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4 On the adaptiveness of territorial behaviour: dependence on strategy space and initial conditions

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In the last two decades the process by which interactions between individuals lead to the emergence of territories has become a focus of theoretical research. The only general evolutionary model of this process so far has been presented by Morrell & Kokko (2005). Comparing the invasion prospects of four discrete behavioural strategies they concluded that high fighting costs lead to the evolution of territoriality whereas low costs result in overlapping home ranges. We show that a simplified non-spatial version of their model reproduces their results. In a spatially explicit dynamic evolutionary version this is however no longer true in general when a continuous range of strategies is assumed. Instead, depending on the initial conditions different strategies with a variety of space use patterns evolve.
4 Dependence on strategy space and initial conditions

4.1 Introduction

In most of the earlier theoretical work on the evolution of territoriality, the proximate process that leads to the formation of territories received very little attention. Most authors focused on territorial behaviour within a population with fully formed territories (e.g. Schoener, 1987; Gintis, 2007). If territory formation was taken into account then it was usually assumed that individuals establish territories by deciding unilaterally which amount of space to defend against competitors (e.g. Parker & Knowlton, 1980; for an exception see Maynard Smith, 1982).

Only in the last two decades a new approach to the theoretical study of territoriality has emerged that explicitly considers how interactions between individuals can lead to the formation of territories (Giuggioli & Kenkre, 2014; Potts & Lewis, 2014). Stamps & Krishnan (1997) were the first to suggest that territories should be seen as an emergent property of local antagonistic interactions between individuals. They proposed to model territorial behaviour as a learning-based process in which individuals adjust the perceived “attractiveness” of an area dependent on their experiences in that area, increasing it after exploration and decreasing it after aggressive interactions. Depending on the specific behavioural rules, a model of this process was indeed able to produce exclusively owned territories or complete sharing of space (Stamps & Krishnan, 1999, 2001).

Stamps & Krishnan (1999) and Stamps & Krishnan (2001) however only studied the proximate consequences of different behavioural strategies and refrained from investigating their evolutionary origins and stability. Expanding on earlier work (Morrell & Kokko, 2003; Adler & Gordon, 2003), Morrell & Kokko (2005) (henceforth abbreviated as M&K) set out to fill this gap by investigating the adaptiveness of territorial behaviour with a simulation model based on the general approach described by Stamps & Krishnan (1999). They determined the relative fitness values and the space use that resulted from interactions of a set of behavioural strategies. From the results of this analysis M&K concluded that if the costs of interactions between individuals are low, overlapping home ranges evolve whereas high costs lead to the evolution of territories.

While these results are interesting and valuable it is unclear how general they are. M&K investigated a very small part of the set of potential strategies by selecting only four specific strategies out of a continuous four-dimensional strategy space. Furthermore their invasion analysis was only based on selection gradients for pairwise interactions at three specific combinations of frequencies in the population (for details see section 2).
In this article we aim to test how well M&K’s results hold up if we generalize their model to a) a continuous strategy space and b) explicit individual-based evolution. We first give a brief overview of M&K’s model. Then we analyse a slightly simplified, spatially implicit analytical model that allows us to find globally evolutionarily stable points. In the second step we present a strict superset of M&K’s model that simulates the actual evolution of the individuals’ behaviour over time without imposing any restrictions on which strategies the population consists of or with which frequencies they occur.

4.2 The original model

We will first give a brief description of the original model as presented by Morrell & Kokko (2005). For a more detailed description please refer to the original article.

Individuals live in a habitat consisting of discrete cells in a 2-dimensional grid. For each individual an occupancy value between 0 and 1 indicates whether and to which degree it uses any given cell. In each time step individuals explore cells adjacent to the ones already occupied by them by increasing the occupancy values in these cells. Fights occur wherever two individuals end up occupying the same grid cell. Fights end either with a draw (with probability $p_{\text{draw}}$) or with one of the individuals winning and the other losing ($p_{\text{win}} = p_{\text{lose}} = (1 - p_{\text{draw}})/2$). Individuals then change the degree of occupancy of the respective cell by adding or subtracting a value $\delta$ dependent on the outcome of the fight. Accordingly, the strategy of an individual consists of a set of $\delta$-values $\delta_{\text{win}}, \delta_{\text{lose}}, \delta_{\text{draw}}$ which correspond to the three possible outcomes win, lose and draw. It is important to note that the consequences of a specific outcome of a fight are described entirely by these $\delta$-values. In this sense win and lose are just convenient labels which are completely interchangeable. A fourth value, $\delta_{\text{empty}}$, describes the change in occupancy when a cell is found empty.

