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Defence, intrusion and the evolutionary stability of territoriality

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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.

Keywords: territorial behaviour, ownership, neighbour-neighbour interactions, resource competition

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23 1. Introduction

24 Territoriality is one of the most conspicuous ways in which access to local resources
25 such as food or nest sites can be organised in animal populations. Territoriality is a sit-
26 uation where many or all of the individuals in a population claim ownership of a piece
27 of the available space in the sense that they have exclusive access to the resources it
28 contains [1]. Due to ubiquitous competition for resources this claim has to be defended
29 against other individuals in the population [2, 3]. Territorial behaviour can therefore
30 only be adaptive if maintenance of ownership is profitable, i.e. if the defence of a terri-
31 tory is less expensive in terms of fitness than the potential damage done by competitors
32 in the absence of defence [3, 4].

33 The main focus in the study of the adaptiveness of territoriality has in the past been
34 on the competition between owners and non-territorial intruders (floaters) either for
35 entire territories [e.g. 5, 6, 7, 8, 9] or for resources within the territory [e.g. 10, 11, 4].

36 The consequences of the competition between territorial neighbours have also been
37 explored, although less thoroughly [12]. Most models of neighbour-neighbour inter-
38 actions assume that conflicts arise from individuals attempting to increase the size of
39 their territories at their neighbours' expense and investigate how the position of the
40 border between two (non-overlapping) territories is negotiated by the respective own-
41 ers [13, 14, 15]. This process can even lead to the exclusion of some individuals from
42 the territorial population [16].

43 Borders of territories are however not impenetrable. To increase its access to re-
44 sources a territory owner could also intrude into a neighbour's territory, effectively
45 "stealing" resources [17]. "Theft" by neighbours can have strong effects on the costs
46 and benefits of territoriality. In low frequencies it can reduce the payoff of having a
47 territory while at the same time increasing the costs of territory defence [e.g. 18, 19, 4].
48 A high incidence of theft would ultimately render territory borders meaningless and
49 would therefore effectively lead to the disappearance of territoriality.

50 It has however been shown that a high level of defence by territory owners can
51 make intrusion into territories costly enough that individuals will restrict themselves
52 to foraging mostly or entirely within their own territories [20, 21]. Whether owners

53 do defend their territories against intruding neighbours on the other hand will depend
54 on the amount of damage done by these intruders relative to the costs (and chances of
55 success) of defence [3, 4].

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

64 In this study we investigate under which conditions stealing of resources by neigh-
65 bours poses a threat to the evolutionary stability of territory defence and when the
66 coevolution of defence and respect for ownership leads to the maintenance of territori-
67 ality.

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

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

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

81 2. The Analytical Model

82 Similar to others [e.g. 22, 20, 14] we model the fitness consequences of single
 83 foraging decisions of individuals. We assume that everything else being equal an indi-
 84 vidual with a higher long-term average resource uptake rate will have a higher fitness.
 85 In the same way fighting in reality can have various negative consequences in terms
 86 of energy costs, time investment, predation risk or risk of injury or death. All of these
 87 however effectively lead to a reduction in fitness. In our model we therefore simplify
 88 things by measuring costs and benefits in units of fitness lost or gained.

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

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

100 2.1. Model description

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

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

111 The payoff an individual obtains from foraging depends on the amount of resources
 112 in the territory it is currently foraging in. Similar to other studies [e.g. 23, 24, 20] we
 113 assume that changes in the amount of resources are slow enough compared to the move-
 114 ment of individuals between territories that short term fluctuations in density have neg-
 115 ligible consequences for the uptake rate of individuals (this assumption is later relaxed
 116 in the simulation). Therefore we approximate foraging success in terms of increase
 117 in fitness as a function $r(D)$ of average number of individuals present on a territory
 118 (henceforth referred to as density) which is equal to the sum of the average proportions
 119 of time all eligible individuals, i.e. the owner (while at home) and all neighbours (while
 120 intruding) spend on the territory. Since we assume exploitation competition, r has to
 121 be a decreasing function.

122 We use a continuous time spatially implicit mathematical model to describe the
 123 dynamics of intrusion, defence and foraging. We analyse evolutionary dynamics within
 124 the model based on a straightforward adaptive dynamics approach [25].

