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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