The fitness of an individual was assumed to be a product of benefits and interaction costs. Benefits equal the sum (over all cells) of the relative occupancy after 100 interaction steps. Interaction costs are calculated as the negative exponential of the number of interactions (in all time steps) scaled by a constant factor $c$ (further referred to as “costs”).

M&K investigated four specific strategies, i.e. four combinations of $\delta$-values: cautious - always retreat after fights ($\delta_{\text{win}} = -0.1, \delta_{\text{lose}} = -0.1, \delta_{\text{draw}} = -0.1, \delta_{\text{empty}} = 0.1$), common sense - only retreat after losing and drawing (0.1,-0.1,-0.1,0.1), daring - only retreat after losing (0.1,-0.1,0.1,0.1), para-
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doxyical - only stay after losing, and drawing, the opposite of common sense (-0.1,0.1,0.1,-0.1). For each combination \( x \) and \( y \) of two (out of these four) strategies M&K measured the fitness of a single individual of one type in a population of individuals of the other type and the respective mean fitness of \( x \)- and \( y \)-individuals when both constitute half of the population. These measures were used to determine which of the four strategies can invade or be invaded by which other strategy.

4.3 Mathematical Model

In the first step we analyse a mathematical description of M&K’s model. In order to make the model mathematically tractable we disregard spatial relationships between habitat sites and simplify the strategy space. This allows us to derive global stability criteria while still being able to test the adaptiveness of avoidance as postulated by M&K.

The model consists of two parts. In the interaction part the distribution of the ownership of sites in the dynamic equilibrium is determined. In the evolution part an expression for the fitness of two competing individuals is derived. The invasion fitness of a rare mutant allows us to determine evolutionarily stable points (Geritz et al., 1998).

Interaction

We model the interaction of two individuals (out of a sufficiently large population) at a time. They compete for a large number of resource sites by abandoning sites and occupying new ones following a specific strategy \( d \).

Sites can be in one of four states: unoccupied \((u)\), owned by individual \( a \) \((a)\), owned by individual \( b \) \((b)\) or shared between \( a \) and \( b \) \((s)\). The proportion of sites in each of these states changes based on two processes: First, during each time step individuals explore new sites by occupying a random fraction \( \epsilon \) of all sites. Second, they abandon shared sites as determined by their strategy \( d \), i.e. a probability of \( d_a \) and \( d_b \), respectively. Given a large number of sites we can describe how the fraction of sites currently in each of the four states changes between time steps:

\[
\begin{pmatrix}
a \\
 b \\
 u \\
 s \\
\end{pmatrix}_{(t+1)} = 
\begin{pmatrix}
1-\epsilon & 0 & \epsilon(1-\epsilon) & d_b(1-d_a) \\
0 & 1-\epsilon & \epsilon(1-\epsilon) & d_a(1-d_b) \\
0 & 0 & (1-\epsilon)^2 & d_a d_b \\
\epsilon & \epsilon & \epsilon^2 & (1-d_a)(1-d_b) \\
\end{pmatrix} \cdot 
\begin{pmatrix}
a \\
 b \\
 u \\
 s \\
\end{pmatrix}_{(t)}
\] (4.1)
4.3 Mathematical Model

From this the long term equilibrium distribution of ownership for given trait values \(d_a\) and \(d_b\) can easily be derived:

\[
\begin{pmatrix}
  a \\
  b \\
  u \\
  s \\
\end{pmatrix}^* (d_a, d_b) = \frac{d_b(2-d_a-\epsilon)}{(2-\epsilon)(\epsilon+d_a+d_b)-d_ab} \\
\frac{d_a(2-d_b-\epsilon)}{(2-\epsilon)(\epsilon+d_a+d_b)-d_ab} \\
\frac{d_a d_b}{(2-\epsilon)(\epsilon+d_a+d_b)-d_ab} \\
\frac{d_b d_a}{\epsilon(2-\epsilon)} \\
\frac{(2-\epsilon)(\epsilon+d_a+d_b)-d_ab}{\epsilon(2-\epsilon)} \\
\end{pmatrix} \quad (4.2)
\]