125 For a list of all model parameters and variables used see table 1.

126 2.2. Fitness

127 To determine the evolutionary dynamics in the model we calculate the fitness of a
 128 single (or rare) mutant (which by definition is identical to its expected long term uptake
 129 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:

$$I = \frac{t_i}{t_i + t_o}. \quad (1)$$

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

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

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

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	
v	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

We can therefore derive the proportion of time spent intruding as

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

133 For a given territory, density (i.e. average number of individuals present) D is then just
134 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 r . 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:

$$\begin{aligned} w(i, e, a) = & (1 - I)r(D_m) \\ & + Ir(D_p) \\ & - N\hat{I}_m dac_o - Id\hat{a}c_i. \end{aligned} \quad (5)$$

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

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

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

141 The density on the mutant’s territory consists of the presence of the mutant itself,
142 $1 - I$ and the density of the resident intruders:

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

143 The contribution of resident intruders to density on the mutant’s territory corresponds
144 to the expected proportion of time each neighbour will spend intruding on the mutant’s

145 territory \hat{I}_m times the number of neighbours. Note that resident neighbours might
 146 spend different amounts of time intruding depending on whether they intrude into the
 147 mutant's or another resident's territory (i.e. $\hat{I}_m \neq \hat{I}_p$). Using the definition of I given
 148 in Eq. 1 we obtain for \hat{I}_m :

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

149 In the following we simplify our notation by defining the time unit as $\frac{1}{d}$ so that d
 150 becomes one and can be dropped from all equations.

151 2.3. Selection gradients

152 Assuming that invasion success of the mutant is predicted by its invasion fitness
 153 selection gradients can be calculated as the derivatives of the mutant's fitness with
 154 respect to the evolving traits. These gradients and their derivatives can then be used to
 155 find evolutionarily singular points and their stability properties [25].

156 From Eq. 5 we can calculate the selection gradients with respect to a , i and e , evalu-
 157 ated at the current resident's strategy $w'_a := \frac{\partial w}{\partial i} \Big|_{(i,e,a)=(\hat{i},\hat{e},\hat{a})}$, $w'_e := \frac{\partial w}{\partial e} \Big|_{(i,e,a)=(\hat{i},\hat{e},\hat{a})}$
 158 and $w'_i := \frac{\partial w}{\partial a} \Big|_{(i,e,a)=(\hat{i},\hat{e},\hat{a})}$.

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

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

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

159 *2.4. Stability*

160 *2.4.1. Intrusion and return rate*

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

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

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

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

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

181 *2.4.2. Aggressiveness*

182 We can derive three straightforward conditions describing the direction of selection
 183 on a (see AppendixA):

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

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

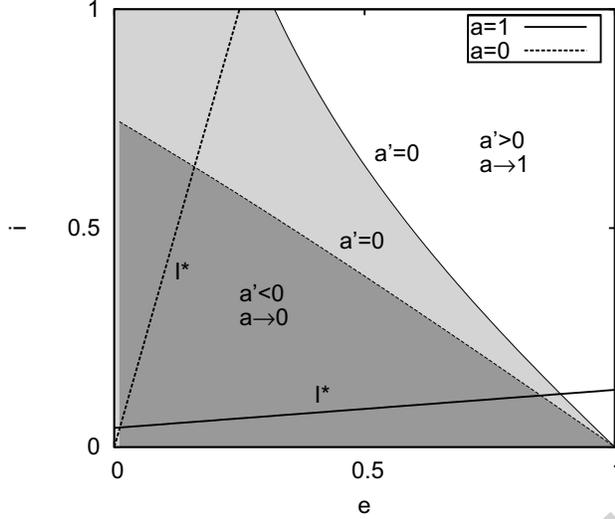


Figure 1: Stability of a dependent on e and i . For values of e and i below the a -isoclines ($a = 1$: thin solid line; $a = 0$: thin dashed line) the selection gradient of a is positive, in the region above the isoclines it is negative. The area between the isoclines (light grey) leads to bistability. 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). ($N = 4$, $\frac{c_i}{|r'(1)|} = 0.9$, $\frac{c_o}{|r'(1)|} = 0.5$)

- greater a is selected for sufficiently large N if

$$e + i > (1 - I) \frac{v|r'(1)|}{c_o} > e \quad (14)$$

- smaller a is selected for ($w'_a < 0$) if

$$(1 - I) \frac{v|r'(1)|}{c_o} < e \quad (15)$$

184 Since a is never convergence stable (see Appendix AppendixB) only the values 0 and
 185 1 can be evolutionary attractors for a .

