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Adaptive strategies of territory formation

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Abstract How do territorial animals gain ownership of an area? Early modelling has considered the evolution of fighting when the winner can claim the right to the resource. Recently, alternative hypotheses have been offered where repeated interactions lead to division of space through ‘nagging’ instead of one decisive fight. However, these models assume that animals avoid areas in which they have taken part in aggressive interactions, but do not consider whether avoidance itself is adaptive. We aim to bridge this gap between mechanistic and adaptive explanations, by presenting a game-theory model where individuals choose whether to return to an area after a fight with a specific outcome (win, loss, draw). We show that avoidance of areas where fights have occurred can be adaptive, but only if benefits of access to the area are low compared to costs of fighting. Otherwise, one individual (typically the winner) responds by returning to the area, and the other (loser) avoids it. In such cases, space is gained by winning fights. We also consider the role of conventions. If responses to fights were purely conventional, paradoxical strategies where losers of fights gain ownership would be equally logical as common-sense ones where winners claim ownership. Paradoxical

solutions can be stable but only when there is little difference in fighting ability between the competitors, when individuals adhere very strictly to a behavioural rule without much random variation, and when the population in its ancient state used a paradoxical strategy.

Keywords Aggression · Animal contests · Fighting · Game theory · Territoriality

Introduction

In territorial animals, ownership of a territory is usually a prerequisite to breeding, indicating strong selection pressure to win such resources. How contests over resources are resolved was the first question that brought game theory to the attention of biologists. Early modelling concentrated on ‘hawk–dove’ games (Maynard Smith and Price 1973; Grafen 1979), which assume that only one of the contestants can win the resource. Such games often include an asymmetry between owners, who have been resident before, and intruders, who have not. These models have been modified to include, for example, size differences (Crowley 2000) or repeated interactions (Houston and McNamara 1991). However, existing game-theory models of conflict focus on winner-takes-all fights for indivisible space.

Other models of territorial settlement, on the other hand, look at the sequential arrival of individuals, such as birds at a nesting area or males at a lek. These models focus on an individual’s timing of arrival (Kokko 1999) or whether it should contest an occupied site or settle in a vacant patch (Broom et al. 1997), rather than looking at simultaneous arrival and exploration of vacant space. However, both these types of model are inappropriate for modelling territorial settlement if aggressive interactions lead to the sharing of space between competitors settling in the same area (e.g. juvenile *Anolis aeneus* lizards, Stamps and Krishnan 1995, 1998). In this case, social interactions during territory establishment may resemble bargaining and negotiation in that both contestants would

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benefit from sharing a divisible resource rather than risking escalated contests.

Consequently, an alternative approach to modelling territory acquisition is advocated by Stamps and Krishnan (1999, 2001). Based on observations of territorial settlement in lizards (Stamps and Krishnan 1997), they model a situation in which no single interaction determines the winning of an entire indivisible territory. Instead, individuals move through a large, suitable, divisible area and increase the use of sites that appear attractive to them. It is important to note that in these models, all sites within the habitat are of equal intrinsic quality; thus, the attractiveness of an area relates solely to the experiences an individual has within it. Fights involve punishment that reduces the attractiveness of an area for both individuals, while entering an area uncontested increases its attractiveness. Thus, through a tendency to avoid areas in which they have taken part in aggressive interactions, regardless of the outcome, and only returning to areas where positive experiences (increasing familiarity) outweigh negative ones (fights), animals can gain exclusive use of space (Stamps and Krishnan 1999). In these models, the gaining of territorial areas occurs through frequent 'nagging' instead of one decisive fight.

Stamps and Krishnan's (1999, 2001) models reproduce several features of territorial systems (Sih and Mateo 2001), and thus are a clear step forward in developing more realistic models of territory acquisition. However, they differ in one crucial respect from game-theory models: they do not evaluate the adaptiveness of the behaviour on which they are based. In particular, one should investigate whether animals benefit from a tendency to avoid areas where they have previously encountered a competitor regardless of the outcome of the encounter, as it is assumed in Stamps and Krishnan (1999, 2001).

Here we develop a new model that addresses these issues, with particular reference to two questions. Firstly, we investigate whether avoidance behaviour is adaptive. In other words, if individuals are given the choice of not returning to an area, or returning less frequently, should they do so (Stamps 1994; Stamps and Krishnan 1999, 2001), or attempt to gain space by winning fights, as dyadic models of territorial contests generally suggest (Maynard Smith and Parker 1976)? Secondly, we ask why respect for ownership can become established in territorial systems. Early game-theory models (e.g. Maynard Smith and Parker 1976; Maynard Smith 1982) suggest that 'paradoxical solutions' to animal conflict—where, for example, owners, or individuals of high resource holding potential (RHP) simply retreat when challenged—can theoretically be as reasonable as the common-sense solutions, in which high RHP individuals or owners are more willing to fight than intruders. A paradoxical evolutionarily stable strategy (ESS) is thus an evolved behavioural convention dictating that an individual of lower RHP, or less to gain from winning a contest (depending on the asymmetry under consideration), obtains access to a disputed resource at the expense

of a more able or motivated contender (Maynard Smith and Parker 1976; Field and Hardy 2000; Kemp 2000).

Later work has extended the basic games, limiting the conditions under which paradoxical solutions can evolve (Enquist and Leimar 1987; Mesterton-Gibbons 1992; Mesterton-Gibbons and Adams 1998), yet in the majority of conflict games, paradoxical solutions remain a feature (Hammerstein and Parker 1982; Parker 1984; Enquist and Leimar 1987; Field and Hardy 2000). For example, Mesterton-Gibbons (1992) analysed owner–intruder games, and found parameter regions where a common-sense 'bourgeois' (aggressive owners) strategy prevailed. This, however, required an a priori assumption that owners are more likely to win fights; otherwise, the paradoxical 'anti-bourgeois' strategy became more likely.