Evolution

We assume fitness of a given trait value \(d\) when interacting with a different trait \(d'\) is a function of the amount of exclusive and shared space that results from the interaction of two individuals showing the respective traits:

\[
w_{d,d'} = w(a^*(d,d'), s^*(d,d')) \quad (4.3)
\]

We now look at the fitness of a mutant \(d_{inv}\) in a uniform resident population \(d_{res}\). If the mutant is rare we can assume that individuals of the resident type only interact with each other whereas the mutant only interacts with residents. We can therefore derive invasion fitness of the mutant \(w_{inv}\) accordingly:

\[
w_{inv} = w(a^*(d_{inv}, d_{res}), s^*(d_{inv}, d_{res})) \quad (4.4)
\]

Evolution of avoidance

The tendency to retreat after encounters \(d\) will increase in the course of evolution if the fitness of a mutant which is very similar to the resident type increases with increasing \(d\) (Geritz et al., 1998):

\[
\frac{\delta w_{inv}}{\delta d_{inv}} \bigg|_{d_{inv}=d_{res}} > 0 \quad (4.5)
\]

Taking the partial derivatives (see equation 4.4) this gives us

\[
\frac{\partial w(a^*(d_{inv}, d_{res}), s^*(d_{inv}, d_{res}))}{\partial a^*(d_{inv}, d_{res})} \cdot \frac{\partial a^*(d_{inv}, d_{res})}{\partial d_{inv}} + \frac{\partial s^*(d_{inv}, d_{res})}{\partial s^*} \bigg|_{d_{inv}=d_{res}} > 0
\]

Using equation 4.2 to calculate the derivatives of \(a^*\) and \(s^*\) with respect to \(d\) and simplifying the result we get the condition

\[
\frac{\partial w}{\partial a} \cdot \frac{2d}{\epsilon(2-d-\epsilon)} + \frac{\partial w}{\partial s} < 0.
\]
Following M&K we assume that fitness increases with the amount of exclusive space thus $\frac{\partial w}{\partial a} > 0$. Further we know that $d$ and $\epsilon$ lie between 0 and 1 so the whole first term $\frac{2d}{\epsilon(2-d-\epsilon)}$ of the left hand side of the inequality has to be positive. It follows that the inequality can only hold if $\frac{\partial w}{\partial s} < 0$. Strength of avoidance $d$ can thus only increase in evolutionary time if a gain of shared space reduces fitness to a sufficient degree. It is also immediately visible that to always share ($d = 0$) can only be evolutionarily stable if $\frac{\partial w}{\partial s} > 0$, i.e. if a decrease in amount of shared space leads to a decrease in fitness.

**Dependence on fighting costs**

The evolutionarily stable value of $d^*$ has to fulfill the condition

$$\frac{\partial w}{\partial a} \cdot \frac{2d^*}{\epsilon(2-d^*-\epsilon)} + \frac{\partial w}{\partial s} = 0.$$ 

Solving for $d^*$ gives

$$d^* = \frac{\partial w}{\partial s} \cdot -\epsilon(2-\epsilon) \left(\frac{2\frac{\partial w}{\partial a} - \epsilon \frac{\partial w}{\partial s}}{\frac{\partial w}{\partial a} - \epsilon \frac{\partial w}{\partial s}} \right).$$ (4.6)

Now we assume that the influence of shared space on fitness ($\frac{\partial w}{\partial s}$) is modulated by a parameter $c$, “fighting costs”. Everything else being equal higher fighting costs should lead to a decrease in fitness and to a more negative influence of shared space on fitness. We can write these two conditions as follows:

$$\frac{\partial w}{\partial c} < 0, \quad \frac{\partial^2 w}{\partial s \partial c} < 0$$ (4.7)

