

Lesley J. Morrell · Hanna Kokko

Bridging the gap between mechanistic and adaptive explanations of territory formation

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Abstract How animals divide space can have fundamental implications for the population dynamics of territorial species. It has recently been proposed that space can be divided if animals tend to avoid fight locations, rather than the winner of fights gaining access to exclusive resources, behaviour that generates exclusive territories in two-dimensional space. A game-theory model has shown that this avoidance behaviour can be adaptive, but the adaptiveness has not been investigated in a spatially realistic context. We present a model that investigates potential strategies for the acquisition of territories when two-dimensional space must be divided between individuals. We examine whether exclusive territories form when animals avoid all encounters with others, or only those encounters that have led to losing fights, under different fighting costs and population densities. Our model suggests that when fighting costs are high, and the population density is low, the most adaptive behaviour is to avoid fight locations, which generates well-defined, exclusive territories in a population that is able to resist invasion by more aggressive strategies. Low fighting costs and high population densities lead to the breakdown of territoriality and the formation of large, over-

lapping home ranges. We also provide a novel reason as to why so-called paradoxical strategies do not exist in nature: if we define a paradoxical strategy as an exact mirror-image of a common-sense one, it must respond in the opposite way to a draw as well as to wins and losses. When this is the case, and draws are common (fight outcomes are often not clear-cut in nature), the common-sense strategy is more often adaptive than a paradoxical alternative.

Keywords Aggression · Fighting · Territoriality · Divisible space · Paradoxical strategy

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L. J. Morrell (✉)
Division of Environmental and Evolutionary Biology,
Institute of Biomedical and Life Sciences,
University of Glasgow,
Graham Kerr Building, Glasgow, G12 8QQ, UK
e-mail: 0103207m@udcf.gla.ac.uk
Tel.: +44-141-3302430
Fax: +44-141-3305971

H. Kokko
Laboratory of Ecological and Evolutionary Dynamics,
Department of Biological and Environmental Sciences,
University of Helsinki,
Helsinki, Finland

H. Kokko
Department of Biological and Environmental Science,
University of Jyväskylä,
Jyväskylä, Finland

Introduction

Territory ownership is a major determinant of fitness in territorial animals, and the question of how individuals gain territories and partition space can have important implications for the dynamics of populations (Gordon 1997; Both and Visser 2003): exclusive use of space will obviously limit the number of individuals capable of breeding, leading to density effects (e.g. Newton 1992; Rodenhouse et al. 1997; Kokko and Sutherland 1998).

A large body of work considers optimum sizes for territories in an economic framework. These models assume that the costs (in terms of numbers of intruders) and benefits (i.e. food resources available) determine territory size, and make predictions concerning the optimal size (e.g. Ebersole 1980; Hixon 1980; Schoener 1983; Schoener 1987). These qualitative predictions have been tested in a range of taxa (Adams 2001). However, the majority of economic models assume that animals are free to adjust their boundaries without constraint from neighbouring territories (Hixon 1980; Schoener 1983; Lima 1984; Adams 2001). In reality, contiguous territories may be compressed below their optimal size by pressure exerted by neighbours (Maynard Smith 1974; Hixon 1980; Patterson 1985; Adams 1998; Keeley 2000; Adams 2001). Clearly, to understand territory formation, it is crucially important to understand the process by which neighbours

influence the location of the boundary between territories. Two major lines of thought have emerged: mechanistic models and models based on adaptive arguments.

Mechanistic models demonstrate the effect of particular rules of behaviour (Adams 2001). Early models used geometric techniques to predict where boundaries are positioned, and suggested that neighbours apply pressure against each other and that boundaries are formed where the pressure is equal (e.g. Maynard Smith 1974; Buckley and Buckley 1977; Patterson 1985; Adams 1998; for a review, see Adams 2001). More recent mechanistic models of territoriality are based on animal movement and interactions between neighbours or neighbouring groups of animals. Examples include models of movement and scent marking to predict spatial patterns in timber wolves (*Canis lupus*; Lewis and Murray 1993; White et al. 1996), and the formation of territories as a learning process governed by positive and negative experiences in different locations (Stamps and Krishnan 1999, 2001). Based on observations of territorial settlement in juvenile *Anolis aeneus* lizards, Stamps and Krishnan (1999, 2001) offer a hypothesis where repeated interactions lead to the division of space through 'nagging' (Sih and Mateo 2001). They model a situation in which the attractiveness of an area to an individual depends on the experiences the individual has within it, and that individuals only return to areas in which positive experiences (increased familiarity with the area) outweigh negative ones (fights), thus showing a tendency to avoid locations where they have been involved in fights. These models reproduce several features of territorial systems and have much biological realism (Sih and Mateo 2001), but they are mechanistic rather than adaptationist, and do not analyse the costs and benefits of different strategies.

To fully evaluate the underlying assumption of these models that avoidance leads to exclusive space use (Adams 2001; Sih and Mateo 2001), some factors should be considered. Models need to be spatially explicit in two dimensions. Additionally, the behaviour of other individuals in the population, and their space use, needs to be considered, and for this, game-theory modelling is needed. In particular, models should not only consider the behaviour of neighbours, but also their space use and its effects on the availability of space. Few models exist that fulfil all these criteria. Game-theory models of territory size (e.g. Parker and Knowlton 1980) tend to be spatially implicit—territories are assumed to be spatially contiguous, but the models do not specify the strategies adopted by different neighbours (Adams 2001).