Here, we consider a particular case of paradoxical versus common-sense strategies, one of crucial importance during initial settlement of previously unoccupied space: if winners and losers of fights behave differently, why should the winner, rather than the loser, become more daring in future fights and claim ownership of an area, all else being equal? If the loser became the new owner, the outcome would share features of other paradoxical solutions. Such an outcome appears counter-intuitive, yet if the outcome of a fight is a simple asymmetry whose outcome is largely determined by chance, an evolutionarily stable strategy could equally well dictate one or the other experience (win or lose) to be used as the cue that makes an animal retreat.

Studies have shown that while common-sense solutions (including both owners winning and larger, or higher RHP, individuals winning) are common in many taxa (fish: Beaugrand et al. 1996; Chellappa et al. 1999; birds: Tobias 1997; insects: Petersen and Hardy 1996; Alcock and Bailey 1997; crustaceans: Jennions and Backwell 1996; mammals: Barnard and Brown 1984), paradoxical solutions are (almost) non-existent. Maynard Smith (1982) quotes studies on *Oecibus civitas* spiders as showing potentially paradoxical behaviour. Owners of webs give up their webs to intruders, leading to a pattern of repeated displacements. We are, however, unaware of any follow-up documenting the same pattern in this or other species (for a current debate concerning butterflies, see Hernandez and Benson 1998; Field and Hardy 2000; Kemp 2000). Furthermore, the above example relates to owner–intruder asymmetry, rather than winner–loser asymmetries, which are relevant when occupying new areas.

This points to a surprisingly unresolved question in the first application of game theory to the study of animal behaviour: if theory continues to predict paradoxical solutions under certain conditions, why do we only ever observe common-sense solutions in nature? Our game-theory approach to the problem of winning space evaluates the stability of both paradoxical and common-sense solutions.

Table 1 Model parameters and definitions

Parameter	Definition
$S = \{S_w, S_L, S_D\}$	Strategy used by an individual, composed of the probability that it returns to the contested area in response to winning, losing, and the fight ending in a draw
α	Proportion of the population that is of high RHP
T	Type of fight (competitors equal or differing in fighting ability)
a	Degree of asymmetry between the two classes of individuals in the population
p	Probability of an individual winning a given fight
q	Probability of an individual losing a given fight
p_d	Probability that a fight ends without a winner or a loser (a draw)
v	Value (benefit) gained from an unsettled contest
V	Value gained from a settled contest
c_w	Cost associated with winning a given fight
c_L	Cost associated with losing a given fight
c_D	Cost associated with participating in a fight which ends in a draw
δ	Amount of error in decision making (behavioural variability)

Methods

The model: background information

Animals compete for access to areas containing necessary resources such as food and nest sites. We can imagine a situation in which two individuals are in conflict over such a space, in an attempt to either extend their current territory or establish a new one. Both individuals are able to withdraw from the contested area to an uncontested area (for example, the core of their existing territory). We aim to investigate the strategies that individuals might use in the course of this pairwise conflict.

A strategy must specify precisely the behaviour of an individual in every possible situation (von Neumann and Morgenstern 1953; Maynard Smith and Parker 1976; Broom et al. 1997). A fight between two contestants can end either in one of them winning, or in a draw, after which each individual will make a decision on how likely it is to return to the location of the fight in the future. This combination of probabilities makes up an individual's strategy. Thus, we define a strategy $S = \{S_w, S_L, S_D\}$, where S_w is the probability of returning to the fight location after winning the fight, S_L is the probability of returning having lost, and S_D is the probability of returning when the fight has ended in a draw. As each probability can take any value from zero to one the strategy set is continuous (Parker 1984), and a potentially infinite number of strategies can be used (see Table 1 for parameter definitions).

We consider situations in which a mutant individual using a strategy $S_m = \{S_{mw}, S_{mL}, S_{mD}\}$ is in conflict with a single member of a population using strategy $S_{pop} = \{S_{pw}, S_{pL}, S_{pD}\}$. We aim to investigate which population strategies are evolutionarily stable against invasion by S_m by calculating a measure of the mutant individual's fitness when $S_m = S_{pop}$ and when $S_m \neq S_{pop}$.

In terms of this model, a common-sense strategy would be one such as $S = \{0.8, 0.2, 0.5\}$, where the animal returns more frequently when it has won than when it has lost. A paradoxical strategy would be one such as $S = \{0.2, 0.8, 0.5\}$ where the probability of returning having lost is greater than the probability of returning having won. In investigating the stability of paradoxical strategies, we ask whether a strategy in which the probability of returning after losing exceeds the probability of returning after winning can ever be an ESS.

In order to investigate the effect of different return strategies on the mutant individual's fitness, we need to consider at least two fights between the contestants. For simplicity, we restrict our analysis to a contest involving exactly two fights, the smallest

number we can use to investigate how the outcome of one fight affects an individual's behaviour in the next. Throughout, 'fight' refers to a single aggressive interaction between two individuals, while 'contest' refers to a series of fights (in this case, two).

We consider three potential outcomes to the contest, depending on which of the two competing individuals chooses to return to the contested area. The mutant individual may not return after the second fight, in which case it gains no increase in fitness from the contest (it may suffer losses; see section on Costs of fighting). If the mutant individual returns but the opponent does not, we assume that the contest has been settled, and the individual gains a large fitness benefit from becoming the sole occupier of the disputed space. If both individuals return, we assume that no further aggressive interaction takes place and the space is shared between the competitors. In this case, we consider the contest to be unsettled, and a smaller benefit is gained by each contestant from the use of the space.

