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Defence, intrusion and the evolutionary stability of territoriality

Martin Hinsch [a,b,*], Jan Komdeur [b,1]

[a] Theoretical Biology, CEES, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands
[b] Animal Ecology, CEES, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands

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ABSTRACT

Territorial behaviour can only be adaptive if its costs are outweighed by its benefits. Territorial individuals incur costs by defending their territories against intruders. Usually these intruders are assumed to be non-territorial floaters attempting to take over the whole territory or neighbours trying to extend the borders of their own territory. We instead investigate how costs and benefits of territorial behaviour are affected by neighbours which invade to steal resources on a territory.

We show analytically that in the absence of defence intrusion into neighbouring territories always pays and that even if territories are defended intrusion levels can still be high. Using a more detailed simulation model we find that territory defence usually disappears from the population even if owners have a strong advantage over intruders in terms of fighting costs or foraging efficiency. Defence and thus territoriality can only be evolutionarily stable if fighting costs for the intruder relative to the productivity of the territory are very high or if crossing the borders between territories carries additional costs.

Our results show that stealing of resources by neighbours can have a considerable effect on the evolutionary stability of territory defence and thus territoriality itself. A more mechanistic model of territorial behaviour is needed to incorporate these kinds of mechanisms into a general theory on the evolution of territoriality.

1. Introduction

Territoriality is one of the most conspicuous ways in which access to local resources such as food or nest sites can be organised in animal populations. Territoriality is a situation where many or all of the individuals in a population claim ownership of a piece of the available space in the sense that they have exclusive access to the resources it contains (Maher and Lott, 1995). Due to ubiquitous competition for resources this claim has to be defended against other individuals in the population (Malthus, 1798; Brown, 1964). Territorial behaviour can therefore only be adaptive if maintenance of ownership is profitable, i.e. if the defence of a territory is less expensive in terms of fitness than the potential damage done by competitors in the absence of defence (Brown, 1964; Schoener, 1987).

The main focus in the study of the adaptiveness of territoriality has in the past been on the competition between owners and non-territorial intruders (floaters) either for entire territories (e.g. Maynard Smith and Parker, 1976; Eshel and Sansone, 1995; Yee, 2003; López-Sepulcre and Kokko, 2005; Gintis, 2007) or for resources within the territory (e.g. Gill and Wolf, 1975; Davies, 1980; Schoener, 1987).

The consequences of the competition between territorial neighbours have also been explored, although less thoroughly (Adams, 2001). Most models of neighbour–neighbour interactions assume that conflicts arise from individuals attempting to increase the size of their territories at their neighbours' expense and investigate how the position of the border between two (non-overlapping) territories is negotiated by the respective owners (MaynardSmith, 1982; Pereira et al., 2003; Mesterton-Gibbons and Adams, 2003). This process can even lead to the exclusion of some individuals from the territorial population (Parker and Knowlton, 1980).

Borders of territories are, however, not impenetrable. To increase its access to resources a territory owner could also intrude into a neighbour's territory, effectively "stealing" resources (Vander Wall and Jenkins, 2003). "Theft" by neighbours can have strong effects on the costs and benefits of territoriality. In low frequencies it can reduce the payoff of having a territory while at the same time increasing the costs of territory defence (e.g. Gill and Wolf, 1979; Hixon, 1980; Schoener, 1987). A high incidence of theft would ultimately render territory borders meaningless and would therefore effectively lead to the disappearance of territoriality.

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* Corresponding author. 134 Steade Rd., S7 1DU Sheffield, UK. Tel.: +44 114 2588687.
E-mail addresses: hinsch.martin@gmail.com (M. Hinsch), j.komdeur@rug.nl (J. Komdeur).
[1] Animal Ecology Group.

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It has, however, been shown that a high level of defence by territory owners can make intrusion into territories costly enough that individuals will restrict themselves to foraging mostly or entirely within their own territories (Adler and Gordon, 2003; Morrell and Kokko, 2005). Whether owners do defend their territories against intruding neighbours on the other hand will depend on the amount of damage done by these intruders relative to the costs (and chances of success) of defence (Brown, 1964; Schoener, 1987).

Whether territoriality can be maintained when theft of resources by neighbours is possible therefore clearly depends on a combination of the economics of both, intrusion and defence against intruders. We would expect that territoriality should break down if either defence is not sufficient to discourage neighbours from intruding or intrusion is too frequent to make defence worth wile. On the other hand territoriality should be self-sustaining if it pays for owners to defend their territories and this defence at the same time makes intrusion costly enough that individuals do not trespass into their neighbours' territories.

In this study we investigate under which conditions stealing of resources by neighbours poses a threat to the evolutionary stability of territory defence and when the coevolution of defence and respect for ownership leads to the maintenance of territoriality.

We use a simple analytical model and a more detailed individual-based simulation to derive our results. In the models we directly track the fitness costs of defence and intrusion. We implement simple resource dynamics to determine the payoff of stealing and the effects of exploitation competition. We investigate which level of territory defence by the neighbour is sufficient to make stealing unprofitable, and whether the potential damage done by intruding neighbours is enough to make defence profitable.