Spatially explicit game-theory approaches to the division of space generally consider how two individuals can negotiate the division of a line into two territories (Maynard Smith 1982; Lewis and Moorcroft 2001; Mesterton-Gibbons and Adams 2003; Pereira et al. 2003; Morrell and Kokko 2003). As an example of models that use adaptive arguments to explain territory size in two-dimensional space, Both and Visser (2003) modelled the circumstances under which contiguous and non-contiguous territories centred on a nest site should be formed.

However, their model fails to satisfy the criterion that individuals' behaviour should influence the availability of space to others: an individual was assumed to be able to expand its territory to a specific size (T) regardless of population density, although doing this was costlier at higher densities.

Thus, no model to date satisfies all our criteria. Perhaps closest to achieving this goal, Adler and Gordon (2003) developed a spatially explicit model of territory size in harvester ants, solving for optimal foraging distances. However, the model by Adler and Gordon (2003) is too specific to serve as a general model of space use as it is strongly focused on the behaviour of ant workers that forage for their colonies.

Here, we develop a model that addresses the issues of multiple competitors and continuous, two-dimensional space, while investigating the adaptiveness of different strategies for territory acquisition. Thus, one of our aims is to combine the spatially explicit approach of mechanistic models with some of the evolutionary aspects of game-theory models, in order to understand the process by which boundaries can form between neighbouring territories.

Methods

Model background

We consider a situation in which a number of individuals, n , arrive in a previously unoccupied area of habitat that can potentially be divided into territories. The aim of the model is to determine how the individuals can partition the habitat into separate territories (Stamps and Krishnan 1999, 2001), rather than investigate the decision to contest an existing territory or settle in an unoccupied one (e.g. Mesterton-Gibbons 1992; Broom et al. 1997). Modelling was performed using MATLAB, and an outline of the model code can be found in the Appendix. The habitat area consists of a number of lattice squares, totalling a^2 squares, where a is the linear size of one dimension (i.e. the total number of squares along one edge) of the two-dimensional area. We assume that all squares in the habitat area are of the same intrinsic quality, that is, we assume that every square has the same potential effect on individual fitness. The space used by an individual will consist of more than one of the squares, and the total habitat area is large enough to support the territories of multiple individuals. To avoid boundary effects, the area is wrapped such that each square has exactly four neighbouring squares, and we assume that individuals moving over a boundary arrive back into the habitat area from the opposite side. This is a standard assumption in spatially explicit individual-based modelling (e.g. Slatkin and Anderson 1984; Bascompte and Solé 1997; Ruckstuhl and Kokko 2002).

Territory expansion and movement

We assume that the initial spatial distribution of individuals is random. Each individual therefore begins at a specific ('arrival') location, (i, j) , allocated at random, and chosen from all the lattice squares (i.e. $1 \leq i \leq a$, $1 \leq j \leq a$). Individual k 's use of space in square (i, j) at time t is denoted by $A(i, j, k, t)$. This quantity reflects the individual's occupancy of the area, and takes values between 0 and 1. Although 'occupancy' could be taken to imply ownership or exclusive use, we simply mean that this parameter reflects an accumulation of an individual's responses to experiences in the area. An individual uses a square if $A(i, j, k, t) > 0$ in that square; note that we do not exclude the possibility that two or more individuals use the same square. Initially, A at an individual's arrival location (i, j)

is set equal to 1, and zero elsewhere. The values of A for each individual develop according to the individual's evolutionary strategy, which dictates the rules of habitat use in previously unfamiliar habitat, as specified below. Within one unit of time, individuals move through all the space they occupy, visiting every square in which A exceeds zero. Movement continues until the end of the settlement period, t_{\max} .

Exploration of empty space

The individual's strategy defines how it reacts to encounters with others. Before we proceed to describing these reactions, we specify how individuals encounter each other in the first place. In order to expand their initial territory of a single square (see above), explore new space and eventually meet other individuals, we assume an intrinsic tendency for an individual to increase the space that it uses. During each time unit, for each individual k , we take each location (i, j) in which $A(i, j, k, t) > 0$, and assume that the surrounding squares $(i-1, j)$, $(i+1, j)$, $(i, j-1)$, $(i, j+1)$ all increase their value of A by the amount $\epsilon A(i, j)$. The rate ϵ is equivalent to animals exploring unknown areas outside those with which they are familiar, in order to expand their home range or territory. To keep the model simple, we assume that ϵ is equal for all individuals, is fixed and does not evolve. We ensure that for each individual, A does not exceed 1, by resetting the value of A to 1 if the addition of ϵ takes it above this value.

Experiences within the territory

We next describe the rules of habitat use that depend on an individual's strategy. We assume that during each visit to a square, individuals can have either an aggressive or a non-aggressive experience. Aggressive interactions between individuals occur wherever their space use overlaps. Thus, a time unit t is defined as being long enough such that individuals can be involved in multiple fights (in different squares) within one time unit. Our time unit thus corresponds to the time to independence, a concept that is used in home range studies to describe the time it takes an individual to use all of its home range (Swihart and Slade 1985; Swihart et al. 1988; Kernohan et al. 2001). Each individual may fight with several others, and/or several times with the same individual in different squares in the habitat area. During one time unit, a fight between individuals k_1 and k_2 will occur wherever $A(i, j, k_1, t) > 0$ and $A(i, j, k_2, t) > 0$. We make the assumption that fights occur wherever space use overlaps for simplicity, and to ensure that the resulting territories are spatially contiguous. Aggressive encounters (fights) can end with a win, a loss or a draw for each individual. We assume that all individuals have equal fighting abilities; following from this, we also assume that all fights end with a random outcome, such that a proportion d of fights will end with a draw. Fights that do not end with a draw end with a clear winner and loser, with equal probability of winning and losing for each individual: $(1-d)/2$.