To investigate the effect of differences in fighting ability on the strategies that individuals use, we assume that the population consists of two classes of individuals, those of good fighting ability or high RHP, and those of lower fighting ability or low RHP. We assume that a fraction α of the population is of high fighting ability (type 1 individuals; type 0 individuals are those of low fighting ability). In such a population, $T_E = \alpha^2 + (1-\alpha)^2$ of fights will occur between equal individuals, in $T_S = \alpha(1-\alpha)$ cases, the mutant individual will be of high RHP (type 1), fighting against an individual of poor fighting ability (type 0), and in $T_W = (1-\alpha)\alpha$ cases, it will be of low RHP, fighting against a good fighter, assuming spatially random mixing of individuals. Thus, when calculating individual fitness (see section on Calculating fitness) we take a weighted mean of the fitness for the three types of fight. Throughout this paper, we use $\alpha = 0.5$. Testing other values is beyond the scope of this paper, but would follow the same principles as described here. Individuals are assumed not to know their own fighting ability. They can, however, observe the outcome of the first fight and adjust their behaviour accordingly.

Fight outcomes

As described above, fights may end up in wins, losses and draws. When two equally matched competitors meet, it is natural to assume that the probability of winning equals the probability of losing: $p = q$; additionally, p_d describes the probability of a fight ending in a draw. We use subscripts such as '10' to denote a high-

Table 2 Calculation of probabilities associated with each outcome, from the point of view of the mutant individual

First fight	Second fight				
	Win	Lose	Draw	No opponent	Avoid
Win	$P_{ww} = p S_{mW} S_{pL} p$	$P_{wl} = p S_{mW} S_{pL} q$	$P_{wd} = p S_{mW} S_{pL} p_d$	$P_{we} = p S_{mW} (1 - S_{pL})$	$P_{wa} = p (1 - S_{mW})$
Lose	$P_{lw} = q S_{mL} S_{pW} p$	$P_{ll} = q S_{mL} S_{pW} q$	$P_{ld} = q S_{mL} S_{pW} p_d$	$P_{le} = q S_{mL} (1 - S_{pW})$	$P_{la} = q (1 - S_{mL})$
Draw	$P_{dw} = p_d S_{mD} S_{pD} p$	$P_{dl} = p_d S_{mD} S_{pD} q$	$P_{dd} = p_d S_{mD} S_{pD} p_d$	$P_{de} = p_d S_{mD} (1 - S_{pD})$	$P_{da} = p_d (1 - S_{mD})$

RHP individual fighting against a low-RHP individual. Where two high-RHP players (1), or two low-RHP players (0) meet, the probabilities of winning, p_{11} and p_{00} , and the probabilities of losing, q_{11} and q_{00} , are:

$$p_{11} = p_{00} = q_{11} = q_{00} = \left(\frac{1 - p_d}{2} \right) \quad (1)$$

In fights between high- and low-RHP players, $p > q$ for the high RHP individual. For simplicity, and to allow us to investigate the impact of varying a single parameter on the ESS, we assume that a fixed proportion of fights end in a draw for each set of parameter values. The limitations of this assumption are discussed later (see Discussion). The probabilities of winning and losing in fights that occur between individuals of differing competitive ability are calculated from the asymmetry in fighting ability between individuals in the population, described by a . This parameter can take values from zero to one. If a takes a value of 1, then in fights between unequal competitors where there is a winner, the victor will always be the individual that is of higher RHP. In asymmetrical situations, the probability that an individual with good fighting ability wins against a poor fighter, p_{10} , and therefore that a poor fighter loses to high-RHP individual, q_{01} , is:

$$p_{10} = q_{01} = \left(\frac{1 + a}{2} \right) (1 - p_d) \quad (2)$$

Likewise, the probability that an individual with high RHP loses to a poor player, q_{10} , and the probability that an individual with low RHP wins over a good player p_{01} , is:

$$p_{01} = q_{10} = \left(\frac{1 - a}{2} \right) (1 - p_d) \quad (3)$$

In the special case where a takes a value of zero, all individuals in the population are identical in fighting ability. Note that when $a=0$, types 1 and 0 become identical, and the model produces identical results regardless of the value of a . For the sake of simplicity we have kept $a=0.5$ for these cases too. At any other value of a the individuals belonging to different groups have true differences in fighting abilities, even though these abilities may be slight.

We use the outcome probabilities above, S_m , and S_{pop} to calculate the probability of each contest outcome (series of two fight outcomes; Table 2). In T_E fights, where individuals are equal, we use p_{11} , p_{00} , q_{11} and q_{00} . In T_S fights, where the mutant is stronger, we use p_{10} and q_{10} , and in T_W fights, where the mutant is weaker, we use p_{01} and q_{01} .

Costs of fighting

The costs associated with fighting are described by c_W (cost of winning a fight), c_L (cost of losing a fight) and c_D (cost of participating in a fight that ends in a draw). To remain biologically meaningful, we assume that the cost of losing a fight must always exceed the cost of winning. We will consider limitations of this assumption in the Discussion. Because studies have shown that the costs of aggression are positively related to the duration or intensity of aggressive encounters (e.g. Hack 1997; Neat et al. 1998a), we assume that all encounters ending with a specific outcome (win, loss or draw) are equal in duration and/or intensity, and so are

equally costly. Where competitors are unequal, we assume that the costs of a specific outcome are the same whether the individual is of good or poor fighting ability. We do not currently include an asymmetry in the ability to bear the costs of an aggressive encounter.

Contest costs are calculated from the cost of a fight outcome, c_W , c_L or c_D , multiplied by the probability of that outcome in the first and second fights; we assume that the cost of successive fights are independent of each other.