This allows us to predict under which conditions territoriality, that is a combination of low intrusion and high defence can be evolutionarily stable even if potential intrusion by neighbours is taken into account.

We will first present the basic version of our model which is simple enough to be analysed mathematically. Then we use a qualitatively equivalent spatially explicit individual-based simulation model to test the validity of some simplifying assumptions and to explore some interesting extensions of the basic model.

2. The analytical model

Similar to others (e.g. Switzer et al., 2001; Adler and Gordon, 2003; Pereira et al., 2003) we model the fitness consequences of single foraging decisions of individuals. We assume that everything else being equal an individual with a higher long-term average resource uptake rate will have a higher fitness. In the same way fighting in reality can have various negative consequences in terms of energy costs, time investment, predation risk or risk of injury or death. All of these, however, effectively lead to a reduction in fitness. In our model we therefore simplify things by measuring costs and benefits in units of fitness lost or gained.

For the sake of simplicity we restrict the effects of intrusion to direct neighbours. In our model individuals therefore at any point in time forage either on their own territory or intrude into one of the neighbouring territories. Intrusion, detection by owners and return to the home territory are assumed to be Poisson processes, i.e. they occur independently and with a constant probability for a given period of time. In the analytical model we approximate these as constant rates.

We ignore the effects of interference competition (with the exception of fighting costs). The only consequence of intrusion is therefore depletion of resources. Resources are assumed to slowly regrow, so that resource level and therefore uptake rate in a territory depends on the long-term average density of individuals (owner and all intruders) in that territory.

2.1. Model description

Individuals in our model inhabit identical territories with a fixed number of N neighbours. The proportion of time they spend as intruders or owners, respectively, as well as the level of aggression in the population is a result of the interaction of three behavioural traits: intrusion rate i, aggressiveness a and return rate e.

Individuals intrude into neighbouring territories with rate i and leave them again – returning to their own territory – either voluntarily with rate e or because they were detected and chased away. Intruding individuals can be detected with rate d by the territory owner which will attack with probability a. If an intruder loses the ensuing fight (probability ν) it returns into its own territory. Fights are costly for the owner (c_o) as well as for the intruder (c_i).

The payoff an individual obtains from foraging depends on the amount of resources in the territory it is currently foraging in. Similar to other studies (e.g. Waser, 1981; Houston et al., 1985; Adler and Gordon, 2003) we assume that changes in the amount of resources are slow enough compared to the movement of individuals between territories that short term fluctuations in density have negligible consequences for the uptake rate of individuals (this assumption is later relaxed in the simulation). Therefore we approximate foraging success in terms of increase in fitness as a function $r(D)$ of average number of individuals present on a territory (henceforth referred to as density) which is equal to the sum of the average proportions of time all eligible individuals, i.e. the owner (while at home) and all neighbours (while intruding) spend on the territory. Since we assume exploitation competition, r has to be a decreasing function.

We use a continuous time spatially implicit mathematical model to describe the dynamics of intrusion, defence and foraging. We analyse evolutionary dynamics within the model based on a straightforward adaptive dynamics approach (Geritz et al., 1998).

For a list of all model parameters and variables used, see Table 1.

2.2. Fitness

To determine the evolutionary dynamics in the model we calculate the fitness of a single (or rare) mutant (which by

Table 1
Model parameters.

Evolving traits	
i	Rate of intrusion
e	Rate of return
a	Probability to attack an intruder
Derived values	
I	Proportion of time spent intruding
D	Average number of individuals on a territory
t_o	Average duration of a stay in the own territory
t_i	Average duration of an intrusion
Functions	
$r(D)$	Uptake rate dependent on average density
Parameters	
ν	Probability that the owner wins a fight
c_o	Fighting costs (owner)
c_i	Fighting costs (intruder)
N	Number of neighbouring territories
d	Detection rate of intruders

definition is identical to its expected long-term uptake rate minus costs of fighting) in a homogeneous resident population.

The average proportion of time an individual spends intruding is denoted as I and can be calculated from the average time spent as intruder (t_i) or owner (t_o), respectively:

$$I = \frac{t_i}{t_i + t_o} \tag{1}$$

Since we approximate the stochastic process with deterministic rates in continuous time the time spent in a state (after entering it) can simply be calculated as the inverse of the rate of leaving the state:

$$t_o(i) = \frac{1}{i} \tag{2}$$

$$t_i(e,a) = \frac{1}{e + adv} \tag{3}$$

We can therefore derive the proportion of time spent intruding as

$$I(i,e,a) = \frac{i}{e + i + adv} \tag{4}$$

For a given territory, density (i.e. average number of individuals present) D is then just the sum of the proportions of time all individuals spend there.