A non-aggressive experience occurs when an individual k visits a square in which $A(i, j, k, t) > 0$, but does not encounter another individual. This occurs when a square used by the individual is not used by any other individuals (i.e. $A(i, j) = 0$ for all other individuals at time t). Thus, in total, there are four potential outcomes for an individual's visit to any given square: a win, a loss, a draw, or the individual can find the space empty. We assume that animals react in different ways to these four outcomes (dictated by their strategies), but a single individual always reacts in the same way to the same outcome; individuals are fixed in this aspect of their behaviour ('behavioural types', Sih et al. 2004). A reaction is an increase or decrease in A in each square, for each individual. After each time-step, a change in A of δ is added to or subtracted from each individual's A in each area, according to the outcome of the visit and the individual strategy. Again, we ensure that the value of A always remains between 0 and 1 by resetting the value to 0 if it becomes negative, and resetting to 1 if it exceeds this value. An

individual's strategy is composed of its reaction to each of the four potential outcomes of a visit to a particular square.

Strategies for territory acquisition

There are potentially a large number of strategies, and considering every one is not feasible in our spatially explicit approach. We therefore consider four biologically interesting strategies, which differ in the way an individual using the strategy responds to the outcome of a fight, or finding a square empty. The strategies differ in their aggressiveness, defined by the behaviour of an individual after a fight: if an individual reacts positively to a fight (i.e. the outcome causes an increase in the occupancy value A), then the individual responds aggressively to that outcome.

Strategy 1: cautious (Ca)

For individuals using this strategy, fights have a negative effect on an individual's occupancy of the area, A , regardless of the outcome of the fight (i.e., whether it won, lost or drew in the fight). Finding the space empty results in an increase in A (after Stamps and Krishnan 1999, 2001). Cautious is the least aggressive strategy we investigate.

Strategy 2: common sense (CS)

Losing or drawing in a fight has a negative effect on occupancy, A , for common-sense individuals. Winning a fight and finding the space empty have a positive effect on A . This is similar to the 'winner-takes-all' strategy of early game-theory models, and is a more aggressive strategy than cautious.

Strategy 3: paradoxical (P)

Positive effects on A result from losing or drawing in a fight; winning and finding the space empty have a negative effect. Individuals using the paradoxical strategy thus behave in exactly the opposite way to common-sense individuals. This strategy implies that intruders gain access to territories while the owners retreat. While deeply counterintuitive, it automatically emerges as a stable solution in many game-theory models of contests over indivisible space (Maynard Smith and Parker 1976; Hammerstein and Parker 1982; Enquist and Leimar 1987; Mesterton-Gibbons 1992).

Strategy 4: daring (D)

Only losing a fight has a negative effect on A . All other experiences have a positive effect. This strategy is thus more aggressive than cautious or common sense, as individuals are more likely to repeatedly encounter opponents.

Two strategies compete at one time, such that a proportion f of individuals use strategy S_1 and $(1-f)$ use S_2 . We aim to investigate the fitness consequences of using different strategies (the calculation of fitness is defined below). We are interested in two basic events: whether a single individual using strategy S_1 can invade a population using S_2 , and once this strategy has invaded, whether it can maintain a superior or equal fitness level as its numbers increase.

Home range size and exclusivity

The home range of an individual is the total number of squares for which $A(i, j, k, t_{\max}) > 0$, at the end of the settlement period, t_{\max} . We also calculate the number of squares used exclusively by each individual. For individual k_1 , this is the number of squares for which $A(i, j, k_1, t_{\max}) > 0$, but $A(i, j, k_{2-n}, t) = 0$.

Individual fitness

The costs associated with fighting are represented by c . We assume that all fights carry equal costs, regardless of the outcome of the fight. Thus, the outcome of a fight itself rather than the costs experienced by an individual determines the individual's response to the fight. We make this assumption to make the model as symmetrical as possible; if we nevertheless find that paradoxical strategies cannot persist, the absence of paradoxical solutions in nature is better explained than had we made assumptions that possibly bias outcomes towards common-sense strategies.

We assume that there is no cost associated with finding a square empty of other individuals. Total contest costs for each individual, C_k , are calculated cumulatively at each time-step. An individual pays the costs associated with the outcome it experiences in each square in each time-step (see Appendix). The benefits gained by each individual, B_k , are calculated at the end of the territory settlement period, t_{max} . Each individual gains benefits B_k from each square it occupies, scaled by its occupancy, A , in that square, and the sum of A in the area for all individuals using the area. Thus, for individual k_1 :

$$B_{k_1} = \sqrt{\frac{\sum_{i,j} A(i,j,k_1,t_{max})}{\sum_{k=1}^n A(i,j,k,t_{max})}}$$

The square root represents a diminishing returns relationship between the number of squares occupied by an individual and the benefits it gains from that area. This is a generally accepted relationship between the size of a territory and the benefits that can be gained from it. For a central place forager, for example, an increase in territory size increases the food available to the territory owner, but increases the time taken to transport it to the nest or retreat (Both and Visser 2003). For territories used purely for feeding, there is a maximum food intake above which fitness no longer increases (Gill and Wolf 1975; Schoener 1983).