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

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

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

206 Therefore the higher switching rates the less effective an increase in aggressive-
 207 ness is in reducing levels of intrusion and consequently exploitation competition by
 208 intruders.

209 We can also see that not surprisingly a high win chance v furthers the stability of
 210 territory defence. Equivalently high fighting costs for the owner c_o relative to the effect
 211 of density on foraging success have a detrimental effect on aggressiveness. Finally
 212 stability of defence increases with the time individuals spend on their own territory
 213 ($1 - I$), since this determines the degree to which they profit from a decrease in intruder
 214 density.

215 3. The simulation model

216 The mathematical model described above trades realism for clarity in a number
 217 of ways. First, it averages over (stochastic) differences between individuals with re-
 218 spect to state and genetic setup. It has been shown that this kind of approximation can
 219 produce strongly misleading results [26]. Second, we assume that individuals always

220 encounter equilibrium resource levels. To test whether these assumptions affect the be-
221 haviour of our model we implemented a spatially explicit individual-based version of
222 the model. As an added benefit this allowed us to easily explore two simple extensions
223 of the model (see below) which would have been difficult to do analytically.

224 3.1. Setup

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

229 At the beginning of each time step individuals can switch territories - either volun-
230 tarily or because they are chased away by owners: In random order they decide whether
231 they want to either intrude (if currently at home) or return (if currently intruding). Cur-
232 rently intruding individuals furthermore are detected, attacked and chased away with
233 the respective probabilities (see analytical model). Subsequently all individuals (again
234 in random order) feed at their current location. All probabilities are calculated equiva-
235 lent to the corresponding rates in the mathematical model. The free parameter detection
236 probability d was arbitrarily set to 0.1.

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

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

244 3.2. Extensions

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

248 In reality however under non-random foraging [e.g. 27] the lack of knowledge
 249 about foraging schedules automatically reduces foraging efficiency for an intruder and
 250 makes intrusion less desirable [11, 24]. This effect of “defence by exploitation” can
 251 become even stronger if individuals on purpose adapt their foraging behaviour so as to
 252 make intrusion unprofitable for example by foraging disproportionately often near the
 253 boundaries of their territories [28, 29, 20]. In the first extension to our basic model we
 254 therefore assumed that intruders forage at a lower efficiency f_i than owners.

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

258 3.3. Results

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

262 In general it turned out that the effect of varying the initial values of i and e con-
 263 formed to the expectations, i.e. higher values decreased the likelihood of the the oc-
 264 currence of defence. Its magnitude however was rather small compared to the effect
 265 of the other parameters. In the following we will therefore only show the results for
 266 $i_0 = e_0 = 0$.

267 3.3.1. Equivalence to the mathematical model

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

273 On the other hand the evolutionary dynamics of the simulation differ considerably
 274 from the expectations based on the analytical model. If the starting value of a is 0 terri-
 275 toriality in the simulation never occurs. For an initial aggressiveness of 1 territoriality
 276 is only kept in runs with very high intrusion costs although variation between replicates

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, \dots, 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

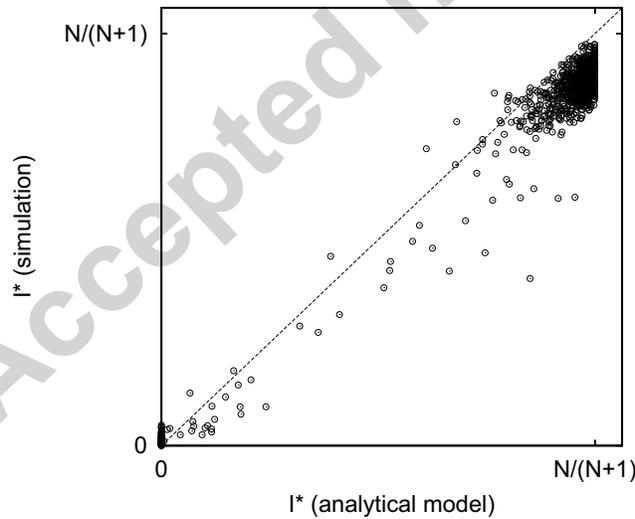


Figure 2: Predicted level of intrusion versus actual intrusion in the basic simulation model (dashed line = identity). The measured level of intrusion after 10000 generations is very close to the evolutionarily stable value of I^* the mathematical model predicts based on the evolved level of aggressiveness a in the simulation. All replicates of all parameter combinations of the basic model are shown.