We define fitness as the sum of the benefits gained through foraging "at home" (proportion of time $1-I$) and in somebody else's territory (proportion of time I) minus the costs of attacking and being attacked. In the following all variables associated with the resident strategy are marked with a ‘ˆ’. If a distinction is necessary behaviour on the mutant's territory is marked with a subscript ‘$_m$’, whereas behaviour taking place on one of the residents' territories is denoted by a ‘$_p$’. For the fitness of a single (or rare) mutant in a homogeneous resident population we obtain

$$w(i,e,a) = (1-I)r(D_m) + Ir(D_p) - N\hat{I}_m dac_o - Id\hat{a}c_i \tag{5}$$

In order to be able to calculate foraging success r we have to determine density on the residents' and the mutant's territory, D_p and D_m, respectively.

The density on a resident's territory (if it is neighbouring the territory of the mutant) is the proportion of time the focal resident is present plus the intrusion by $N-1$ other residents and the mutant. Assuming for the sake of tractability that the focal resident's time at home is not influenced by the mutant's behaviour we obtain

$$D_p(i,e) = 1 - \hat{I}_p + \frac{N-1}{N}\hat{I}_p + \frac{1}{N}I_p. \tag{6}$$

The density on the mutant's territory consists of the presence of the mutant itself, $1-I$ and the density of the resident intruders:

$$D_m(i,e,a) = 1 - I + N\hat{I}_m \tag{7}$$

The contribution of resident intruders to density on the mutant's territory corresponds to the expected proportion of time each neighbour will spend intruding on the mutant's territory $\hat{I}_m$ times the number of neighbours. Note that resident neighbours might spend different amounts of time intruding depending on whether they intrude into the mutant's or another resident's territory (i.e. $\hat{I}_m \neq \hat{I}_p$). Using the definition of I given in Eq. (1) we obtain for $\hat{I}_m$:

$$\begin{aligned}\hat{I}_m(a) &= \frac{1}{N}\frac{\hat{t}_{i,m}}{\hat{t}_o + \frac{1}{N}\hat{t}_{i,m} + \frac{N-1}{N}\hat{t}_{i,p}}\\ &= \frac{1}{N}\frac{\frac{1}{\hat{e}+dav}}{\frac{1}{\hat{i}} + \frac{1}{N}\frac{1}{\hat{e}+dav} + \frac{N-1}{N}\frac{1}{\hat{e}+d\hat{a}v}}\end{aligned} \tag{8}$$

In the following we simplify our notation by defining the time unit as $1/d$ so that d becomes one and can be dropped from all equations.

2.3. Selection gradients

Assuming that invasion success of the mutant is predicted by its invasion fitness selection gradients can be calculated as the derivatives of the mutant's fitness with respect to the evolving traits. These gradients and their derivatives can then be used to find evolutionarily singular points and their stability properties (Geritz et al., 1998).

From Eq. (5) we can calculate the selection gradients with respect to a, i and e, evaluated at the current resident's strategy $w'_a := \partial w/\partial i|_{(i,e,a)=(\hat{\imath},\hat{e},\hat{a})}$, $w'_e := \partial w/\partial e|_{(i,e,a)=(\hat{\imath},\hat{e},\hat{a})}$ and $w'_i := \partial w/\partial a|_{(i,e,a)=(\hat{\imath},\hat{e},\hat{a})}$:

$$w'_i = \left(\left(\frac{N+1}{N}I - 1\right)r'(1) - ac_i\right)\frac{\partial I}{\partial i} \tag{9}$$

$$w'_e = \left(\left(\frac{N+1}{N}I - 1\right)r'(1) - ac_i\right)\frac{\partial I}{\partial e} \tag{10}$$

$$w'_a = (1-I)|r'(1)|N\left|\frac{\partial \hat{I}_m}{\partial a}\right| - c_o\left(I - aN\left|\frac{\partial \hat{I}_m}{\partial a}\right|\right) \tag{11}$$

2.4. Stability

2.4.1. Intrusion and return rate

Since we know that level of intrusion has to increase with i and decrease with e it follows from Eqs. (9) and (10) that $\mathrm{sign}(w'_i) = -\mathrm{sign}(w'_e)$, which means in particular that $w'_i = 0 \Leftrightarrow w'_e = 0$. Thus, any evolutionarily singular point (sensu 25) for i is also a singular point for e and vice versa. We further see from Eqs. (9) and (10) that whether a given combination of i and e is a singularity depends only on the value of a and the resulting level of intrusion I. Therefore for each given value of a there has to be a line of evolutionarily singular different combinations $(i,e)^*$ which lead to the same singular I^*. Setting $w'_i = 0$ we can solve for this point:

$$I^*(a) = \frac{N}{N+1}\left(1 - \frac{ac_i}{|r'(1)|}\right) \tag{12}$$

The singular point I^* turns out to be convergence stable (assuming negative density dependence $r' < 0$) and continuously stable if r is concave around 1.

This result can be explained by the fact that the benefits as well as the costs of intrusion are only a function of the proportion of time spent on the foreign territory not of the frequency of switching between territories.