The fitness of individual k , W_k , depends multiplicatively on the benefits gained (B_k) from the space it uses and the costs it pays (C_k) during fighting, scaled such that increasing costs lead to fitness approaching zero:

$$W_k = B_k e^{-C_k}$$

The multiplicative form indicates that territories are necessary to gain fitness, and an individual that uses none of the available space, gaining no benefits ($B=0$) will have no fitness (but will remain extant), but neither will an individual whose costs of fighting are so high that survival is very improbable (e^{-C}). This form also ensures that fitness (a relative concept) never becomes negative. The negative exponential function indicates that each fight reduces the fitness benefits that can be gained by the same proportion. Strategy fitness W_S is estimated as the mean fitness of all individuals using strategy S after 20 iterations of the model.

Evolutionary stability of strategies

We investigated whether a population of each of the strategies is stable against invasion by a single mutant individual using one of the alternative strategies ($f=1/n$). We investigate whether populations are stable against mutants under different levels of costs (c) and population density (n). The details of the algorithm are provided in the Appendix. If a strategy is susceptible to invasion by a mutant, we can investigate whether the mutant strategy gains higher or lower mean fitness than the population when its numbers increase ($f=0.5$). Here we consider only a single generation: a potentially fruitful avenue of further research would be to allow the frequency of individuals using a certain strategy to evolve over many generations. The model also allows us to compare the fitness of populations of a single strategy, and the territories they gain. Since our model is stochastic, the stability of a population has to be interpreted in the following conservative way: a mutant is able to

invade a population if its fitness is equal to or greater than the mean strategy fitness of the population (solid lines in Fig. 3 and Fig. 4, 'Y' in Table 2). A mutant cannot invade a population if the population has greater mean fitness than the mutant (dashed lines in Fig. 3 and Fig. 4, 'X' in Table 2). Invadability was investigated using paired t -tests; P -values were Bonferroni corrected (Rice 1989) within a set of parameter values. Under some parameter values, either the mutant, or the population, or both, gain fitness of zero (when both the invader and the population gain zero fitness; shown by a dotted line in Fig. 3 and Fig. 4), and thus cannot invade or resist invasion.

Preliminary simulations

Preliminary investigations of the simulation model revealed that spatially contiguous territories were established for each individual, and that 100 time-steps ($t_{max}=100$) were sufficient for space use to approach equilibrium. At equilibrium, when space was divided, there was variation between individuals in the number of squares used, even when all individuals were equal and using the same strategy.

Results

Population performance

We first compare the performance of strategies in isolation from each other. When all individuals in the population are using the same strategy, a population of cautious individuals displays the highest mean fitness, followed by populations of common-sense individuals. Populations of daring (D) and paradoxical (P) individuals gain very low fitness, much lower than that of cautious (Ca) and common-sense (CS) individuals when the costs associated with fighting are low (Fig. 1, open bars). This

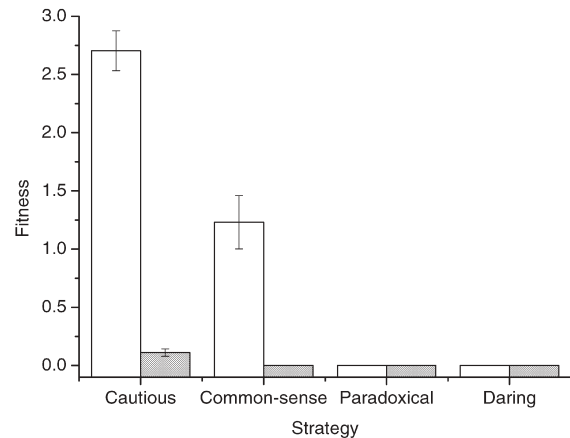


Fig. 1 Mean (\pm SD) fitness gained by individuals using each strategy when all individuals in the population are using the same strategy, for low costs [$c=0.0001$, open bars; ANOVA: $F_{3,76}=1,613.15$, $P<0.001$, Tukey's B post-hoc test revealed that cautious (Ca) and common-sense (CS) strategies differ from one another, and also differ from the paradoxical (P) and daring (D) strategies] and intermediate costs ($c=0.001$, filled bars; ANOVA: $F_{3,76}=223.54$, $P<0.001$. Tukey's B post-hoc test revealed that P, D and CS have similar fitness, but C gained higher fitness). Parameter values used: $n=10$, $a=15$, $d=0.8$, $\delta=0.1$, $\epsilon=0.1$, $t_{max}=100$. The model was run 20 times for each strategy

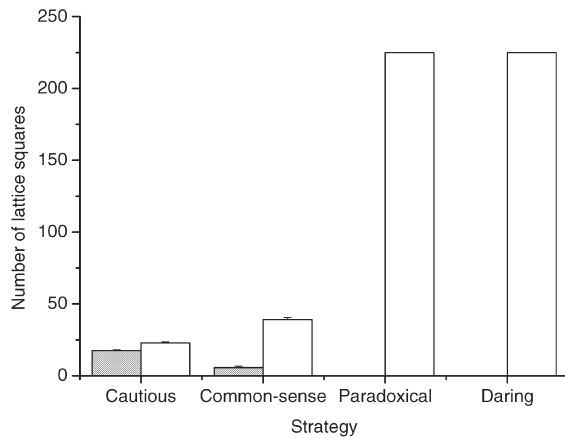


Fig. 2 Mean (\pm SD) number of lattice squares occupied exclusively by one individual (filled bars; ANOVA: $F_{3,76}=4,114.26$, $P<0.001$, Tukey's B post-hoc test revealed $Ca>CS>P$ and D , abbreviations as Fig. 1) and total number of squares used by each individual, including those occupied exclusively (open bars; ANOVA: $F_{3,76}=431,010.65$, $P<0.001$. Tukey's B post-hoc test revealed P and $D>CS >Ca$), when all individuals in the population use the same strategy. Parameter values used: $n=10$, $a=15$, $d=0.8$, $\delta=0.1$, $\epsilon=0.1$, $c=0.0001$, $t_{max}=100$. The model was run 20 times for each strategy