The likelihood that an individual wins one of the two fights in which it is involved (P_{W1}) is the sum of the probabilities of winning the first fight, when the outcome of the second fight was a loss or a draw, or one or both of the competitors did not return for the second, plus the sum of the probabilities of winning the second fight, when the first fight ended with a loss or draw for the individual in question (Table 2). Thus:

$$P_{W1} = P_{wl} + P_{wd} + P_{we} + P_{wa} + P_{lw} + P_{dw} \quad (4)$$

The subscripts w, l, d, refer to an outcome of a win, loss or draw in the first (first position) or second (second position) fight. In the case where the opponent does not return, we use the subscript e, and where the mutant does not return, a. The probability of winning both fights is described by P_{ww} . The probabilities of losing and drawing in one and both fights are calculated analogously to Eq. (4) and P_{ww} . The total costs associated with fighting are:

$$C = c_W(2P_{ww} + P_{W1}) + c_L(2P_{ll} + P_{L1}) + c_D(2P_{dd} + P_{D1}) \quad (5)$$

Benefits of fighting

The benefits gained from ownership of the disputed territory are described by v and V for unsettled and settled contests, respectively. In an unsettled contest, both contestants return after the second fight. In this case, the mutant has access to a resource of value v . In a settled dispute, where the opponent does not return after the first or second fights and the mutant has sole use of the disputed territory, the resource has a value of V . V is always equal to or greater than v . The actual benefits gained from settled contests, B_S , are calculated from the probability of the contest being settled (the sum of Table 3) multiplied by V . Benefits from unsettled contest, B_U , are calculated from the probability of contests where both the mutant and the opponent return after the second fight (the sum of Table 4) multiplied by V . No benefits are gained when the mutant does not return after the first or second fight.

Calculating fitness

Fitness is defined as the difference between the benefits of using the space and the costs paid during the contest. For example, we can imagine a situation where the population is using strategy $S_{pop} = \{0.5, 0.5, 0.5\}$, and a mutant individual uses strategy $S_m = \{0.1, 0.2, 0.8\}$. To present a simple example, we assume that in this case no fights end in a draw ($p_d=0$) and all individuals are equal with respect to their fighting ability ($a=0$). Other parameters are set as $v=1$, $V=5$, $c_W=0.1$, $c_L=0.2$ and $c_D=0.1$. We calculate the costs paid by the mutant when fighting members of the population as $C=0.1613$. Unsettled gains are $B_U=0.0056$ and settled gains are $B_S=0.4031$. Fitness of the mutant, W , is calculated as:

Table 3 Return probabilities after the second fight, where only the mutant returns

First fight	Second fight				
	Win	Loss	Draw	No opponent	Avoid
Win	$M_{ww}=P_{ww} S_{mW} (1-S_{pL})$	$M_{wl}=P_{wl} S_{mL} (1-S_{pW})$	$M_{wd}=P_{wd} S_{mD} (1-S_{pD})$	$M_{we}=P_{we}$	0
Loss	$M_{lw}=P_{lw} S_{mW} (1-S_{pL})$	$M_{ll}=P_{ll} S_{mL} (1-S_{pW})$	$M_{ld}=P_{ld} S_{mD} (1-S_{pD})$	$M_{le}=P_{le}$	0
Draw	$M_{dw}=P_{dw} S_{mW} (1-S_{pL})$	$M_{dl}=P_{dl} S_{mL} (1-S_{pW})$	$M_{dd}=P_{dd} S_{mD} (1-S_{pD})$	$M_{de}=P_{de}$	0

Table 4 Return probabilities after the second fight, where both competitors return

First fight	Second fight				
	Win	Loss	Draw	No opponent	Avoid
Win	$R_{ww}=P_{ww} S_{mW} S_{pL}$	$R_{wl}=P_{wl} S_{mL} S_{pW}$	$R_{wd}=P_{wd} S_{mD} S_{pD}$	0	0
Loss	$R_{lw}=P_{lw} S_{mW} S_{pL}$	$R_{ll}=P_{ll} S_{mL} S_{pW}$	$R_{ld}=P_{ld} S_{mD} S_{pD}$	0	0
Draw	$R_{dw}=P_{dw} S_{mW} S_{pL}$	$R_{dl}=P_{dl} S_{mL} S_{pW}$	$R_{dd}=P_{dd} S_{mD} S_{pD}$	0	0

$$W = B_U + B_s - C \quad (6)$$

and thus is equal to 0.2474.

Finding the ESS

To find the strategies that are evolutionarily stable, we check whether the population strategy can be invaded by a mutant using a different strategy, then we check if it can be invaded by another mutant strategy, until all possible mutants have been checked. An evolutionary stable strategy occurs when all mutants deviating from the population strategy have lower fitness than the population strategy, meaning that the population strategy can not be invaded by an alternative strategy.

Returning to the previous example, we can calculate whether or not the mutant strategy S_m is able to invade a population that is using strategy S_{pop} . We calculate the fitness of a random member of the population (i.e. an individual using S_{pop}) against the population as a whole. In this case, W for S_{pop} equals 0.375. Comparing this to the fitness of the mutant using S_m against S_{pop} (0.2474), we see that the population member has higher fitness than the mutant, and thus the population is stable against invasions by a mutant using S_m .

As there are a potentially infinite number of strategies that can be tested, it is impossible to test them all in the manner outlined above. Instead, we use convergence techniques (Houston and McNamara 1999) to find ESSs. A standard technique for finding an ESS in a dynamic game is through iteration of the best response map (McNamara et al. 2000). This procedure starts with an arbitrary strategy and finds the sequence of strategies where each strategy is the best response to the previous strategy in the sequence. A problem of this method is that the sequence sometimes oscillates without converging towards the ESS. By incorporating errors in decision making, oscillation can be eliminated. 'Errors' here refer to the biologically realistic assumption that individuals do not always use the strategy that yields them the highest fitness, especially if the fitness difference between two options (e.g. return or do not return to an area) is small. By including errors, it is thus assumed that the probability of making an error decreases as the cost of making it increases (McNamara et al. 1997).