We see that without defence intrusion into neighbouring territories clearly pays: Setting a to 0 in Eq. (12) leads to $I^* = N/(N+1)$, i.e. an individual should spend exactly the same amount of time in its own as in each of its neighbour's territories. If territories are defended the amount of intrusion decreases and can even disappear completely if fighting costs for the intruders are high, resource production is low or detection rate is high. In general intrusion increases with the number of neighbours per territory.

2.4.2. Aggressiveness

We can derive three straightforward conditions describing the direction of selection on a (see Appendix A):

- greater a is selected for ($w'_a > 0$) if

$$(1-I)\frac{v|r'(1)|}{c_o} > e + i \tag{13}$$

- greater a is selected for sufficiently large N if
$$e+i > (1-I)\frac{v|r'(1)|}{c_o} > e \tag{14}$$

- smaller a is selected for ($w'_a < 0$) if
$$(1-I)\frac{v|r'(1)|}{c_o} < e \tag{15}$$

Since a is never convergence stable (see Appendix B) only the values 0 and 1 can be evolutionary attractors for a.

We see that although for the evolution of intrusion and return rate only the actual proportion of time spent intruding is relevant, the evolutionary stability of defence also depends on the frequency of intrusion events. For the same level of intrusion I, low intrusion and return rates (i, e) can lead to maintenance of defence whereas high rates will make it disappear (see Fig. 1).

A closer look at how small changes in the mutant's aggressiveness affect realised fighting costs and foraging success reveals the underlying mechanism (see Eq. (11)). The sensitivity of (realised) fighting costs against changes in aggressiveness depends on intruder density (and therefore on the proportion of time individuals spend intruding) whereas the sensitivity of foraging success depends on the *change* in density with aggressiveness.

We can see from Eqs. (3) and (4), however, that under high switching rates (i.e. high i and e) aggressiveness (and thus change of aggressiveness) has a much less pronounced effect on density as well as leaving rates of intruders than under low switching rates even if the actual intruder density (and therefore attack rate adI) is the same in both cases. To put it differently: if we assume two scenarios with the same proportion of time spent intruding but different frequencies of moving between territories then in the scenario with the higher frequency of movement a single intrusion bout of an individual is less likely to have been terminated by an attack and more likely by voluntary return to the home territory resulting in weaker effects of aggressiveness.

Therefore the higher switching rates the less effective an increase in aggressiveness is in reducing levels of intrusion and consequently exploitation competition by intruders.

We can also see that not surprisingly a high win chance v furthers the stability of territory defence. Equivalently high fighting costs for the owner c_o relative to the effect of density on foraging success have a detrimental effect on aggressiveness. Finally stability of defence increases with the time individuals spend on their own territory ($1-I$), since this determines the degree to which they profit from a decrease in intruder density.

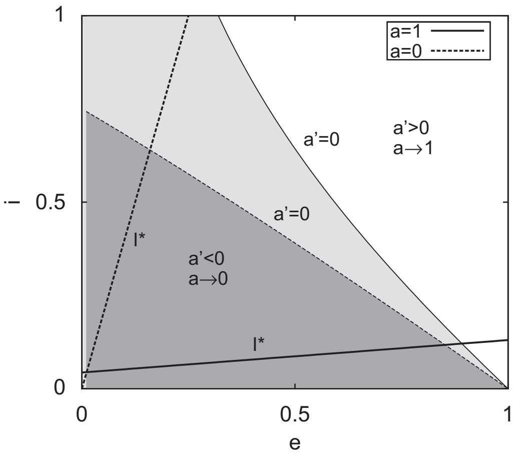

Fig. 1. Stability of a dependent on e and i. For values of e and i below the a-isoclines ($a=1$: thin solid line; $a=0$: thin dashed line) the selection gradient of a is positive, in the region above the isoclines it is negative. The area between the isoclines (light grey) leads to bistability. Also shown are the combinations of e and i which lead to a stable level of intrusion I for $a=0$ (fat dashed line) and $a=1$ (fat solid line). ($N=4$, $c_i/|r'(1)|=0.9$, $c_o/|r'(1)|=0.5$).

3. The simulation model

The mathematical model described above trades realism for clarity in a number of ways. First, it averages over (stochastic) differences between individuals with respect to state and genetic setup. It has been shown that this kind of approximation can produce strongly misleading results (Huston et al., 1988). Second, we assume that individuals always encounter equilibrium resource levels. To test whether these assumptions affect the behaviour of our model we implemented a spatially explicit individual-based version of the model. As an added benefit this allowed us to easily explore two simple extensions of the model (see below) which would have been difficult to do analytically.

3.1. Setup

Territories are placed on a regular grid of size 30 times 30. Territories to the left, right, above and below are considered adjacent (thus $N=4$)—grid edges are assumed to wrap around (leading to a torus-shaped world). Each territory is always owned by exactly one individual.

At the beginning of each time step individuals can switch territories—either voluntarily or because they are chased away by owners: In random order they decide whether they want to either intrude (if currently at home) or return (if currently intruding). Currently intruding individuals furthermore are detected, attacked and chased away with the respective probabilities (see analytical model). Subsequently all individuals (again in random order) feed at their current location. All probabilities are calculated equivalent to the corresponding rates in the mathematical model. The free parameter detection probability d was arbitrarily set to 0.1.