pattern also exists when the costs of fighting are intermediate, although fitness values are lower when costs are higher, and common sense does not differ from paradoxical and daring strategies (Fig. 1, filled bars). At high fighting costs, fitness values are very low for all populations (not shown). Thus, in a 'good for the species' point of view that ignores invasibilities, the least aggressive strategies that show avoidance behaviour perform best.

An important question to ask in a discussion of territoriality is whether the strategies under consideration can divide space and form stable territories. When all individuals in the population are using the same strategy, and draws occur relatively often ($d=0.8$), a population of cautious individuals gains the most exclusive space (Fig. 2, filled bars), followed by a population of common-sense individuals. Populations of individuals using the daring or paradoxical strategies do not get any exclusive space, instead, all individuals share overlapping home ranges (Fig. 2, open bars).

Evolutionary stability: cautious, common sense and daring

In an evolutionary setting, the important question is whether a population using a particular strategy is stable against invasion by a single mutant individual using a different strategy, and how this is affected by different costs of fighting and population density. We compare three of our four strategies, cautious, common sense and daring, representing increasing aggressiveness in individuals using the strategies. We will consider the success of the paradoxical strategy in a separate section below.

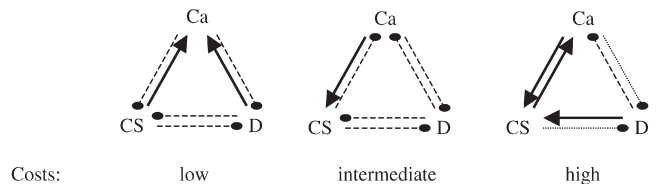


Fig. 3 The effect of increasing the costs of fighting on the ability of an individual using each strategy to invade populations using each alternative strategy. Solid arrows indicate that an invader using the strategy at the foot of the arrow is able to invade a population of individuals using the strategy at the head of the arrow. Dashed lines indicate that invasion of the population at the ● is not possible, and dotted lines indicate that both the invader and the population gain zero fitness when invasion into the population at the ● is attempted, based on 20 runs for each invasion. Abbreviations used: *Ca* cautious, *CS* common sense, *D* daring. Parameter values used: low costs: $c=0.0001$, intermediate costs: $c=0.001$, high costs: $c=0.005$, $n=10$, $a=15$, $d=0.8$, $t_{max}=100$, $\delta=0.1$, $\epsilon=0.1$

Increasing the costs of fighting alters the ability of strategies both to invade and resist invasion by other strategies (Fig. 3). At low costs of fighting ($c=0.0001$), cautious strategies are unable to invade or resist invasion by either of the more aggressive strategies, but as the costs increase to an intermediate level ($c=0.001$), cautious is able to invade a common-sense population, and resist invasion by both common-sense and daring strategies. When the costs of fighting are high ($c=0.005$), cautious continues to invade common sense, but can once again be invaded by common sense. This is due to the extremely low fitness gained by both types of individuals, when the costs of fighting are high.

Common-sense populations are resistant to invasion when the costs of fighting are low, but increasing costs means that they can be invaded, first by the cautious strategy (intermediate costs) and then by the daring strategy (high costs; Fig. 3). Both common-sense and cautious strategies are unable to invade a daring population regardless of the costs of fighting. When fighting costs are high, fitness can decline to zero for both the invader and invading strategy. Daring is a relatively ineffective strategy as an invader: a single daring individual can only invade cautious populations when the costs of fighting are low, and common-sense populations when the costs are high. It is, however, stable against invasion by both common-sense and cautious individuals when draws occur commonly ($d=0.8$), regardless of the costs of fighting.

Increasing the number of individuals present in the habitat area also influences whether individuals using one strategy can invade a population using a different strategy (Fig. 4). In general, increasing the density of individuals increases the likelihood that the more aggressive strategies are successful as invaders. At low population density ($n=5$), cautious can invade common-sense populations, but all other invasions are unsuccessful. Increasing the density to $n=10$ results in cautious populations no longer being stable against invasions from common-sense and daring individuals, and further increasing to $n=15$ means that common-sense populations can now be invaded by

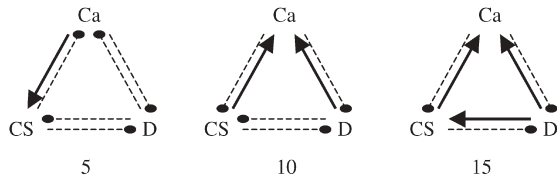


Fig. 4 The effect of increasing population density on the ability of individuals using each strategy to invade populations using each alternative strategy, based on 20 runs for each invasion. Abbreviations and arrows see Fig. 3. Parameter values used: $c=0.0001$, $a=15$, $d=0.8$, $t=100$, $\delta=0.1$, $\epsilon=0.1$

daring individuals, whereas under lower population densities these populations are stable against invasion.