As a strategy S consists of S_W , S_L and S_D , we vary each in turn to find the best response, and update S . We calculate fitness for an animal using (in the first instance) $S_W=1$ or $S_W=0$, against a member of the population using S_{pop} . Denoting the fitness of the strategy $\{1, S_L, S_D\}$ by W_1 and that of $\{0, S_L, S_D\}$ by W_0 , we can calculate the fitness difference between using $S_W=1$ and $S_W=0$ as $d=W_1-W_0$. The best response with error (behavioural variability) is then calculated as:

$$S_{Wn} = \left(\frac{1}{1 + e^{-d/\delta}} \right) \quad (7)$$

The amount of error is indicated by the parameter δ . Increasing δ means more variability in behaviour: if δ is small, the animal is highly likely to choose the better option even if the fitness difference between the two behavioural options is small. As δ approaches infinity, the individual chooses either action with a probability that approaches 1/2: animals become increasingly unable to differentiate between actions with similar consequences. Using this method, the value for S_{Wn} depends on the fitness consequences of the two options ($S_W=1$ and $S_W=0$) when they compete against a population using S_{Wn-1} . Other components of the strategy (S_L and S_D) are calculated analogously.

The iteration then proceeds as follows:

1. Choose an initial population strategy $S_0=\{S_{W0}, S_{L0}, S_{D0}\}$.
2. Calculate S_{W1} according to Eq. 7.
3. Calculate S_{L1} analogously to Eq. 7.
4. Calculate S_{D1} analogously to Eq. 7.
5. Create the new $S_1=\{S_{W1}, S_{L1}, S_{D1}\}$.
6. Repeat steps 2–5 to find the new population strategy S_2 .

Steps 2–6 are repeated over n time-steps. This quickly produces an ESS where $S_n=\{S_{Wn}, S_{Ln}, S_{Dn}\}$.

Results

By altering the values given to the various parameters, we investigated the ESS solutions that emerged from the model under different conditions.

Is avoidance behaviour adaptive?

First, we investigated whether it is adaptive for both winners and losers (or for individuals who experienced a draw) to avoid areas of conflict. We found no situations in which both previous winners and losers avoided the contested area completely. However, Fig. 1 shows that in some cases (low value of V), individuals return with less than 50% probability no matter what the outcome of the previous fight. This confirms that avoidance behaviour is indeed sometimes beneficial regardless of the outcome of

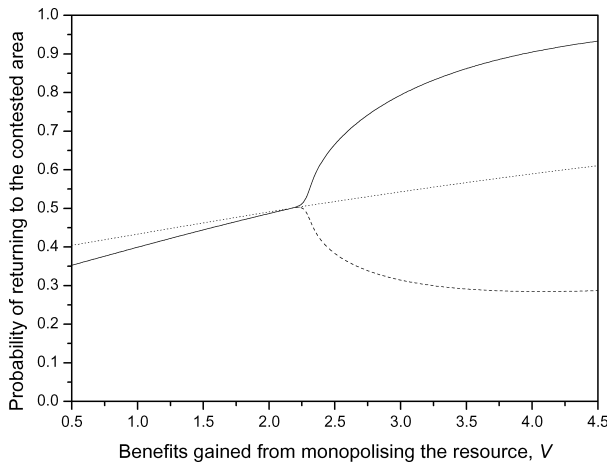


Fig. 1 Evolutionarily stable return probabilities after winning (S_W , solid line), losing (S_L ; dashed line) and after a draw (S_D ; dotted line), for a population starting its evolution from a common-sense strategy $S_{pop}=\{1, 0, 0.5\}$. Other parameter values used: $\alpha=0.5$, $v=1$, $c_W=2.5$, $c_L=5$, $c_D=2.5$, $a=0$, $p_d=0.2$, $\delta=0.5$; value of resource V as indicated on the x -axis. In some cases (when the value of monopolising, V is low), both winners and losers avoid the contested area more than half the time, at other times, winners return but losers avoid the area (high V)

the fight; also note that a return probability of less than 50% guarantees that the result is not merely due to errors in decision-making (random variation in behaviour), but that staying away truly generates higher fitness than returning. This is intuitive, when the benefits (V) are small compared to the costs of meeting an opponent and fighting. Likewise, there is an intuitive explanation as to why complete avoidance behaviour (neither competitor ever returns to the area of conflict) nevertheless does not evolve: if one participant (say, the loser) always stays away, there is no cost for the other (say, the winner) to return and claim the reward V .

Common-sense versus paradoxical solutions

We define a paradoxical solution as one where the probability of returning having won a fight is lower than the probability of returning having lost. In Fig. 1, all solutions were derived assuming that $S_{pop}=\{1, 0, 0.5\}$ was the ancestral strategy from which evolution starts. This strategy is common-sense, and it is therefore not surprising that solutions are common-sense too (Fig. 1). We now turn to the question of whether common-sense and paradoxical solutions are equivalent in the model. In other words, if evolution starts from a common-sense or a paradoxical strategy (the initial population strategy), will stable solutions turn out common-sense or paradoxical?

If solutions are entirely based on conventions, then the convention ‘losers return, winners do not’ is as logical as the one that specifies the opposite. However, if true fighting ability plays a role, we might expect that winners of the first fight (who are more likely to be good than bad