The change of the evolutionarily stable degree of avoidance $d^*$ with fighting cost derives as

$$\frac{\partial d^*}{\partial c} = -2\epsilon(2-\epsilon) \frac{\frac{\partial w}{\partial a} \cdot \frac{\partial^2 w}{\partial s \partial c} - \frac{\partial w}{\partial s} \cdot \frac{\partial w}{\partial a} \cdot \frac{\partial w}{\partial s}}{\left(2\frac{\partial w}{\partial a} - \epsilon \frac{\partial w}{\partial s}\right)^2}.$$ 

Therefore the value of $d^*$ increases with increasing $c$ when

$$\frac{\partial w}{\partial s} \cdot \frac{\partial^2 w}{\partial a \partial c} > \frac{\partial w}{\partial a} \cdot \frac{\partial w}{\partial s \partial c}.$$ (4.8)

Since we know that fitness increases with amount of exclusive space $a (\frac{\partial w}{\partial a} > 0)$, according to our definition of costs in inequality 4.7 the right hand side of inequality 4.8 has to be negative. From before we also can say that for a
positive evolutionarily stable value of $d$ to exist fitness has to decrease with shared space. If we further assume that the fitness gain through exclusive space at least does not increase with higher costs the left hand side becomes positive or zero and the condition holds.

To recapitulate, when fitness decreases with increasing amount of shared space avoidance becomes adaptive and the evolutionarily stable value of avoidance increases with increasing fighting costs.

**Example**

We will illustrate these results with a concrete fitness function. Following M&K we define fitness as a product of benefits and costs:

$$ w := B \cdot C = (a + \frac{1}{2}s)e^{-cs} \quad (4.9) $$

Although possible, analysis of the full model with this fitness function leads to very complicated expressions for the evolutionarily stable trait value. For this example we therefore use a simplified version of the model which shows the same qualitative behaviour. We assume that $a$ and $b$ never leave or enter a site at the same time. Then sites, once occupied, can not become unoccupied any more so that $u = 0$ at equilibrium. This allows us to only consider the states $a$, $b$, and $s$. Further the terms $e^2$ and $d_a d_b$ disappear, leaving us with a simple equation for the change of space use over time:

$$ \begin{pmatrix} a \\ b \\ s \end{pmatrix} (t+1) = \begin{pmatrix} a \\ b \\ s \end{pmatrix} (t) \cdot \begin{pmatrix} 1 - \epsilon & 0 & d_b \\ 0 & 1 - \epsilon & d_a \\ \epsilon & \epsilon & 1 - d_a - d_b \end{pmatrix} \quad (4.10) $$

The equilibrium state of the simplified model derives as

$$ \begin{pmatrix} a \\ b \\ s \end{pmatrix}^\ast (d_a, d_b) = \begin{pmatrix} \frac{d_b}{d_a + d_b + \epsilon} \\ \frac{d_a}{d_a + d_b + \epsilon} \\ \epsilon \frac{d_a}{d_a + d_b + \epsilon} \end{pmatrix}. \quad (4.11) $$

If we plug this into 5.5 and insert the result into the condition for an ESS

$$ \left. \frac{\delta w_{\text{inv}}}{\delta d_{\text{inv}}} \right|_{d_{\text{inv}} = d_{\text{res}}} = 0 $$

we get a simple expression for the ESS at $d^\ast$:

$$ d^\ast = \frac{\epsilon}{2} (c - 1) $$
From this we can calculate the evolutionarily stable space use as:

$$\begin{pmatrix} a \\ b \\ s \end{pmatrix}^* = \begin{pmatrix} \frac{c-1}{2c} \\ \frac{c-1}{2c} \\ \frac{1}{c} \end{pmatrix}$$

We see that under low costs individuals will not abandon sites after an encounter ($d^*$ close to 0) leading to shared space ($s$ close to 1) whereas high costs result in complete avoidance and therefore mainly exclusive space ($a, b$ close to $\frac{1}{2}$).

### 4.4 Spatially explicit Simulations

In order to allow for evolution to take place we slightly extended M&K’s model:

Each individual has a genome consisting of a single set of four $\delta$-values which is transmitted to its offspring during clonal reproduction. The mutation probability per gene and generation is 0.01. Genes are mutated by adding a random value uniformly distributed between $-0.025$ and $0.025$.