To keep things simple we opted for very basic resource dynamics. Each time step the resource level in each territory is increased by a fixed amount R. Feeding individuals reduce the resource level by a fixed proportion f.

After 3000 time steps the population reproduces, generating a new generation of individuals which completely replaces the old population. The expected number of offspring of an individual is determined by its fitness, i.e. the sum of all benefits and costs it accrued during its lifetime relative to the average population fitness.

3.2. Extensions

In the basic model the only costs to intrusion are the fighting costs from a potential attack (c_i). Apart from that – assuming equal resource levels – foraging on a foreign territory is exactly equivalent to foraging at home.

In reality, however, under non-random foraging (e.g. Gill and Wolf, 1977) the lack of knowledge about foraging schedules automatically reduces foraging efficiency for an intruder and makes intrusion less desirable (Davies, 1980; Houston et al., 1985). This effect of "defence by exploitation" can become even stronger if individuals on purpose adapt their foraging behaviour so as to make intrusion unprofitable for example by foraging disproportionately often near the boundaries of their territories (Davies and Houston, 1981; Possingham, 1989; Adler and Gordon, 2003).

In the first extension to our basic model we therefore assumed that intruders forage at a lower efficiency f_i than owners.

In addition it is in many situations conceivable that the movement between territories itself is costly in terms of time, energy or predation risk. We simulated this by making individuals pay a fixed amount of energy c_s on each return or intrusion.

3.3. Results

For all model variants we varied fighting costs c_i and c_o and initial values of the traits a, i and e. For each parameter combination we ran ten replicates for 10 000 time steps. For a list of all parameter combinations used, see Table 2.

In general it turned out that the effect of varying the initial values of i and e conformed to the expectations, i.e. higher values decreased the likelihood of the occurrence of defence. Its magnitude, however, was rather small compared to the effect of the other parameters. In the following we will therefore only show the results for $i_0 = e_0 = 0$.

3.3.1. Equivalence to the mathematical model

All mechanistic aspects of the mathematical model are reproduced very accurately by the IBM. Given a set of parameters and trait values we can exactly predict the resulting intrusion rates, foraging rates and attack rates in the simulation with the mathematical model (not shown). Similarly the predicted stable level of intrusion I^* corresponds very well to the value reached in the simulation (see Fig. 2).

On the other hand the evolutionary dynamics of the simulation differ considerably from the expectations based on the analytical model. If the starting value of a is 0 territoriality in the simulation never occurs. For an initial aggressiveness of 1 territoriality is only kept in runs with very high intrusion costs although variation between replicates is considerable (Fig. 3a and c). A closer look shows that although the level of intrusion in the simulation generally is consistent with the analytical predictions (see above) the values of e and i undergo strong directional drift towards higher values. As our mathematical analysis implies (see Fig. 1) this will lead to a breakdown of territoriality as soon as the population moves into the unstable zone for high values of e and i.

This unexpected effect can be explained by non-equilibrium resource dynamics in the individual-based model. The equilibrium level of resources in a territory depends on the long-term average number of individuals present which is one. The density experienced by a focal individual is, however, either one if it is alone or higher than one if other individuals are present, which leads to an average higher than one. Therefore on average an individual will find itself in a situation where resource levels (due to its own and its conspecifics' presence) are slowly decreasing towards levels below equilibrium. The surrounding territories on the other hand have an average density <1 (since the focal individual is not present) and are thus moving towards a higher equilibrium resource level. Individuals therefore profit from increasing switching rate to avoid local depletion.

3.3.2. Owner advantage

Assuming that intruders forage less efficiently than owners surprisingly does have only little effect on the outcome of the simulations even for low values of intruder efficiency f (see Fig. 3 B,D). The slow increase of e and i over time still leads to the breakdown of territoriality in most scenarios.

3.3.3. Switching costs

Already moderate switching costs are sufficient to counteract the selection for higher switching frequency which considerably stabilises territoriality (Fig. 4a and c). For low fighting costs for the

Table 2
Parameter values (simulation).

v	Probability that the owner wins a fight	0.5
N	Number of neighbouring territories	4
d	Detection rate (of intruders)	0.1
Basic simulation model		
i_0	Initial rate of intrusion	0,1
e_0	Initial rate of return	0,1
a_0	Initial probability to attack an intruder	0,1
c_o	Fighting costs (owner)	0.1, 0.4
c_i	Fighting costs (intruder)	0.1, 1, 2, …, 5
Owner advantage		
f_i	Foraging efficiency of intruders	0.9, 0.5
Switching costs		
c_s	Costs of moving between territories	0.1, 1.0

