

Respect for property rights: when does it pay to defend territory?

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ABSTRACT

Question: Should habitat-selecting individuals respect the property rights of territory holders or challenge them for ownership?

Definitions: Ideal despotic individuals challenge others for high-quality territories and defend them against rivals. Ideal pre-emptive individuals seek only unoccupied space and surrender it when challenged by despots.

Approach: Computer simulations of an evolutionary game between ideal despotic and ideal pre-emptive habitat selectors.

Features of the model: Individuals of each strategy choose between two habitats. Pure strategies grow for 1000 generations after which one individual possessing the alternative strategy is allowed to invade. If the invasion fails within 10 generations, invasion is attempted again with twice as many individuals (maximum of four attempts with 1, 2, 4, and 8 individuals respectively). Each simulation is repeated 99 times.

Ranges of key variables: Habitat quality: mean population growth rate = 1 vs. 1.5; standard deviation = 0.25; sampling effort = 10; defence costs = 0–0.5 in increments of 0.01; challenge cost = 0.02; search cost = 0.02; stochastic frequency = 2 or 3; stochastic mortality = 2–4.

Conclusions: The two strategies frequently co-existed. The pre-emptive strategy outperformed the despotic strategy. Pre-emptive individuals gained additional advantages when resident, and when defence costs were high. Thus, real populations of territorial species are rather likely to also exhibit mixed strategies where respect for property rights may trump overt conflict.

Keywords: co-existence, evolutionary game, habitat selection, ideal despotic distribution, ideal pre-emptive distribution, mixed strategies, territory.

INTRODUCTION

There is thus plenty of further scope for developing a theory of how conflicts over space are reflected in carrying capacities of environments and stability properties of populations. (López-Sepulcre and Kokko, 2005: 327)

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Individuals of numerous species occupy exclusive territories that they mark with scent, sound, and visual displays. The markings and displays are often described as mechanisms of territorial defence designed to dissuade invaders. Even so, territorial disputes are common in many species, and the outcomes can be manipulated by altering aggressiveness or fighting ability (e.g. Adams, 2001). But individuals of many other species appear to simply respect the proprietary rights of territory holders. Thus, we evaluate the conditions under which individuals should engage in territorial contests versus the conditions under which non-territory holders should simply search for unoccupied space in which to establish their own territory.

The vast literature on the evolution of territoriality typically addresses the problem of territory acquisition and retention as arising from solution of an optimality or game-theoretic analysis of the respective costs and benefits of territory defence (for a review, see Adams, 2001). A thorough understanding of the evolution of territoriality must also include the feedback from population dynamics onto the fitness payoffs associated with alternative territorial strategies (López-Sepulcre and Kokko, 2005). These population-dependent feedbacks onto strategies of territory defence versus acquiescence are embedded deeply in density-dependent habitat selection theory.

We begin with a short review of the two competing strategies of habitat selection that conjoin territorial behaviour with population density. These strategies represent the extremes of a continuum ranging from complete respect for territorial ownership (pre-emptive habitat selection) to overt aggression associated with territorial dominance and defence (despotic habitat selection). We then describe computer simulations that incorporate the three major elements expected from despotic habitat selection (López-Sepulcre *et al.*, 2010): (1) competition is targeted towards the best territories; (2) competition and territorial defence reduce fitness; (3) territorial conflict is associated with uneven spatial distributions of territory quality. We illustrate how the simulations differentiate between despotic and pre-emptive strategies, how we allow each strategy to stabilize before assessing whether it can be invaded by the other strategy, and how we incorporate stochastic dynamics. We are especially interested in determining whether the two strategies can co-exist with one another. If so, do the proportions of the overall mixed strategy vary with the cost of territorial defence and stochasticity? We conclude by discussing the implications of the simulations to our understanding of territoriality, habitat selection, and population dynamics.

TERRITORIALITY AND HABITAT SELECTION

Mechanisms of territorial behaviour are typically encapsulated in two related spatial distributions. The ideal-despotic distribution (Fretwell and Lucas, 1969) applies when individuals defend territories against rivals. Dominant individuals are assumed to occupy territories in habitat with the highest mean quality. Despots reduce the fitness expectations of all individuals that they encounter. Subordinate individuals are thus forced into habitat with lower mean quality and achieve lower average fitness than do their dominant neighbours.