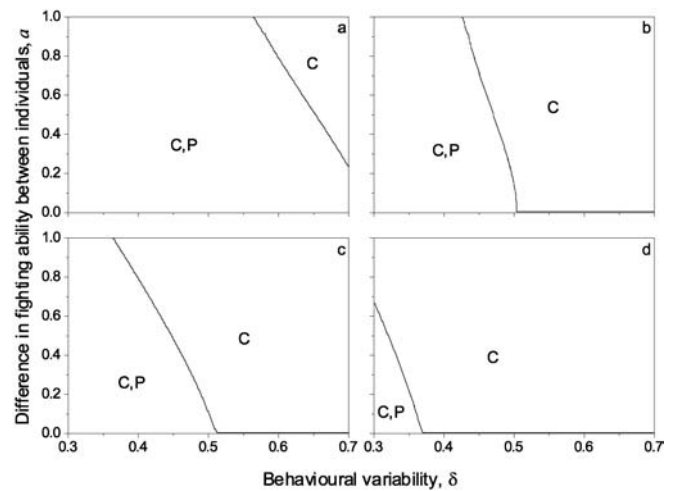


Fig. 2a–d Stability of common-sense (C) and paradoxical (P) strategies at various values of behavioural variability (δ) and population-wide difference in fighting ability (a). Where both C and P exist, either can be stable depending on the initial strategy in the ancient population. Each panel shows stabilities for different values of monopolising the resource, V , and costs of fighting c_W , c_L and c_D . **a** $V=5$, $c_W=3$, $c_L=6$, **b** $V=5$, $c_W=2$, $c_L=4$, $c_D=2$; **c** $V=2$, $c_W=3$, $c_L=6$, $c_D=3$; and **d** $V=2$, $c_W=2$, $c_L=4$, $c_D=2$. Other parameter values used for all panels: $\alpha=0.5$, $v=1$, $p_d=0.2$. Ancient strategies: for common-sense, $S_{pop}=\{1, 0, 0.5\}$; for paradoxical, $S_{pop}=\{0, 1, 0.5\}$

fighters) are more likely to win the latter fight too. Therefore, they suffer lower fighting costs, and should be more prone to return than losers. This would lead to the evolution of a common-sense strategy even if starting from a paradoxical ancestral strategy.

Figure 2 shows how δ (the magnitude of behavioural variability) and a (the asymmetry between individuals) affect whether both paradoxical and common-sense strategies can be stable, or whether a common-sense strategy evolves irrespective of whether the ancient population was common-sense or paradoxical. When animals adhere to a behavioural rule without much variation (small δ), both types of population strategies are stable regardless of the asymmetry between individuals. When behaviour is more variable (large δ), asymmetries between fighters allow common-sense solutions to evolve from paradoxical population strategies. Thus, when the difference between good and poor fighters is large, paradoxical strategies are unlikely to be stable, except when behaviour shows little random variation.

Figure 2 also shows how the stability of paradoxical strategies is affected by the relative costs and benefits of fighting. Fig. 2a shows that when both costs and benefits are high, paradoxical solutions persist over much of the parameter space, evolving to common-sense solutions only when variability δ and asymmetries in fighting ability a are high. When the costs of fighting are reduced (Fig. 2b), common-sense solutions evolve from paradoxical ancestral strategies when there is less variation in behaviour (lower δ) and asymmetries are smaller (lower a). A similar pattern is seen when the benefits of fighting

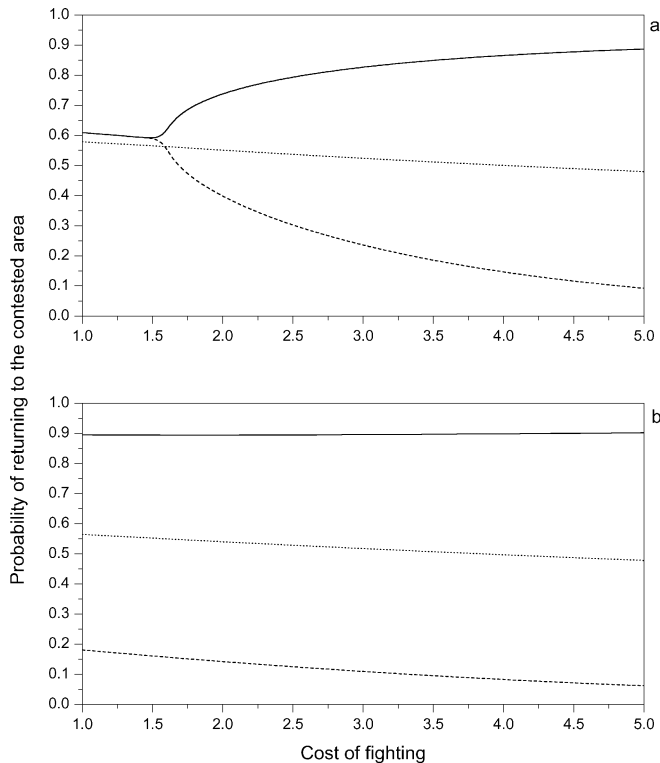


Fig. 3 Return probabilities with **a** $a=0$, **b** $a=1$. *Solid line*: evolutionarily stable strategy (ESS) probability of returning having won, *dashed line*: probability of returning having lost, *dotted line*: probability of returning after a draw. Parameter values used: $\alpha=0.5$, $c_L=6$, $v=1$, $V=3$, $p_d=0.2$, $\delta=0.5$, Initial $S_{pop}=\{1, 0, 0.5\}$. Cost of winning (c_W) and a draw (c_D) as indicated on the x -axis

are reduced (Fig. 2c). Finally, Fig. 2d shows that when both the costs and benefits of fighting are low, common-sense solutions prevail over the majority of the parameter space. Paradoxical solutions are only stable when there is very little behavioural variation (small d) and animals differ only slightly in their fighting ability (small a). Additionally, paradoxical solutions are stable when all individuals are identical with respect to their fighting ability ($a=0$).

Strength of conventions

A convention is a rule based on arbitrary cues that allows quick resolution of potentially protracted disputes (Mesterton-Gibbons and Adams 2003). In game theory, 'convention' is generally used to describe pure strategies (Maynard Smith and Parker 1976; Parker 1984), however, we use a slightly broader meaning: we assume that behaviour can vary (McNamara et al. 1997), and thus we do not obtain pure strategies. We have therefore used 'convention' to mean a situation where either one of two possible outcomes (winning, losing) can function equally well as the cue that makes an animal to return to the contested area, and it is sufficient that the behaviour is statistically associated with the cue.