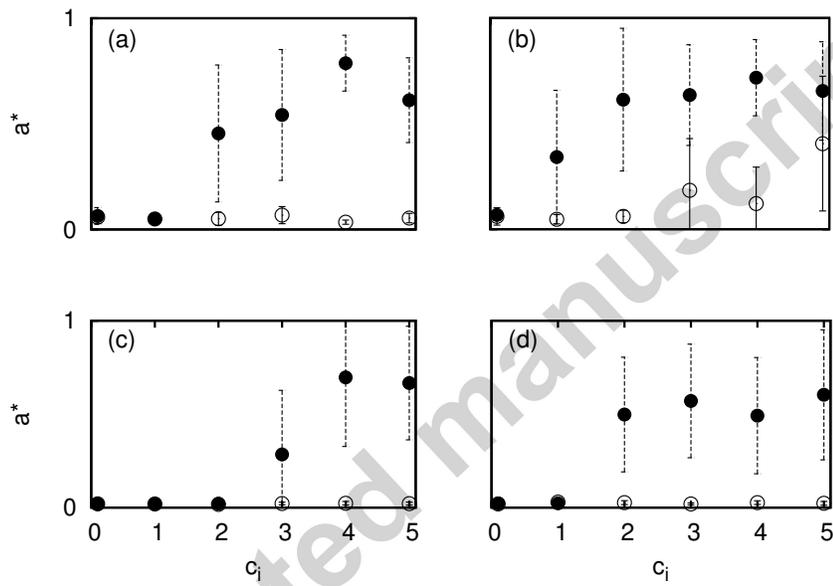


Figure 3: Evolved level of aggressiveness a versus fighting costs for the intruder c_i for high ($a_0 = 1$, solid line, filled circles) and low ($a_0 = 0$, dashed line, open circles) values of initial aggressiveness. Results are shown for different values of fighting costs for the owner (top: $c_o = 0.1$; 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.

277 is considerable (Fig. 3 a, c). A closer look shows that although the level of intrusion
 278 in the simulation generally is consistent with the analytical predictions (see above) the
 279 values of e and i undergo strong directional drift towards higher values. As our math-
 280 ematical analysis implies (see Fig. 1) this will lead to a breakdown of territoriality as
 281 soon as the population moves into the unstable zone for high values of e and i .

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

293 3.3.2. *Owner advantage*

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

298 3.3.3. *Switching costs*

299 Already moderate switching costs are sufficient to counteract the selection for
 300 higher switching frequency which considerably stabilises territoriality (Fig. 4 a, c). For
 301 low fighting costs for the owner c_o territoriality even emerges from a non-territorial
 302 population (Fig. 4 a). For high switching costs most populations end up being territo-
 303 rial independent of initial aggressiveness and fighting costs (Fig. 4 b, d). Interestingly
 304 under the presence of switching costs low fighting costs for the intruder c_i seem to
 305 promote rather than hinder territoriality.