Long-term invasion potential

Once an individual using a different strategy has invaded a population, it may reproduce and increase in number. Thus, we can investigate the effect of an increased frequency of the invading strategy (increasing f of strategy S_1). As an example, we chose to investigate the effect of equal numbers of each of the two strategies present in the population ($f=0.5$), for one of the population densities considered above ($n=10$). When the daring strategy is present in the population at $f=0.5$, those individuals always gain higher mean fitness than the cautious or common-sense individuals they share the habitat with (Table 1). This suggests that even if common-sense or cautious individuals are able to invade a daring population, their numbers are unlikely to increase.

In populations consisting of five individuals using the common-sense strategy and five individuals using the cautious strategy, the individuals using the common-sense strategy gain highest fitness when the costs of fighting are low ($c=0.0001$) or intermediate ($c=0.001$), but the cautious individuals gain higher fitness when the costs of fighting are high ($c=0.005$). At low fighting costs, a common-sense individual can invade a cautious population (Fig. 3), and its fitness is also higher when it makes up 50% of the population (Table 1). At intermediate costs, a cautious individual can invade a common-sense population (Fig. 3), but it gains lower fitness than the common-sense individuals when they are equal in number (Table 1). When fighting costs are high, both cautious and

Table 2 The ability of common-sense (CS) and paradoxical (P) strategies to invade populations using each alternative strategy, for two different probabilities that the fight ends without a clear winner and loser, d . Abbreviations as in Table 1, plus: Y mutant can invade, X mutant cannot invade. Parameter values used: $c=0.001$, $n=10$, $a=15$, $\delta=0.1$, $\epsilon=0.1$, $t=100$, 20 runs for each invasion

Population	$d=0.8$		$d=0.2$	
	CS Mutant	P Mutant	CS Mutant	P Mutant
C	X	X	X	X
CS	-	X	-	Y
D	X	Y	Y	Y
P	X	-	Y	-

common-sense individuals can invade populations of the other strategy (Fig. 3), but at 50%, the cautious strategy prevails (Table 1). Thus, under high fighting costs, cautious individuals have the potential to invade common-sense populations over a longer time period, but common-sense individuals do not have the potential to invade cautious populations.

The importance of draws: common-sense and paradoxical strategies

We now investigate whether an individual using the common-sense or paradoxical strategy can invade populations using other strategies, when draws occur either commonly ($d=0.8$) or less commonly ($d=0.2$). When draws are common, there is a clear difference between the common-sense and paradoxical strategies: a single paradoxical individual can invade a daring population, but a common-sense individual cannot (Table 2). However, when draws are less common, both common-sense and paradoxical strategies can invade daring populations, and also invade populations of each other, and, in this way, behave identically (Table 2).

We also compare the fitness and territories gained by common-sense and paradoxical populations (i.e. the population performance, see above), and investigate the effect of changing the probability of a draw. When draws are common ($d=0.8$), the common-sense strategy gains more exclusive space (Fig. 2) and higher fitness than paradoxical when the costs of fighting are low ($c=0.0001$; Fig. 1). When draws occur only less frequently ($d=0.2$), the fitness of common-sense individuals decreases (mean fitness

Table 1 Relative fitness when strategies are equally common in the population, showing the strategy that gains higher fitness, for different levels of fighting costs. Abbreviations used: Ca cautious, CS common sense, D daring. Low costs: $c=0.0001$; intermediate costs: $c=0.001$; high costs: $c=0.005$. Other parameters used: $n=10$, $a=15$, $d=0.8$, $t=100$, $\delta=0.1$, $\epsilon=0.1$, 20 runs for each parameter and strategy combination

Strategy pair	Costs		
	Low	Intermediate	High
Cautious	Common sense	CS	Ca
Cautious	Daring	D	D
Common sense	Daring	D	D

$\pm 2SE = 1.46 \times 10^{-7} \pm 3.57 \times 10^{-9}$, $d = 0.2$, other parameter values as Fig. 1). Common-sense territories decrease from 5.65 ± 4.226 (mean $\pm 2SE$) exclusive squares when draws are common, to no exclusive squares when draws are less common ($d = 0.2$, other parameter values as Fig. 2). Paradoxical individuals gain no exclusive space in either case. Thus, when draws occur less commonly, common-sense individuals become much more similar to paradoxical individuals than when draws are a common outcome of fights.

Discussion

Our modelling clearly shows that spatial division is a more complicated issue than a strategy's success in contests over one resource item would predict. Models such as hawk-dove games (Maynard Smith and Price 1973; Grafen 1979; Houston and McNamara 1991; Mesterton-Gibbons 1992; Crowley 2000), concentrate on what happens when two contestants have already met, and a fight ensues. Other approaches assume that space can only be gained as the result of winning contests (Maynard Smith 1982; Pereira et al. 2003). This ignores the possibility that individuals may gain space simply by being 'cautious', that is, by being deterred from space that is contested, and seek other empty spaces instead (Stamps and Krishnan 1995, 1998, 1999, 2001). To find out the success of such a strategy, it is necessary to realise that a strategy can have positive fitness even if it loses ownership of one particular location; in other words, a spatially explicit treatment is needed.