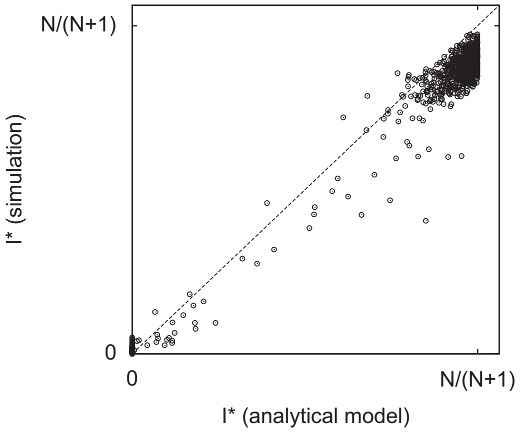

Fig. 2. Predicted level of intrusion versus actual intrusion in the basic simulation model (dashed line = identity). The measured level of intrusion after 10 000 generations is very close to the evolutionarily stable value of I^* the mathematical model predicts based on the evolved level of aggressiveness a in the simulation. All replicates of all parameter combinations of the basic model are shown.

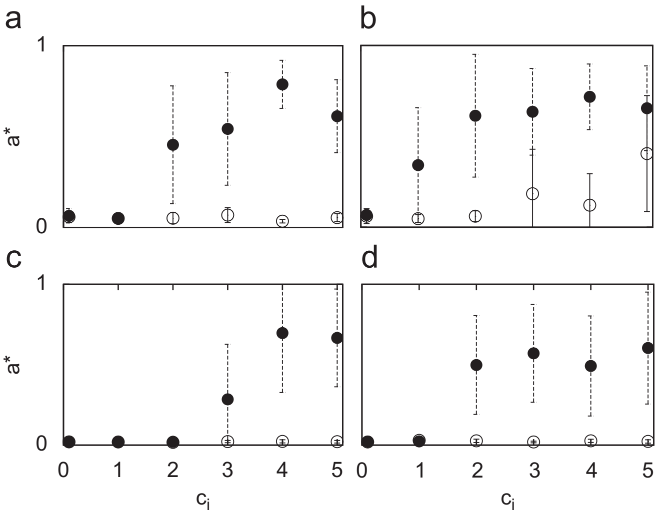

Fig. 3. Evolved level of aggressiveness a versus fighting costs for the intruder c_i for high ($a_0 = 1$, solid line, filled circles) and low ($a_0 = 0$, dashed line, open circles) values of initial aggressiveness. Results are shown for different values of fighting costs for the owner (top: $c_0 = 0.1$; bottom: $c_o = 0.4$) and owner advantage (left: no owner advantage; right: $f = 0.5$). High aggressiveness and therefore territoriality only persists for high intrusion costs and high initial aggressiveness. Owner advantage and fighting costs for the owner have little effect.

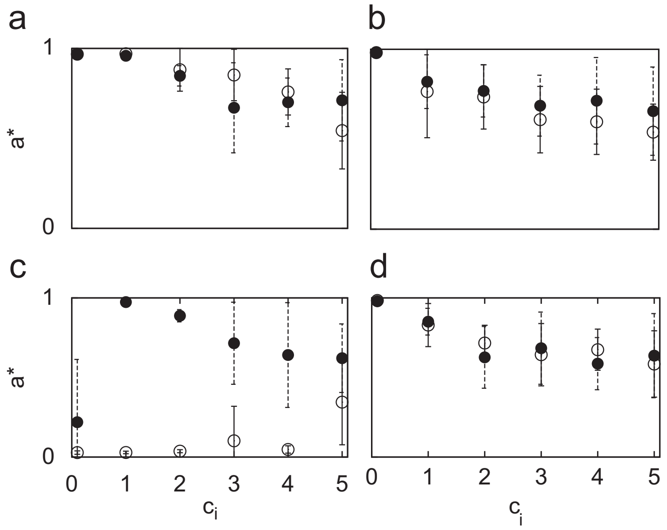

Fig. 4. Evolved level of aggressiveness a versus fighting costs for the intruder c_i for high ($a_0=1$, solid line, filled circles) and low ($a_0=0$, dashed line, open circles) values of initial aggressiveness. Results are shown for different values of fighting costs for the intruder (top: $c_o=0.1$; bottom: $c_0=0.4$) and different switching costs (left: $c_s=0.1$; right: $c_s=1$). Already moderate switching costs strongly favour the stability and even the emergence of territoriality.

owner c_o territoriality even emerges from a non-territorial population (Fig. 4a). For high switching costs most populations end up being territorial independent of initial aggressiveness and fighting costs (Fig. 4b and d). Interestingly under the presence of switching costs low fighting costs for the intruder c_i seem to promote rather than hinder territoriality.

4. Discussion

Our results show that in territorial populations the incentive for stealing resources from neighbours can be strong enough that defence becomes uneconomical and disappears. Only if being attacked by territory owners has severe fitness consequences for intruders or if crossing the borders between territories is costly per se can intrusion levels be kept low enough to enable territory defence.