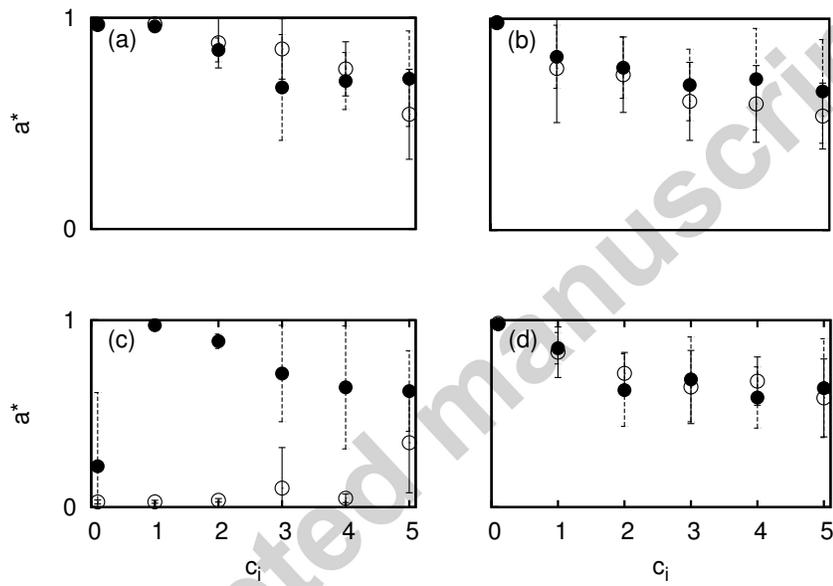


Figure 4: Evolved level of aggressiveness a versus fighting costs for the intruder c_i for high ($a_0 = 1$, solid line, filled circles) and low ($a_0 = 0$, dashed line, open circles) values of initial aggressiveness. Results are shown for different values of fighting costs for the intruder (top: $c_o = 0.1$; bottom: $c_o = 0.4$) 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.

306 4. Discussion

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

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

323 The results of our calculations concerning the selection on intrusion and defence
324 respectively partially confirm earlier studies. Similar to [20] and [21] we find that ter-
325 ritory defence can prevent intrusion by making it costly with defence becoming more
326 effective the higher the fighting costs and the weaker the effects of density dependence.
327 As previous studies on economic defendability [see 4] we see in our model that costs
328 and efficacy of defence, the gain in terms of reduction of competition and the amount
329 of intrusion influence economic defendability. The combination of both confirms our
330 expectations - without defence intrusion leads to the complete disappearance of terri-
331 toriality. High intrusion levels on the other hand make defence uneconomical.

332 A factor which surprisingly had barely any effect on the stability of territoriality
333 was the owner advantage in foraging rate. This is interesting since this has been seen
334 as one of the primary reasons for the respect of ownership by territorial neighbours
335 [28, 29]. At least partially this puzzling result might be explained by the fact that

336 the spatial distribution of resources within a territory is not represented in our model.
337 If we assume that intruders forage preferentially close to their own territory then the
338 depletion they cause will be concentrated in these areas which might make intrusion
339 less worthwhile.

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

349 If movement between territories is costly on the other hand frequent intrusion is
350 selected against and territoriality becomes stable. This effect certainly does play a
351 role in natural systems where territories are large or separated by uninhabited space
352 or where individuals start their foraging activities from a central point in the territory.
353 There are however also many examples where territories are tightly packed with no (at
354 least for the human observer) discernible interstitial space [e.g. 10, 11, 30, 31, 20]. In
355 these cases it is difficult to see why “switching” between territories should be costly.

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

361 In addition a decrease of detection rate while intruding can lead to a trade-off be-
362 tween intrusion and “guarding” the territory (a similar effect has been shown for mate-
363 guarding by [32]). This could in some cases stabilise territoriality.

364 In general our results show that the interactions between territorial neighbours are
365 economically relevant. This means that calculations of economic defendability of ter-
366 ritories [as done e.g. by 10, 33, 24] are incomplete in the sense that they have to be

367 complemented by an analysis which includes the expected intrusion rate by neighbours.
368 This might lead to very different results. For example, although our model predicts that
369 in the territorial case intruders into territories will always be attacked by the owner, the
370 actual level of intrusion still can vary a lot depending on resource production, fighting
371 costs and number of neighbours. In contrast to older models of economic defendability
372 against floaters [e.g. 33, 4], in our model even if defence is high individuals can there-
373 fore still lose considerable amounts of their resources to intruders without however that
374 this necessarily makes defence unprofitable. This might serve as an explanation for the
375 high levels of reciprocal pilferage found in some food-caching species [17, 34].

376 More generally our results show that floating intruders do not pose the only threat
377 to the maintenance of territoriality, an assumption which underlies most models of
378 the evolution of territoriality [12]. We see that interactions between neighbours “per
379 default” act as a force destabilising territoriality. In order to understand the factors
380 which determine the evolutionary stability of territoriality it is therefore necessary to
381 take the economics of interactions between neighbours into account. A theory of the
382 evolution of territoriality needs to be able to explain which mechanisms maintain the
383 partitioning of space between neighbours.

384 There are numerous possibilities to extend our basic approach.

385 There is a wealth of empirical information on the effects of resource properties such
386 as abundance, distribution or predictability [35]. It would be fairly straightforward to
387 take these into account in the simulation model and thus test whether our framework
388 can predict the observed correlations.