Morrell and Kokko (2003) showed, in a simple one-dimensional three-compartment model, that cautious-type strategies can be successful if the value of monopolisation of a resource item is low, for example, when the contest is over a moderately small expansion of a territory, rather than territory ownership itself. Lewis and Moorcroft (2001) have likewise shown, in a model inspired by scent-marking wolf packs, that strategies that yield minimal conflict with neighbours can be evolutionarily successful. Here we have shown that this idea holds in a general setting, with interactions that resemble hawk-dove encounters of early game-theory models, but interpreted in a spatially explicit framework that allows assessment of whether territories form, validating some of our earlier findings (Morrell and Kokko 2003). When fighting costs are high relative to the value of the resource, evolutionarily stable behaviour generates well-defined, exclusive territories, either through cautious or common-sense behaviour, due to avoidance following aggressive encounters. By contrast, if costs of fighting are low compared to resource value, territoriality breaks down and evolution proceeds to the formation of large, overlapping home ranges, where avoidance of fight locations does not occur. That increasing costs favour strategies that avoid conflict is well known from early game theory (Maynard Smith and Price 1973; Maynard Smith and Parker 1976; Parker and Knowlton 1980), and costly conflicts can lead to the

evolution of exclusive territories in ant colonies (Adler and Gordon 2003).

In our model, high fight costs lead to the formation of territories through avoidance behaviour. However, once territories are established, interactions between neighbours tend to be of low intensity and low cost, compared to interactions between territory owners and intruders (the 'dear enemy phenomenon'; Getty 1987; Ydenberg et al. 1988; Temeles 1994). Such reduced aggression emerges as the result of increasing familiarity between individuals that interact frequently (e.g. Morris et al. 1995; Höjesjö et al. 1998; Utne-Palm and Hart 2000), after the settlement period considered in the model. In the case of overlapping home ranges and very low fight costs, one should note that the terms 'fighting costs' and 'aggressive' may become misleading; a better interpretation of a 'fight' in such a case is a low-cost interaction between individuals who share space, e.g. through resource depletion without overt aggression. The evolutionarily stable behaviour in such a case is the most aggressive behaviour, daring, and it simply describes any non-territorial species, for which the costs of sharing space with conspecifics are not sufficient to deter any individual from using any particular region of the area, and which responds in an optimistic way to interactions with others.

We assume that all fights carry the same cost, regardless of the outcome. In some cases, winners and losers pay equal costs (Smith and Taylor 1992). In others, losers incur higher costs than winners (Neat et al. 1998), while in some cases, the energetic cost of winning may even exceed that of losing (Hack 1997). One might expect an individual to respond more strongly to fights that carry greater costs, for example, an individual using a cautious strategy might be less likely to return to a location in which it has suffered high fight costs (perhaps through losing) than one in which it has suffered lower costs because it won the fight (Stamps and Krishnan 2001). Our assumption that all fights are equally costly and have an equal magnitude of effect allows us to investigate the effect of the fight outcome itself rather than a response to the costs paid as a result of the fight.

In addition to investigating the costs of fighting, our spatially explicit treatment also allows us to consider effects of population density. Clearly, being cautious only pays if there is sufficient empty space available to be won. In denser populations, common-sense strategies can prevail, and in the densest populations, territoriality breaks down. This pattern fits in well with the ideas of economic defensibility of territories (Brown 1964; Adams 2001; Both and Visser 2003), and with game-theory findings that increasing density favours individuals that act more aggressively (e.g. Parker and Knowlton 1980; Mesterton-Gibbons 1992).

The costs and benefits of territory maintenance have commonly been found to change with intruder pressure (e.g. Iguchi and Hino 1996; Praw and Grant 1999; Adams 2001), and there is some evidence to suggest that population density affects territorial behaviour. In lizards, individuals gain more exclusive home ranges at low den-

sities than at high densities (Stamps and Krishnan 1998). In juvenile salmonid fish, territorial behaviour occurs only at low population densities; at high densities, individuals share space, and little aggression occurs (Kallenberg 1958). However, in the funnel-web spider *Agelenopsis aperta*, the costs of maintaining territories in habitats near saturation is higher than that in habitats where space is more readily available, but territorial behaviour does not appear to vary (Riechert 1979, 1981), perhaps due to external constraints such as gene flow (Hammerstein and Riechert 1988).

A limitation of our model is that population density is a parameter that can take different values, rather than be a consequence of the population dynamics that the individual behaviour generates (Eshel and Sansone 1995; Mylius and Diekmann 1995; Kokko and Lundberg 2001). However, our results are consistent with other work in this area. Considering territorial turnover in a setting with a fixed number of breeding spots, Dunham et al. (1995) showed that a non-aggressive 'waiting' strategy prevailed when injury rate was high and if territory owners had a high death rate. Both factors have the effect of lowering population density, lending support to the idea that life histories that lead to much vacant space in the environment allow spatial strategies with relatively non-aggressive behaviour to prevail in a population, with ownership fully respected. At a higher density individuals may get more 'desperate' (sensu Grafen 1987).