The population always consists of 300 individuals. At the beginning of a generation the individuals are randomly distributed over 20 patches, with a fixed number of 15 individuals per patch. Subsequently interactions take place in each patch during 100 within-generation time steps in exactly the same way as in the original model. At the end of a generation all 300 individuals are lumped together into one population again. An individual’s probability to reproduce is determined by its relative fitness with respect to the whole population. After reproduction all parent individuals die.

In situations where conventions, i.e. arbitrary population-wide agreements are used to settle conflicts the composition of the starting population can determine which convention will emerge in the population (Maynard Smith, 1982). We therefore tested six different initial conditions, i.e. ways of determining the genetic composition of the population at the beginning of the simulation runs. In the first scenario we started with a “neutral” population with all $\delta$ values set to zero. In the second scenario we initialized all individuals in the population at random by drawing for each $\delta$ a value between $-0.2$ and $0.2$ (a range which includes all strategies used by M&K). Finally for each of the four strategies used by M&K we started a set of simulations where initially all individuals followed that strategy.

Of M&K’s three parameters we kept draw probability and patch size fixed (at 0.2 and 15 respectively) and only varied interaction costs. For each scen-
4.5 Results

Figure 4.1: Mean and standard deviation of evolved $\delta$-values for a) low and b) high costs. Since $\delta_{\text{win}}$ and $\delta_{\text{lose}}$ are interchangeable (see model description in the text) their absolute difference is used. For each of the scenarios starting with a single strategy (neutral=0, cautious=CA, common sense=CS, daring=DA and paradoxical=PA) the starting point (open circles) and the outcome after 15000 generations (filled circles) is shown.

ario we ran 20 replicates over 15000 generations both at low ($c = 0.0001$) and high fighting costs ($c = 0.005$).

4.5 Results

Strategies

The outcome of evolution of the $\delta$-values shows some general patterns. In the majority of the cases the evolved values are negative. In most runs $\delta_{\text{empty}}$ reaches a value around -0.065 (not shown). However there is no single strategy (i.e. combination of $\delta$-values) or group of strategies which evolves under all starting conditions. Only when starting with neutral and cautious initial conditions under low fighting costs the same strategies evolve (see Fig. 4.1). For all other starting points the $\delta$-values evolved after 15000 generations differ markedly from each other.

Even given the same initial population, differences between replicates are large, especially under high fighting costs (Fig. 4.1). The only exceptions are again neutral and cautious initial conditions under low fighting costs, where in all replicates very similar combinations of $\delta$-values evolve.

In all cases the $\delta$-values after 15000 generations differ considerably from the starting points. This indicates that all initial conditions tested - including the four strategies used by M&K - are evolutionarily unstable.
Space use

As can be seen in Fig. 4.2 a variety of patterns of space use evolves. The shape of the areas occupied by individuals varies strongly. In some cases they inhabit compact contiguous areas (Fig. 4.2 b,e), in others the cells owned by an individual are spread out over the whole habitat (Fig. 4.2 d,f). The degree of sharing varies as well, ranging from nearly all space being shared (Fig. 4.2 a, b) to exclusively used areas (Fig. 4.2 e).

With few exceptions fighting costs as well as initialization seem to have little systematic effect on which patterns occur. Only when starting with a neutral or a cautious population a clear picture emerges, with low costs leading to compact overlapping home ranges (Fig. 4.2 b) and high costs to exclusive and contiguous territories (Fig. 4.2 e).

These two patterns also occur under random initial conditions. In addition however we also see patterns c, d and f (Fig. 4.2). In these cases the cells occupied by an individual no longer form a compact contiguous area. Patterns d and f further show a high turnover rate with ownership of nearly all cells changing between time steps (not shown).

The patterns which evolve when starting with one of the four strategies used by M&K differ considerably. Starting with cautious leads to very similar results as the neutral scenario showing nearly identical spatial patterns. Letting all individuals start with common sense leads for low costs to the evolution of a pattern of spread out dots (Fig. 4.2 d). In all other cases we encounter a mixture of all patterns seen so far including some intermediate ones. In some cases we even see “extinction” where no individuals occupy any space at all (not shown).

