dominant punishes the subordinate, but when roles are reversed, is unprepared to transgress strongly) 'paradoxical punishment, common sense transgression'; and 'paradoxical punishment, paradoxical transgression'. But the most likely states are a form of mutual non-punishment in which the dominant takes resources from the subordinate but not vice versa, or a form of common sense punishment in which the dominant punishes the subordinate, and yet transgresses strongly against it when roles are reversed.

investment^{48,64,66}. In some cases, punishment can have considerable costs to offspring. In European coots and moorhens, parents usually feed whichever offspring is closest to them but discourage 'greedy' young that persistently follow them closely after they have been fed by picking them up and shaking them^{66,67}. On occasion, persistent young are even killed⁶⁶. Although killing offspring is presumably non-adaptive, it may generally be to the parent's advantage to teach its progeny not to attempt to monopolize resources by lowering the benefits of persistent attempts to feed.

■ **The enforcement of cooperative behaviour.** Compared to other explanations of cooperative behaviour, relatively little attention has been paid to the possibility that cooperative behaviour occurs because dominant breeders coerce subordinates to assist them⁶⁸⁻⁷⁰. Previous models of the punishment and its benefits are shared equally among group members⁷¹⁻⁷⁹, an assumption that weakens the benefits of punishing because it favours individuals that cooperate but do not punish. In practice, dominant animals are usually more likely than other group members to punish non-cooperators and commonly gain a disproportionate share of reproduction. These inequalities substantially strengthen the benefits of punishing defectors and cooperation can often be maintained by punishment, especially if individuals learn responses for specific dyads (Box 1).

Enforced cooperation is probably common in animal societies. Punishment frequently occurs in dyadic interactions between cooperating individuals: chimpanzees, for example, form supportive coalitions to gain access to resources and will attack allies that fail to support them in competitive interactions with third parties¹⁹. In some primitively eusocial *Polistes* wasps, dominant workers may inherit the queen's role, and conflicts of interest consequently arise between queens and dominant workers over how much time and energy the latter should invest in rearing sibs⁸⁰. Queens are regularly aggressive to inactive workers, chasing, biting, grappling or bumping them, and experimental removal or cooling of queens rapidly lowers the level of worker activity^{81,82}. Similar behaviour occurs in the primitively eusocial naked mole rat where queens direct repeated aggression at lazy workers⁸³. And in superb fairy wrens, helpers that are experimentally removed from the group at times when the group is raising young (when they play a major role in providing food) are usually attacked and harassed by the dominant male on their return, whereas helpers removed during the non-breeding season are never attacked⁸⁴.

In a few cases, subordinate members of cooperatively breeding groups punish dominant individuals that infringe their fitness, as Box 3 predicts. For example, in primitively eusocial paper wasps *Polistes fuscatus*, colonies are founded by small groups of sisters that initially cooperate to build and defend the nest and feed the young⁸⁵. Queens are ranked in a dominance hierarchy and the dominant queen regulates the reproduction of subordinates by eating around a third of their eggs. Excessive egg-eating by the dominant queen (mimicked by experimental removal of subordinates' eggs) elicits an increase in the frequency of aggression directed at the dominant by her subordinate sisters⁸⁵.

Conclusions

Theoretical studies confirm that where individuals live in stable social groups, conflicts of interest between group members are likely to lead to the evolution of punishing tactics and negative reciprocity. Empirical research on social vertebrates shows that a high proportion of aggressive interactions involve reciprocal threats or attacks between individuals and their kin or allies. By punishing actions that infringe their interests, dominant animals teach subordinates to behave in a fashion that increases (or avoids reducing) the dominant's fitness. As selection is likely to favour subordinates who test dominance relationships from time to time, punishment is likely to be a continuing feature of domi-

Several studies show that attacks by males can have substantial costs to females⁴⁷. Serious wounding is not uncommon^{58,59}: for example, anestrus female olive baboons are seriously wounded by males around once a year³³. Wounds may subsequently lead to death, abortion or loss of subsequent reproductive performance^{47,52}. Males have even been seen to kill females belonging to their harem or social group in several mammals, including elephant seals⁶⁰, red deer (F. E. Guinness, personal communication) and grey langurs⁶¹.