In the absence of defence stealing from neighbours is always profitable in our model since individuals can effectively save up on their own resources by living off the neighbour's resources for some time. This simple and intuitively plausible result leads to some interesting conclusions. First of all it means that everything else being equal resource dynamics create a force counteracting territoriality and furthering the "diluting" of territories by mutual intrusion. Therefore in general, in order to explain the existence of territories some additional effect has to be found which compensates for the profitability of stealing. If we abstract a bit from the details of our particular model we further see that this conclusion might even apply to other scenarios of resource partitioning. In every situation where not using a resource increases its future value we would similarly expect stealing to be profitable.

The results of our calculations concerning the selection on intrusion and defence, respectively, partially confirm earlier studies. Similar to Adler and Gordon (2003) and Morrell and Kokko (2005) we find that territory defence can prevent intrusion by making it costly with defence becoming more effective the higher the fighting costs and the weaker the effects of density dependence. As previous studies on economic defendability (see Schoener, 1987) we see in our model that costs and efficacy of defence, the gain in terms of reduction of competition and the amount of intrusion influence economic defendability. The combination of both confirms our expectations—without defence intrusion leads to the complete disappearance of territoriality. High intrusion levels on the other hand make defence uneconomical.

A factor which surprisingly had barely any effect on the stability of territoriality was the owner advantage in foraging rate. This is interesting since this has been seen as one of the primary reasons for the respect of ownership by territorial neighbours (Davies and Houston, 1981; Possingham, 1989). At least partially this puzzling result might be explained by the fact that the spatial distribution of resources within a territory is not represented in our model. If we assume that intruders forage preferentially close to their own territory then the depletion they cause will be concentrated in these areas which might make intrusion less worthwhile.

An unexpected result from our analytical model was that not only the absolute level of intrusion but also the frequency of intrusion events determines the efficiency of defence. It turns out that this effect is quite important. In combination with the fact that defence results in selection on intrusion *levels* and not frequency it causes any factor that affects intrusion frequency to directly determine the evolutionary stability of territoriality. This is confirmed by our simulation results. In the scenario most directly corresponding to the analytical model resource dynamics lead to a strong enough selection for higher intrusion frequency to let defence and thus territoriality disappear in nearly all cases.

If movement between territories is costly on the other hand frequent intrusion is selected against and territoriality becomes stable. This effect certainly does play a role in natural systems where territories are large or separated by uninhabited space or where individuals start their foraging activities from a central point in the territory. There are, however, also many examples where territories are tightly packed with no (at least for the human observer) discernible interstitial space (e.g. Gill and Wolf, 1975; Davies, 1980; Ebersole, 1980; Komdeur and Edelaar, 2001; Adler and Gordon, 2003). In these cases it is difficult to see why "switching" between territories should be costly.

It is, however, imaginable that the frequency with which individuals can move back and forth between their own and a neighbour's territory is directly limited by the individuals' movement speed or the food resource's handling time. As can bee seen in Fig. 1 this can be sufficient to make defence evolutionarily stable. This also gives us an interesting relationship which could be testable by cross-species comparison.

In addition a decrease of detection rate while intruding can lead to a trade-off between intrusion and "guarding" the territory (a similar effect has been shown for mate-guarding by Kokko and Morrell, 2005). This could in some cases stabilise territoriality.

In general our results show that the interactions between territorial neighbours are economically relevant. This means that calculations of economic defendability of territories (as done e.g. by Gill and Wolf, 1975; Carpenter and McMillen, 1976; Houston et al., 1985) are incomplete in the sense that they have to be complemented by an analysis which includes the expected intrusion rate by neighbours. This might lead to very different results. For example, although our model predicts that in the territorial case intruders into territories will always be attacked by the owner, the actual level of intrusion still can vary a lot depending on resource production, fighting costs and number of neighbours. In contrast to older models of economic defendability against floaters (e.g. Carpenter and McMillen, 1976; Schoener, 1987), in our model even if defence is high individuals can therefore still lose considerable amounts of their resources to intruders without, however, that this necessarily makes defence unprofitable. This might serve as an explanation for the high levels of reciprocal pilferage found in some food-caching species (Vander Wall and Jenkins, 2003; Dally et al., 2006).

More generally our results show that floating intruders do not pose the only threat to the maintenance of territoriality, an assumption which underlies most models of the evolution of territoriality (Adams, 2001). We see that interactions between neighbours "per default" act as a force destabilising territoriality. In order to understand the factors which determine the evolutionary stability of territoriality it is therefore necessary to take the economics of interactions between neighbours into account. A theory of the evolution of territoriality needs to be able to explain which mechanisms maintain the partitioning of space between neighbours.

There are numerous possibilities to extend our basic approach.

There is a wealth of empirical information on the effects of resource properties such as abundance, distribution or predictability (Maher and Lott, 2000). It would be fairly straightforward to take these into account in the simulation model and thus test whether our framework can predict the observed correlations.

Our model is fairly simple in terms of "game-theoretic structure". It has been shown for simple conflict models that for example variations in fighting ability, access to information about the opponent or the ability to change the behaviour in repeated interactions can have tremendous effects on the outcome (e.g. Leimar and Enquist, 1984; van Doorn et al., 2003). It can certainly be expected that conflicts between territory owners are no exception to this.