All types of patterns occur for low as well as for high fighting costs with -per pattern- only slight differences in the amount of exclusive space between scenarios. Nevertheless for most initial conditions the amount of exclusive space clearly increases with fighting costs (Fig. 4.3).

This effect is strongest when starting out with a neutral or a cautious population (Fig. 4.3 a,c). It is still clearly visible for the cautious initial conditions (Fig. 4.3 a,c) and weak when starting with daring, common sense (Fig. 4.3 d) or paradoxical (Fig. 4.3 f).

4.6 Discussion

Our results show that the choice of strategy space as well as taking into account spatial effects strongly influence which behavioural strategies evolve as well as which pattern of shared space these strategies produce. While the
Figure 4.2: Examples for typical evolved patterns of space use. Each of the small grids indicates the space use (immediately before reproduction) of one of the 15 individuals inhabiting a patch. Cells in which the focal individual is the only occupant (exclusive space) are indicated by circles; cells which it does not occupy (occupancy zero) are left empty, filled cells are those it shares with other individuals (shared space). In cases a-d most occupied space is shared by several occupants whereas in e and f each cell is owned by a single individual. The space used by an individual can form a compact contiguous area (b, e) or consist of disconnected single cells (d, f). Scenarios and initial conditions are: a - CS, high costs; b - neutral, low costs; c - PA, low costs; d - random, low costs; e - neutral, high costs; f - DA, high costs
Figure 4.3: Exclusive space versus total occupied space per individual after 15000 generations for low (empty circles) and high costs (filled circles). Each circle represents one replicate. Points on the diagonal represent cases where there is no shared space (exclusive space = total space). The further away from the diagonal, the more cells are shared between individuals.
simplified non-spatial analytical model confirms M&K’s results - high interaction costs lead to avoidance and thus exclusive space - the results of the simulation present a considerably more complicated picture.

We see that with the introduction of spatial effects and in a slightly more complicated strategy space the composition of the starting population determines to a large degree the outcome of evolution. The evolved $\delta$-values differ strongly between runs with different initializations and even in scenarios with a homogeneous initial population the variability between replicates is very high (see Fig. 4.1). This indicates that within the continuous strategy space not just a single evolutionarily stable strategy exists. Furthermore not only the genetic composition of the initial population but also stochastic effects seem to determine to a big extent which combination of $\delta$-values evolves. (see Fig. 4.2).

It is known from game theory that games with multiple parameters tend to have multiple equilibria (e.g. Haigh, 1975; Broom & Cannings, 1999). Therefore the possibility exists that an increase in the number of available strategies will lead to the appearance of additional stable equilibria which might not be accessible from every initial condition. This has for example been shown for the Iterated Prisoner’s Dilemma (Lindgren, 1992; Brembs, 1996) and for models of social dominance (Van Doorn et al., 2003a,b). Therefore it is not surprising that the four strategies used by M&K turn out to be evolutionarily unstable within the continuous strategy space and that the analysis based on them resulted in a different and much simpler picture of the evolutionary dynamics.

For the six different initial conditions we investigated, only the results of the neutral and the cautious scenarios lend themselves to easy interpretation. The same stable combination of $\delta$-values is reached in all replicates for low fighting costs, while the variation in evolved strategies is limited for high costs (see Fig. 4.1). The corresponding spatial patterns are clearly identifiable as either overlapping home ranges (low costs) or territories (high costs) which is in line with our mathematical analysis and M&K’s main conclusions.

For all other starting conditions, however, we see a very different picture. Corresponding to the variability in $\delta$-values the resulting patterns of space use are very diverse. Several patterns are difficult to classify as either territorial or non-territorial (see Fig. 4.2). Furthermore for most starting conditions no clear effect of fighting costs on the pattern of space use is detectable (not shown).

Despite the variety of spatial patterns however we see that in most scenarios the amount of exclusive space per individual is significantly higher un-
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under high than under low fighting costs (Fig. 4.3). This indicates that the trend of higher costs leading to less sharing of space which was found by M&K and in our analytical model is a general phenomenon, confirming earlier results (e.g. Adler & Gordon, 2003; Morrell & Kokko, 2003). Future research will have to investigate under which conditions a high amount of exclusive space is indicative of territorial behaviour.

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