■ **Parent/offspring conflict.** Conflicts of interest between parents and their offspring often occur over the duration or level of parental investment^{62,63} and parents often adopt punishing tactics adapted to modify the behaviour of their offspring. In vertebrates, females will bite, peck, kick or slap juveniles that persistently attempt to suck or solicit other forms of

nance relationships. Punishment is commonly used to constrain the demands of offspring; to establish dominance relationships and mating bonds; to persuade reluctant helpers to cooperate; and to discourage thieves, cheats, parasites and even predators. Punishers are generally dominant individuals who can punish at little cost—although subordinates may sometimes wait for favourable opportunities to punish dominant individuals at times when they cannot retaliate effectively.

Punishing tactics have important consequences for other aspects of social behaviour. Both punishers and their victims may minimize the risk of retaliatory aggression by ritualized reconciliatory behaviour, involving affiliative behaviour or close physical contact shortly after an aggressive interaction⁸⁶. For example, pairs of long-tailed macaques that were given the opportunity to show reconciliatory behaviour after induced conflicts, subsequently showed closer proximity to each other than pairs that had been experimentally prevented from reconciling⁸⁷. Following conflicts, both contestants may seek reconciliation with members of each others' kin groups, while their relatives may also seek reconciliation with each other^{27,31,56,86}.

In many social vertebrates, dominant individuals will also intervene to end aggressive exchanges, possibly because repeated aggression between other group members can reduce their fitness. For example, in cercopithecine monkeys, both dominant males and dominant females will intervene in quarrels between other group members^{88,89}. In captive chimpanzees, intervention on the side of weaker individuals may help high ranking males to consolidate and maintain their social position: rising males initially support winners in quarrels between other group members but switch to supporting losers as soon as they reach the alpha position¹⁹. Subordinate individuals may also intervene to encourage reconciliation: for example, females will apparently help to bring rival males together after a conflict by grooming or presenting to them¹⁹. They probably have a direct interest in doing so, for females are commonly attacked during prolonged aggressive interactions between males.

It is clear that analogies exist between punishing tactics in social animals and retaliatory aggression among humans. Retaliation is a common feature of aggressive interactions between individuals¹² as well as between groups⁹⁰: obvious examples include retaliatory expulsions of diplomats and tit for tat sectarian killings. In some tribal societies, individuals are permitted to punish minor infringements of their interests themselves, while the punishment of more severe offences is either carried out by community action or is delegated to particular individuals^{91–93}, an arrangement likely to limit the extent of negative reciprocity and minimize disruption within the group. Even here, there are parallels with aggressive behaviour in animal societies: in some social Hymenoptera, group members may cooperate to punish or prevent defection⁹⁴, whereas in some social primates, subordinate individuals will draw the attention of dominant animals to actions by other group members that are likely to infringe their interests¹⁹.

Although negative reciprocity provides a theoretical framework for research on the evolution of aggression in social animals, there are many questions that have yet to be explored. How does the involvement of other individuals affect punishing strategies? What is the optimal magnitude of punishment? What tactics should individuals adopt? Should they exact retribution proportional to the damage to their interests? Should they escalate—like opposing regiments during the First World War, who punished breaches of informal peace pacts on the basis of two or three for one⁷⁶. Or should they de-escalate, thereby signalling a readiness to terminate the conflict?

Firm experimental evidence that individual animals punish other group members whose behaviour is likely to depress their fitness and that punishment reduces the risk of repetition is now badly needed. The factors affecting the magnitude and frequency of punishments and the effects of asymmetries between contestants need to be explored. As reciprocal attacks are often widely

spaced in time and may be modified by intervening interactions between contestants and other individuals, these questions pose methodological as well as conceptual challenges for behavioural scientists. Their solution will require a novel mixture of quantitative ethology, cognitive psychology and evolutionary biology. □

T. H. Clutton-Brock is in the Large Animal Research Group, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK; G. A. Parker is in the Population Biology Research Group, Department of Environmental and Evolutionary Biology, University of Liverpool, Brownlow Street, Liverpool L69 3BX, UK.