When a paradoxical solution is stable, it means that animals rely on a convention to settle fights: one outcome (losing) determines a higher probability of returning, which could lead to ownership even though it does not have a positive relationship with the ability to defend a territory. We have demonstrated that conventional behaviour of this type can be stable if fighting ability does not differ much between individuals, and they follow behavioural rules strictly (Fig. 2).

Figure 3a shows the common-sense solution in a case where individuals do not differ in fighting ability at all ($a=0$). Thus, their fate in the first fight does not give them any information about their fighting ability; if they nevertheless adjust their behaviour according to the fight outcome, it must be due to a convention. The asymmetry in fight outcome is the only factor influencing the choice of strategy, equivalent to asymmetries such as owner or intruder determining outcomes in other game-theory models (Maynard Smith and Parker 1976; Maynard Smith 1982; Leimar and Enquist 1984; Enquist and Leimar 1987). Conventions clearly become stronger when the costs of fighting increase: winner and loser behaviour becomes markedly different when fighting costs are large (Fig. 3a). In the case where there are true differences in fighting ability (Fig. 3b), losers gain information about their fighting ability in the first fight, and they consequently avoid the area even if costs of fighting are low.

Additionally, as the value of sharing the resource, v , increases, the probability of losers returning increases (not shown). This is intuitive; when a resource is worth sharing (high v), it makes sense for both winners and losers to return to claim a part of it, even though this may involve further aggressive interactions.

Discussion

Is avoidance adaptive?

Contrary to the assumptions of some models (Stamps and Krishnan 1999, 2001), our results suggest that a tendency to avoid areas in which fights have occurred is not always an adaptive strategy for territorial animals. In some cases, however, avoidance behaviour is beneficial, no matter what the outcome of the fight (low values of V , Fig. 1). This is intuitive when the benefits (V) of fighting are small compared to the costs of meeting an opponent and fighting.

An interesting phenomenon is that the probability of returning can decrease with increasing the value V of the resource. This happens for losers of fights when winners become much more prone to return after fights, which in turn increases the costs of returning to losers (Fig. 1). At large values of V , individuals respond to winning by returning to the area. When losers do not do so, winners have effectively claimed ownership of the area (Fig. 1, large V). When one participant (in this case, the loser) stays away, it makes sense for the other (the winner) to return to the contested area and claim the benefits V . As it

is unlikely to meet the loser again, there are no costs associated with returning.

In their model of territory acquisition by unequal competitors, Stamps and Krishnan (2001) found that individuals suffering lower fighting costs acquire larger territories than individuals suffering from higher fighting costs. In the current model, when the benefits are higher, winners (who suffer lower fight costs) have a higher tendency to return to the contested area than losers, which could lead to the establishment of larger territories. Our model thus also supports the finding that the costs experienced by an individual could affect their final territory size (Stamps and Krishnan 2001).

Additionally, our findings support the assumption of early game-theory models that animals can win space by winning fights (Maynard Smith and Price 1973; Grafen 1979; Maynard Smith 1982), if their opponent avoids the area having lost. The costs of fighting relative to the benefits of winning determine whether general avoidance (as in Stamps and Krishnan 1999, 2001) or a 'winner-takes-all' pattern evolves.

Common-sense versus paradoxical solutions

We also found that sometimes paradoxical (losers have a higher probability of returning than winners) and common-sense (winners are more likely to return) solutions both exist and at other times, only common-sense strategies are stable (Fig. 2). This reflects the findings of other game-theory models, which show a limited set of conditions under which paradoxical strategies can evolve (Maynard Smith and Parker 1976; Hammerstein and Parker 1982; Enquist and Leimar 1987; Mesterton-Gibbons 1992). Both variation in fighting ability, a , variability in behaviour, δ , and the costs and benefits of fighting play a role in determining whether a paradoxical ancestral population strategy evolves to a common-sense or paradoxical solution in the current game. Why is this the case? When individuals differ little in fighting ability (small a), an individual gains little information on its own RHP from fighting. Overly high fight costs can then be avoided simply based on conventions, and paradoxical strategies can remain stable. When there are large differences in fighting ability (large a), winners of the first fight (likely to be of high RHP) are likely to also win the second fight, suffer lower fighting costs and be more likely to return than losers. This leads to the evolution of a common-sense strategy even when the ancestral strategy is paradoxical.

However, even when differences in fighting ability exist, paradoxical strategies can be stable if animals strictly adhere to behavioural rules (small δ). This means that an initial convention that was in use in an ancient population remains stable. But when there is some behavioural variability (large δ), individuals who in reality are better fighters sometimes return to contested areas even if the initial convention dictates they should not. As these individuals tend to win, the convention gets

broken down and true fighting ability takes over as a decisive feature of the system.

When the costs and benefits of fighting are low, paradoxical solutions are no longer stable, and evolve to common-sense ESSs (Fig. 2). When the benefits are low, losers can no longer offset the high costs of losing by returning to claim the resource, and so gain higher fitness by not returning, and the paradoxical convention breaks down. Conventions also tend to break down when benefits of fighting are low. This implies that the fitness difference between returning and avoiding is small. The cost of making errors is thus small, and therefore errors occur more frequently (McNamara et al. 1997), which in turn implies that selection does not strongly prevent individuals from choosing the alternative behaviour. When original rules of behaviour are not strictly followed, the signature of the true fighting ability can become dominating, and a common-sense ESS evolves.