389 Our model is fairly simple in terms of “game-theoretic structure”. It has been
390 shown for simple conflict models that for example variations in fighting ability, access
391 to information about the opponent or the ability to change the behaviour in repeated
392 interactions can have tremendous effects on the outcome [e.g. 36, 37]. It can certainly
393 be expected that conflicts between territory owners are no exception to this.

394 Another very interesting area for future research will be to integrate our model with
395 other aspect of territorial behaviour. Additional processes which likely are tightly in-
396 terlinked with the direct competition between neighbours are the founding of territories
397 [38, 31], the emergence of territory borders [39, 40, 14], and the defence of territories

398 against floaters [41, 6, 8].

399 Finally, every theory requires empirical validation. A number of detailed data sets
400 on the energy budgets of foraging and territory defence for example for sunbirds [10],
401 honeycreepers [33] and wagtails [24] have been used to test the validity of classical
402 models of economic defendability. The same data could be used to calculate for exam-
403 ple the expected level of intrusion based on our model.

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

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503 **AppendixA. direction of selection for a**

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

$$\begin{aligned}
 w'_a &= (1-I)r'(1)N\frac{\partial \hat{I}_m}{\partial a} \\
 &\quad - c_o \left(I + aN\frac{\partial \hat{I}_m}{\partial a} \right) \\
 &= N\frac{\partial \hat{I}_m}{\partial a}((1-I)r'(1) - c_o a) - c_o I
 \end{aligned} \tag{A.1}$$

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

$$\begin{aligned}
 w'_a &> 0 \\
 \Leftrightarrow 0 &< N\frac{\partial \hat{I}_m}{\partial a}((1-I)r'(1) - c_o a) - c_o I \\
 \Leftrightarrow c_o \frac{I}{N} &< \frac{\partial \hat{I}_m}{\partial a}((1-I)r'(1) - c_o a) \quad \left| \frac{I}{N} = \hat{I}_m \text{ for } a = \hat{a} \right. \\
 \Leftrightarrow \frac{\hat{I}_m}{\frac{\partial \hat{I}_m}{\partial a}} &> (1-I)\frac{r'(1)}{c_o} - a
 \end{aligned} \tag{A.2}$$

505 With

$$\begin{aligned}
 \frac{\partial \hat{I}_m}{\partial a} &= -\frac{t_i \frac{\partial \hat{t}_{i,m}}{\partial a}}{(t_o + t_i)^2 N^2} + \frac{t_i \frac{\partial \hat{t}_{i,m}}{\partial a}}{(t_o + t_i)N} \\
 &= -\hat{I}_m^2 \frac{\partial \hat{t}_{i,m}}{t_i} + \hat{I}_m \frac{\partial \hat{t}_{i,m}}{t_i} \quad \left| \frac{\partial \hat{t}_{i,m}}{\partial a} = -vt_i^2 \right. \\
 &= -v\hat{I}_m t_i (1 - \hat{I}_m),
 \end{aligned} \tag{A.3}$$

506 we continue from A.2:

$$\begin{aligned}
& w'_a > 0 \\
\Leftrightarrow \frac{\hat{I}_m}{-v\hat{I}_m t_i(1-\hat{I}_m)} & > (1-I)\frac{r'(1)}{c_o} - a \\
\Leftrightarrow \frac{1}{t_i(1-\hat{I}_m)} - av & < (1-I)\frac{r'(1)v}{c_o} \\
\Leftrightarrow \frac{e+av}{1-\frac{1}{N}I} - av & < (1-I)\frac{r'(1)v}{c_o}. \tag{A.4}
\end{aligned}$$

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

$$e < \frac{e+av}{1-\frac{1}{N}I} - av \leq e + i \tag{A.5}$$

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

511 **Appendix B. no convergence stable a^***

512 Assuming a convergence stable point a^* , values of $a < a^*$ have to result in a
513 positive selection gradient whereas the selection gradient for values $a > a^*$ has to be
514 negative. Therefore condition A.4 has to be fulfilled for values smaller than and not
515 fulfilled for values greater than a^* .

A simple transformation of Eq. A.4 yields:

$$\frac{(1-I)\frac{r'(1)v}{c_o}}{\frac{e+av}{1-\frac{1}{N}I} - av} > 1 \tag{B.1}$$

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