On the absence of paradoxical strategies in nature

Theoretical models often produce paradoxical solutions to contests over the acquisition of indivisible space (Maynard Smith and Parker 1976; Hammerstein and Parker 1982; Maynard Smith 1982; Enquist and Leimar 1987; Mesterton-Gibbons 1992), so that owners retreat when challenged by intruders. Such solutions are found when asymmetries in resource holding potential are small or absent (RHP; Parker 1974), yet they rarely occur in nature (but see Burgess 1976; Fernet and Smith 1976; Peeke et al. 1998). Our model provides a novel explanation for the absence of paradoxical strategies in nature that does not rely on RHP asymmetries. If a large proportion of fights end without a clear winner or loser (Bleistein et al. 1994; Stamps and Krishnan 1994a, 1994b, 1997, 1998; Adams 1998; Stamps 1999; Draud et al. 2004), then the common-sense strategy wins over the paradoxical alternative because it responds more adaptively to draws. The common-sense strategy behaves cautiously after a draw. The paradoxical strategy's response resembles that of daring, with the associated benefits and costs: it can invade daringly, but is not able to form stable territories and persist on its own if repeated encounters are costly.

Had we defined the paradoxical strategy as different from the common-sense one with respect to responses to wins and losses only, we would not have found the above asymmetry in the outcome (this would correspond to swapping the labels 'win' and 'loss', without paying at-

tention to the biological meaning). Under such a definition, any fitness difference between the paradoxical and common-sense strategies would have to arise through other mechanisms (e.g. Mesterton-Gibbons 1992, Morrell and Kokko 2003). However, our fitness comparisons rely on cognitive 'rules of thumb': behavioural mechanisms dictate that one is likely to find correlated responses to situations that resemble each other. Since both loss and draw entail not acquiring the desired resource, swapping the response to one outcome is likely to influence the decisions made in another situation too.

Conclusions

To summarise, our model has shown that it is possible to bridge the gap between spatially explicit, two-dimensional, mechanistic models of territory formation and adaptive models of animal conflict. Our model also shows that avoidance of high fighting costs easily results in solutions where individuals settle and agree on boundary locations even though some individuals end up with much smaller spaces than others—despite every individual being equal in our model. In our model, the space was uniform, with no habitat gradients or landmarks that could serve as territorial boundaries.

An interesting case for future development is the inclusion of landmarks: arbitrary features of the landscape that can be used as conventions dictating the boundaries of territories, and therefore reduce the frequency of aggressive encounters (Eason et al. 1999; LaManna and Eason 2003; Mesterton-Gibbons and Adams 2003). In a two-player setting with a one-dimensional (linear) territory, landmark use has been found to be a stable convention (Mesterton-Gibbons and Adams 2003), even if it significantly reduces territory sizes for the owner of the smaller territory. Investigating the limits of such conventions in a spatially realistic setting, and examining its population consequences, would be a fruitful avenue of further research.

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Appendix: model of spatial division

The following steps outline the simulation model of spatial division.

1. Define the strategies and other parameters used in the model. Select the two strategies S_1 and S_2 to be tested against each other.
2. n individuals are each allocated one of the two selected strategies. The number of individuals allocated each

- strategy is determined by the parameter f . For a single invading mutant, $f=1/n$. The first fn individuals are allocated strategy S_1 , and the remainder, strategy S_2
3. The n individuals arrive in a grid of squares measuring a squares by a squares. The grid of squares is wrapped such that each square has exactly four neighbouring squares. The initial location of each individual (i, j) is determined randomly, and is independent of the location of all other individuals.
 4. A for each individual (k) is set to 1 in the initial location square (i, j) , such that $A(i, j, k, t_1)=1$. A in all other squares is set to zero.
 5. For each individual, A in all squares surrounding its initial location increase by ϵA (which in this case is equal to ϵ).
 6. Each individual uses all squares in which $A(i, j, k, t)>0$. For each individual, k_1 to k_n , we compare the location identities of all squares in which $A(i, j, k, t)>0$ with the location identities of all other individuals.
 7. For each possible pair of individuals, we record the location where both $A(i, j, k_1, t)>0$ and $A(i, j, k_2, t)>0$. At this location, a fight takes place.
 8. The outcome of the fight is determined randomly, with a probability d that the fight ends in a draw. If a number drawn from a random number distribution is less than $(1-d)/2$, we record that individual k_1 won the fight, and individual k_2 lost. If the random number is between $(1-d)/2$ and d , we record a loss for individual k_1 and a win for individual k_2 . Otherwise, we record a draw for both individuals. This step is repeated for all possible pairs of individuals in all locations where both $A(i, j, k_1, t)>0$ and $A(i, j, k_2, t)>0$.
 9. For each fight, the costs to the each of the participants is recorded, and added to any existing costs already paid by the individual from other fights in the same or previous time-steps.
 10. As a result of the outcome of fights, $A(i, j, k, t)$ changes in accordance with the individual strategy, by a value δ . For each fight recorded above, we determine how A will change as a result of the value of δ and the strategy used by the individuals involved in that fight. These changes (some of which are positive and some negative) are recorded for each square for each individual.
 11. If there is no fight in a particular square for a particular individual, A changes in accordance to their response to finding the space empty. Combining steps 10 and 11 gives a change in A for each square, for each individual.
 12. When all the changes as a result of the fights have been recorded, they are added to the original A value for each square. Any A values which then exceed 1 or are below zero are set to 1 and 0 respectively.
 13. At each location (i, j) in which $A(i, j, k, t)>0$, the surrounding squares $(i-1, j)$, $(i+1, j)$, $(i, j-1)$, $(i, j+1)$ all increase their value of A by the amount $\epsilon A(i, j)$.
 14. Steps 6–13 are repeated for t_{\max} times. After this, the simulation ends.

15. At the end of the simulation, individual fitness, home range size and number of squares used exclusively are calculated, and grouped according to the strategy used by the individual. Strategy means are then calculated and collected.
16. The entire simulation is repeated 20 times.

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