Our finding that fighting ability plays a greater role in settling disputes when the asymmetry in fighting ability is greater is not surprising. Many empirical studies show that body size (generally an indicator of fighting ability) plays an important role in determining the outcome of fights (Beaugrand et al. 1996; Jennions and Backwell 1996; Petersen and Hardy 1996; Johnsson et al. 1999). The finding that conventions can be important when asymmetries are small is reflected in empirical studies where owners tend to win fights against intruders when their fighting ability appears to be equal to or lower than that of their opponent (Beaugrand et al. 1996; Jennions and Backwell 1996; Alcock and Bailey 1997; Chellappa et al. 1999; Johnsson et al. 1999; Wenseleers et al. 2002).

However, it has been suggested that residents tend to win not because of arbitrary conventions but because they have greater motivation to fight, as their valuation of the resource is greater, a finding supported by empirical data (birds, Krebs 1982; Tobias 1997; fish, Neat et al. 1998b; Johnsson and Forser 2002; insects, Alcock and Bailey 1997; crustaceans, Edsman and Jonsson 1996). Our results suggest that conventions are not necessarily falsified if some asymmetry (e.g. in resource-holding potential, or in valuing the resource) can be shown to exist. While avoidance behaviour by the loser is stronger when asymmetries exist (Fig. 3b), it persists in the absence of asymmetries too (Fig. 3a).

As the costs of fighting increase, strategies where winners return with increasing probability and losers with decreasing probability become stable (Fig. 3). This suggests that as fighting becomes costly, conventions become stronger even if strategies are common-sense (note that the information content gained by the initial fight does not change when costs change). If fighting is costly, then it would benefit individuals to avoid fighting whenever possible, and a strategy where only one of the contestants would return would allow animals to avoid a second fight in that location but enable one of them to gain the benefits associated with returning to it. As the benefit associated with monopolising the resource, V , increases (Fig. 1), we also see an increasing difference in

the behaviour of winners and losers. As paradoxical strategies are stable at high values of V (Fig. 2), this suggests that conventions play a role here, too, otherwise we would expect the individual of greater fighting ability to always return more frequently and a common-sense solution to emerge.

According to our results, the fact that paradoxical strategies are not seen in nature probably relates to the fact that fighting abilities indeed almost always vary between individuals, and there usually is some behavioural variation (as in almost any biological trait). This highlights the general importance of not assuming that individuals always optimise their behaviour in every single instance (McNamara et al. 1997). In addition, paradoxical strategies are not seen when the costs and benefits of fighting are low. In nature, animals probably do not engage in extremely costly fights for small areas of extremely valuable space. Instead, low cost aggression, such as chases and displays, rather than escalated fights, is common (butterflies, Davies 1978; Hardy 1998; damselflies, Waage 1988; spiders, Riechert 1978; lizards, Stamps and Krishnan 1997, 1998). Additionally, the patches of space contested may be relatively low in value in comparison to an entire territory, for example, when individuals are contesting small areas of feeding territories rather than the centre of a breeding territory.

Limitations of the model

As with all models, we have made some assumptions that should be evaluated critically. Individuals in our model only gain information regarding their fighting ability from the fights; they do not know their own fighting ability beforehand. A longer series of fights would enable an individual to gain more accurate information, as each fight would enable them to update the information they possess (Enquist and Leimar 1983). If individuals can gain more accurate information, or have prior information regarding their fighting ability, common-sense solutions would be strengthened as individuals would be able to more accurately assess their chances of winning or losing a fight and participate or avoid accordingly.

In addition, the 'winner and loser' effect (Dugatkin 1997; Hsu and Wolf 1999, 2001) may have an influence on the behaviour of an individual. According to this effect, an animal is more likely to win (lose) in fights following a fight that it has already won (lost). In our model, winning probabilities themselves do not change as a result of prior experience. However, the fact that winners become more daring in terms of returning to the area could be interpreted as similar to the winner effect. Winner effects clearly have the potential to further enhance the stability of common-sense solutions.

In the model, we assume that the parameters describing asymmetries in fighting ability, a , and the probability that fights end in a draw (p_d) are independent. Although one could expect that draws would occur more frequently when individuals are equally matched (possibly with

draws occurring 100% of the time), there are also situations in which equally matched competitors fight until there is a clear winner (Davies 1978; Waage 1988; Gribbin and Thompson 1991; Kemp and Wiklund 2001), and likewise, there are situations where draws occur even though one would expect the better fighter to win (Stamps and Krishnan 1997). It is important to note that the model is able to produce solutions for any given combination of fight outcome probabilities that may occur in nature.

We assume a relationship between the outcome of a fight and its cost, namely that losing is always more costly than winning. A limitation of this assumption is that this relationship between fight outcome and associated cost does not hold true for all species. Experimental studies have shown that while in some cases, losers do incur higher costs than winners (Chellappa and Huntingford 1989; Neat et al. 1998a), in other cases there is no difference in the costs incurred (Smith and Taylor 1992). The energetic cost spent by winners may even exceed that of losers (Hack 1997), which presumably could lead to a wider diversity of outcomes than we have derived. For simplicity, we also assume that all fights ending in the same outcome carry the same cost. This can be viewed as an average cost, as an aggressive interaction can take many different forms, ranging from threat display and avoidance to escalated contests, which are likely to carry very different costs to both the winner and the loser (Chellappa and Huntingford 1989; Smith and Taylor 1992; Brick 1998; Neat et al. 1998a).

Experimental findings suggest that territory owners abandon territory defence when the costs of fighting become too high (Carpenter 1987; Tricas 1989). Fighting costs in the experimental studies are generally associated with the number of intruders on the territory (e.g. Myers et al. 1979; Carpenter et al. 1983; Carpenter 1987; Tricas 1989; Keeley 2000; review in Adams 2001). Our model considers the cost of each interaction, rather than the number of interactions, so that there is scope for further study. Considering the dynamics of space use when there are multiple intruders and continuous space, while evaluating the adaptive value of strategies, would be a clear next step in combining the spatially explicit approach of mechanistic models (Stamps and Krishnan 1999, 2001) with the evolutionary aspects of game-theory models.

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