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ARTICLES

Regulation of PLC-mediated signalling *in vivo* by CDP-diacylglycerol synthase

Louisa Wu, Barbara Niemeyer, Nansi Colley, Michael Socolich & Charles S. Zuker*

Howard Hughes Medical Institute and Departments of Biology and Neurosciences, University of California at San Diego, La Jolla, California 92093-0649, USA

CDP-diacylglycerol synthase (CDS) is an enzyme required for the regeneration of the signalling molecule phosphatidylinositol-4,5-bisphosphate (PtdInsP₂) from phosphatidic acid. A photo-receptor cell-specific isoform of CDS from *Drosophila* is a key regulator of phototransduction, a G-protein-coupled signalling cascade mediated by phospholipase C. *cds* mutants cannot sustain a light-activated current as a result of depletion of PtdInsP₂. Overexpression of CDS increases the amplitude of the light response, demonstrating that availability of PtdInsP₂ is a determinant in the gain of this pathway. *cds* mutants undergo light-dependent retinal degeneration which can be suppressed by a mutation in phospholipase C. Thus, enzymes involved in PtdInsP₂ metabolism regulate phosphoinositide-mediated signalling cascades *in vivo*.

PHOSPHOINOSITIDE-MEDIATED signalling pathways are a ubiquitous mode of intracellular signal transduction in eukaryotic cells. Phosphoinositides and their cleavage products are a class of second messengers that can be found downstream of many tyrosine kinase receptors and G-protein-coupled seven-transmembrane-helix receptors^{1,2}. These second messengers are involved in cell growth and oncogenesis^{3,4}, differentiation and development^{5,6}, the action of neurotransmitters and hormones⁷, and sensory perception (olfaction, taste and vision)^{8–10}. The signals from many of these different cascades converge on the activation of a phospholipase C (PLC). PLC catalyses the hydrolysis of the minor membrane phospholipid phosphatidylinositol-4,5-bisphosphate (PtdInsP₂) into the second messengers inositol trisphosphate (InsP₃) and diacylglycerol (DAG)^{1,2}. InsP₃ mobilizes internal stores of calcium, which affects and modulates many cellular processes¹¹; DAG activates members of the protein kinase C (PKC) family of proteins¹².

Given the central role of PtdInsP₂ in signalling, it may be expected that its levels would be tightly modulated in the cell. Although PtdInsP₂-mediated signalling pathways have been studied in great detail in a number of systems, little is known

about the metabolic machinery that couples PtdInsP₂ synthesis with its availability for signalling. Recent studies have demonstrated that in order to reconstitute PLC activity in permeabilized cells, phosphatidylinositol transfer protein (PtdIns-TP), a protein required for the transfer of phosphoinositides between intracellular membranes, must be added back to the preparation¹³. These results argue that PtdInsP₂ is synthesized on demand (as opposed to being stored) and suggest that its metabolism plays an important and direct role in the regulation of phosphoinositide-mediated cascades.

Failure to regulate components of phosphoinositide signalling cascades can lead to severe cellular dysfunction¹⁴. For instance, uncontrolled signalling from a PLC-mediated pathway can lead to calcium cytotoxicity¹⁵. Hyperactivation of PKC may lead to uncontrolled cell growth and tumorigenesis¹². Also, it is hypothesized that the therapeutic effects of lithium in manic-depression therapy involve the depletion of internal inositol¹⁶. This may limit the amount of PtdInsP₂ that can be made in these 'overactive' brain cells and restore signalling to normal levels. Thus, enzymes involved in PtdInsP₂ metabolism may serve as important targets for pharmacological intervention of normal and abnormal signalling pathways.

Phototransduction in *Drosophila* is an ideal model system for the study of G-protein-coupled phospholipase-C-mediated sig-

* To whom correspondence should be addressed.