Alternatively, individuals may seek territories of highest quality irrespective of which habitat such opportunities occur in [the ideal-pre-emptive distribution (Pulliam, 1988), also embedded in site-dependent habitat selection (Rodenhous *et al.*, 1997; McPeck *et al.*, 2001)]. Models of pre-emptive habitat selection imagine that individuals respect the territorial boundaries of others and search for unoccupied space in which to establish their own territory (Pulliam and

Danielson, 1991). Territory holders pre-empt occupation of the best sites and thus reduce the fitness expectations of subsequent individuals seeking their own territory. Unlike despotic individuals, pre-emptive habitat selectors do not reduce fitness through direct encounters. Individuals living in habitat with many high-quality territories will achieve higher mean fitness than will individuals living in habitats with fewer territories of high quality.

We know that territorial behaviour, in whatever guise, can either yield differences in mean fitness among habitats, or alter population dynamics and equalize fitness among habitats [as occurs in Seychelles magpie robins (López-Sepulcre *et al.*, 2010)]. But no-one has yet modelled the expected outcomes emerging from systems where both despotic and pre-emptive strategies compete for space. We imagine two scenarios under which pre-emption can yield higher fitness than despotism. First, if search costs are low between habitats with different distributions of breeding-site qualities (*sensu* Pulliam, 1988), individuals may be able to discover high-quality, unoccupied space in which to breed. Second, if the cost of territorial encounters is excessive, individuals who respect existing territories might achieve higher fitness by searching for unoccupied space. Respect for territory could evolve even if invaders can usurp existing territories. Having exhausted their advantage by winning a contest against the resident, they then lose to new rivals seeking the same advantage.

The potential of each scenario depends on density. If densities are low, space for potentially high-quality territories will be relatively common and easily encountered during search. Low density also implies high opportunity to find territories of near-equal quality to those already occupied. Resources might better be allocated to search (pre-emption) rather than to territorial defence and conquest. But if densities are high, the opportunity to find unoccupied space will be low, and resources might best be allocated to aggression even though encounters among individuals, and their cumulative costs, will increase.

Population density depends on, and feeds back onto, the fitness accrued by individuals. If mean fitness declines monotonically with increasing density, populations will converge towards either a constant density or towards some repeated pattern of densities through time. Few populations exist in such ‘constant’ environments. Most individuals live instead with stochastic variation that alters fitness and densities in both space and time. Any evaluation of respect for property rights must, therefore, include stochastic dynamics.

THE MODEL

We assess the densities attained by the two territorial strategies by modelling the behaviour of an asexual semelparous organism occupying a virtual landscape consisting of two habitats. The landscape is defined by frequency distributions of habitat quality. Each habitat comprises 500 breeding sites. Population size in each habitat is thus a direct measure of population density. An individual has sole use of the breeding site it occupies. Site quality is drawn from a normal distribution of net reproductive rates (R_0) that an individual will achieve by occupying a site. An individual’s fitness is reduced by costs associated with finding and defending breeding sites. The sequence of dynamics is recruitment followed by dispersal and stochastic mortality. The model updates population sizes once each generation.

Individuals search a minimum number of breeding sites sequentially, aspire to occupy a site that yields at least one descendant [aspiration level (Posch *et al.*, 1999)], and incur a cost (a deduction in site quality) for every site sampled (Table 1). Individuals assess occupied sites, but pre-emptive individuals do not evict occupants. We embed assessment costs (which

Table 1. Variables and parameter values used to simulate competition between ideal despotic and ideal pre-emptive habitat selectors choosing breeding sites of variable quality in two habitats