Another very interesting area for future research will be to integrate our model with other aspect of territorial behaviour. Additional processes which likely are tightly interlinked with the direct competition between neighbours are the founding of territories (Broom et al., 1997; Komdeur and Edelaar, 2001), the emergence of territory borders (Stamps and Krishnan, 1999; Lewis and Moorcroft, 2001; Pereira et al., 2003), and the defence of territories against floaters (Mesterton-Gibbons, 1992; Eshel and Sansone, 1995; López-Sepulcre and Kokko, 2005).

Finally, every theory requires empirical validation. A number of detailed data sets on the energy budgets of foraging and territory defence for example for sunbirds (Gill and Wolf, 1975), honeycreepers (Carpenter and McMillen, 1976) and wagtails (Houston et al., 1985) have been used to test the validity of classical models of economic defendability. The same data could be used to calculate for example the expected level of intrusion based on our model.

The work presented here is a first step towards a better understanding of the role defence of territories against theft by neighbours plays in the evolution of territoriality. It suggests, however, that trying to understand territorial behaviour in terms of foraging decisions of individuals rather than competition for indivisible resources might lead to more general valuable insights.

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Appendix A. Direction of selection for *a*

We start with the selection gradient for a (Eq. (11)).

$$w'_a = (1-I)r'(1)N\frac{\partial\hat{I}_m}{\partial a} - c_o\left(I + aN\frac{\partial\hat{I}_m}{\partial a}\right) = N\frac{\partial\hat{I}_m}{\partial a}((1-I)r'(1)-c_o a)-c_o I \tag{A1}$$

From this we can derive a condition for a positive selection gradient on a:

$$\begin{aligned} w'_a > 0 \Leftrightarrow\ & 0 < N\frac{\partial\hat{I}_m}{\partial a}((1-I)r'(1)-c_o a)-c_o I \\ \Leftrightarrow\ & c_o\frac{I}{N} < \frac{\partial\hat{I}_m}{\partial a}((1-I)r'(1)-c_o a) \quad \left|\frac{I}{N} = \hat{I}_m \quad \text{for } a=\hat{a}\right. \\ \Leftrightarrow\ & \frac{\hat{I}_m}{\frac{\partial\hat{I}_m}{\partial a}} > (1-I)\frac{r'(1)}{c_o} - a \end{aligned} \tag{A2}$$

With

$$\begin{aligned} \frac{\partial\hat{I}_m}{\partial a} &= -\frac{t_i\frac{\partial\hat{t}_{i,m}}{\partial a}}{(t_o+t_i)^2N^2} + \frac{t_i\frac{\partial\hat{t}_{i,m}}{\partial a}}{(t_o+t_i)N} = -\hat{I}_m^2\frac{\frac{\partial\hat{t}_{i,m}}{\partial a}}{t_i} + \hat{I}_m\frac{\frac{\partial\hat{t}_{i,m}}{\partial a}}{t_i} \quad \left|\frac{\partial\hat{t}_{i,m}}{\partial a} = -\nu t_i^2\right. \\ &= -\nu\hat{I}_m t_i(1-\hat{I}_m), \end{aligned} \tag{A3}$$

we continue from (A2)

$$\begin{aligned} w'_a > 0 \Leftrightarrow\ & \frac{\hat{I}_m}{-\nu\hat{I}_m t_i(1-\hat{I}_m)} > (1-I)\frac{r'(1)}{c_o} - a \\ \Leftrightarrow\ & \frac{1}{t_i(1-\hat{I}_m)} - a\nu < (1-I)\frac{r'(1)\nu}{c_o} \Leftrightarrow \frac{e+a\nu}{1-\frac{1}{N}I} - a\nu < (1-I)\frac{r'(1)\nu}{c_o}. \end{aligned} \tag{A4}$$

We can now consider the left hand side of the last condition. Letting N go from 1 to ∞ (and taking into account that $1-I=(e+a\nu)/(e+i+a\nu)$, see Eq. (4)) we see that

$$e < \frac{e+a\nu}{1-\frac{1}{N}I} - a\nu \le e+i \tag{A5}$$

always holds, which leads us to conditions (13) to (15) as described in the main text.

Appendix B. No convergence stable a^*

Assuming a convergence stable point a^*, values of $a < a^*$ have to result in a positive selection gradient, whereas the selection gradient for values $a > a^*$ has to be negative. Therefore condition (A4) has to be fulfilled for values smaller than and not fulfilled for values greater than a^*.

A simple transformation of Eq. (A4) yields

$$\frac{(1-I)\frac{r'(1)\nu}{c_o}}{\frac{e+a\nu}{1-\frac{1}{N}I} - a\nu} > 1 \tag{B1}$$

As the reader can easily verify the derivative with respect to a of the left hand side is always positive, therefore if the condition holds for a given value a_0 it will also hold for all $a > a_0$. Thus no convergence stable value a^* can exist.

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