Variable	Definition	Parameter value
Mean A	Mean of normally distributed breeding sites in Habitat A	1
Dev A	Standard deviation of normally distributed sites in Habitat A	0.25
Mean B	Mean of normally distributed breeding sites in Habitat B	1.5
Dev B	Standard deviation of normally distributed sites in Habitat B	0.25
Sample	Initial number of breeding sites sampled	10
Search	Reduction in R_0 for each site sampled (search cost)	0.02
Defence	Reduction in R_0 caused by defending a site (ideal despotic only)	0–0.5 (0.01)
Challenge	Reduction in R_0 for each site contested (ideal despotic only)	0.02
Threshold	Maximum cost an individual can accrue (Search + Challenge)	1
Severity	Percent mortality drawn from a uniform distribution	2–4 (1)
Frequency	Frequency of stochastic mortality (from a uniform distribution)	2 or 3 (1)

Note: Values in parentheses represent the increments used during iteration.

may simply be deciphering olfactory, visible or audible cues) within those associated with searching for a site. Searching ends when an individual has found an available breeding site after searching the minimum number of sites, or when costs cumulate to a threshold value (cost threshold, fixed at 1 for these simulations).

In the first round of simulations, each pre-emptive individual searches the entire landscape for unoccupied sites. Upon reaching its cost threshold, the individual occupies the best unoccupied site found. If no empty sites were sampled, the individual remains in the final habitat it sampled as a non-breeding floater. Once ‘settled’, another randomly chosen individual begins its search under the same rules. The simulation ends when all individuals complete their search.

Ideal despotic individuals, and pre-emptive individuals in the second round of simulations, search similarly except that they sample sites from only the habitat that maximizes their expected fitness. If an ideal despotic individual samples an occupied site in which the resident accrued higher search costs than the searching contestant, the searching individual can usurp that site but must pay a confrontation cost to do so. The ousted individual accrues an appropriation encumbrance that is added to its cumulated search costs; it then resumes its search for a new site, subject to its cost threshold. If costs equal or exceed the threshold, the individual becomes a floater in the habitat it previously occupied. Costs thus reflect both density- and frequency-dependent processes of breeding-site selection.

Floaters do not occupy breeding sites, but do depress the fitness of all breeding individuals in the habitat by an amount proportional to their combined demand on shared resources. Each floater is assumed to consume enough resources to maintain itself without reproduction and thus reduces the summed R_0 achieved by all breeding individuals in the habitat by one. The assumption that all floaters have equal effect appears justified in our simulations because the number of floaters is always a minor proportion (usually zero) of total population size. If floaters become abundant, however, their combined effects are less likely to be additive, and the model would need to account for their cumulative influence on breeders’ fitness (for example, by including an appropriate floater \times breeder interaction term).

We calculated the expectation of fitness to be obtained by individuals in each habitat as the value of all unoccupied sites minus the number of floaters. This simple metric implicitly incorporates the density dependence of site availability and quality, as well as the density-dependent effects of floaters. For either strategy, if no site in the initial sample yields $R_0 > 1$, the individual continues searching until it finds such a site, or until it reaches its cost threshold. It then occupies the best-sampled and unoccupied site. If all sampled sites are occupied, the individual is classified as a non-territorial and non-breeding individual (floater; reduces the summed R_0 by one).

The simulations incorporate two phases: population growth and strategy invasion. In the population growth phase, pure populations of each strategy are initiated with 10 individuals, and grow in isolation from the other strategy, but in identical habitats. After all individuals select breeding sites (or habitats by floaters), both populations suffer identical stochastic mortality. The frequency and severity (percent) of stochastic mortality are drawn from separate uniform distributions where the maximum possible value varies among different simulations. The model then adds

$$\Sigma(R_i - c_i) - V_T \quad (1)$$

individuals to each habitat, where R_i is the value of a site occupied by breeding individual i , c_i is the total cost accrued by that individual (positive values of the term in parentheses are rounded down to ensure that only ‘whole’ offspring are recruited; negative values are rounded to zero because these individuals have no effect on the breeding success of other individuals), and V_T is the total number of non-territorial individuals in the habitat (non-territorial floaters depreciate mean fitness by pilfering occupied productive sites). Each simulation records population dynamics for 1000 generations.

The invasion phase is initiated immediately following population growth. The simulation begins with a single individual of one strategy invading the mean population size achieved during population growth by the alternative resident strategy (unless the resident strategy ‘fails’ during population growth, in which case its initial population size is set at 10). The first individual is chosen at random from the two strategies. Afterwards, the choice of invading individuals alternates between strategies. The invasion protocol thus limits the ability of whichever strategy is numerically dominant to monopolize access to the best sites available. If the invading strategy becomes extinct within 10 generations, it is reintroduced at twice the density (two individuals). This protocol repeats with four and then eight individuals if extinction recurs within 10 generations. The possibility for multiple invasion episodes reduces the likelihood of failure associated with single invaders as well as failures caused by strings of poor sampling choices, or during strings of stochastically high mortality. The invasion phase records the densities of each strategy for a total of 500 generations unless one or the other of the strategies becomes extinct. In this latter case, the simulation ends after 100 generations beyond the extinction event. We replicated each scenario 99 times (99 invasion scenarios for each strategy).

We began the first round of simulations by searching for a set of parameter values (Table 1) that reliably ensured persistence of both resident strategies for 1000 generations in stable environments (no stochastic mortality). Using these parameter values, we then explored the relative effects of variation in defence and challenge costs on population size. We did so because we assumed that these variables are the two that are most likely to influence a strategy’s relative population size. Differences in habitat quality, search costs, sampling effort, and cost thresholds interact to determine mean population size but have no

direct effect on a strategy's success relative to its competitor. Population sizes were far more sensitive to variation in defence costs than to variation in challenge costs, so all subsequent simulations varied only defence costs in stochastic environments (defence cost was varied from 0 to 0.5, mortality either 2, 3, or 4%, frequency of stochastic events either 2 or 3). All simulations were modelled with Python 2.5.

We summarized each pair of 99 simulations by calculating the mean population sizes (in the final generation) of both resident and invading strategies. The stochastic assignment of habitat quality and sampling resulted in several simulation attempts where the mean final population size of a strategy comprised 10 or fewer individuals. Although these populations persisted in our simulations, we deemed their habitat distributions as uncharacteristic of the simulations' intent, and also deemed their populations vulnerable to extinction. We eliminated these unusual occurrences and ranked the remaining densities from smallest to largest. We then calculated the number of times the two strategies co-existed as well as the number of occurrences where only a single strategy persisted. We assessed whether the frequency of strategies depended on input factors and their interactions with stepwise logistic regression. We used multiple linear regression to provide insight into a parsimonious model capable of predicting density [dependent variable = rank density, independent variables = defence cost plus indicator variables for the type of habitat selection strategy (ideal-despotic, ID; ideal pre-emptive, IP), whether the strategy was resident or the invader, as well as the severity and frequency of stochastic mortality and their interactions]. We confirmed the selection of variables by contrasting Akaike's Information Criterion (AIC) in a GLM assessing differences in rank density. We selected the model with the lowest AIC to best represent the data if the next highest AIC increased by at least 2, otherwise we chose the model with the fewest number of parameters (Burnham and Anderson, 2002). All analyses were conducted with IBM SPSS Statistics, v.20.

We were concerned that differences between strategies in search opportunities might mask the effects of dominance on a strategy's density. Despotic individuals sampled only the habitat with the highest mean territory quality while pre-emptive individuals sampled from both. We thus repeated the simulations (second round) where pre-emptive individuals also sampled only from the best habitat. Paired output from the two types of simulations was not significantly different for the parameter values we use here. Simulations using identical search strategies took much longer to complete, so we discontinued the comparisons and report results only from simulations where pre-emptive individuals sampled both habitats.

RESULTS

Persisting and co-existing strategies

The majority of 'populations' persisted over the entire 500 generations following invasion (703 of the 1224 possible; Table 2). The ideal pre-emptive strategy was far more likely to persist than was the despotic strategy (451 vs. 252 populations). In all instances but one, if the ideal despotic strategy persisted, so too did pre-emption.

Table 2. Co-existence, persistence, and extinction of two simulated habitat-selection strategies occupying two habitats with stochastic mortality

Strategy	Number of occurrences			
	Co-exist	Persists alone	Extinct	Total
ID _{Resident}	137	1	168	306
ID _{Invader}	114	0	192	306
IP _{Resident}	114	112	80	306
IP _{Invader}	137	88	81	306

Note: ID_{Resident} = ideal despotic resident, ID_{Invader} = ideal despotic invader, IP_{Resident} = ideal pre-emptive resident, IP_{Invader} = ideal pre-emptive invader.

Table 3. Results from a stepwise logistic regression analysis contrasting simulated ideal despotic (coded 1) and ideal pre-emptive habitat selectors choosing breeding sites of variable quality in two habitats undergoing stochastic variation in mortality ($\chi^2 = 54.5$, $P < 0.001$)

Variable	<i>B</i>	Wald	d.f.	<i>P</i>
Constant	0.30	4.45	1	0.035
Defence cost	-4.28	49.21	1	<0.001

Predictors of persistence

The probability of persistence by ideal despotic habitat selectors declined with increasing costs of territorial defence (stepwise logistic regression: $\chi^2 = 54.5$, $P < 0.001$; Table 3). No other simulation variable (residency, frequency, severity), or interaction, entered the model. Even though the model had low classification success (64.3%), it is nevertheless clear that despotic habitat selectors were more likely to persist when defence costs were low than when they were high (Fig. 1).

Population density

Ranked density depended on whether individuals used the despotic or pre-emptive strategy, whether they represented the resident or invading strategy, the severity of the stochastic effect, and the interaction between strategy and residency ($F_{5,697} = 301.38$, $P < 0.001$; Table 4). The mean values of ranked density for both indicator variables representing the stochastic effect were less than the grand mean (Severity3 = 269.4; Severity4 = 159.1; Grand Mean = 299.2). The ideal pre-emptive strategy consistently achieved a higher rank density than the despotic strategy. The resident strategy also achieved a higher rank density than the invading strategy, but this difference was associated mainly with ideal pre-emptive habitat selectors (Fig. 2).

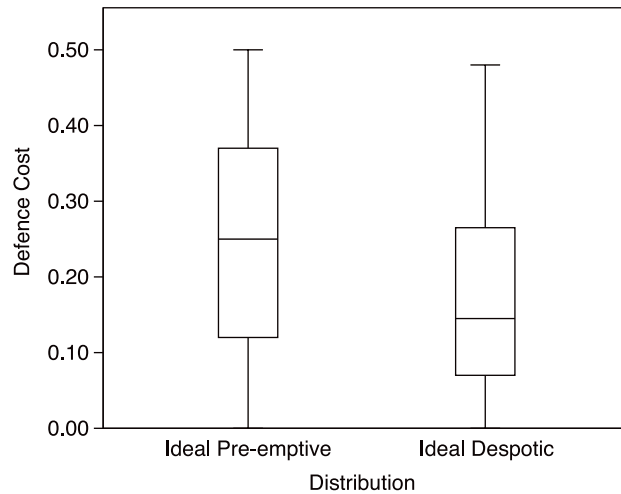


Fig. 1. Boxplots illustrating differences in defence costs between persisting populations of ideal despotic and ideal pre-emptive habitat selectors. Boxes delimit the first and third quartiles, whiskers detail the minimum (0) and maximum values, and the horizontal lines within boxes represent the median value.

Table 4. Comparisons among models predicting rank density (GLM)

Model	<i>F</i>	d.f.	<i>P</i>	AIC
Distribution + Residency + Severity3 + Severity4 + Distribution × Residency	301.38	5, 697	<0.001	2904.77
Distribution + Residency + Severity3 + Severity4 + Distribution × Residency + Distribution × Severity3 + Distribution × Severity4	220.45	7, 695	<0.001	2903.1
Distribution + Residency + Severity3 + Severity4 + Distribution × Residency + Distribution × Severity4	253.49	6, 696	<0.001	2904.68
Distribution + Residency + Severity4 + Distribution × Residency	367.04	4, 698	<0.001	2908.39
Distribution + Residency + Severity3 + Severity4	343.34	4, 698	<0.001	2922.06

Note: Indicator variables as follows: Distribution distinguishes ideal pre-emptive from ideal despotic habitat selection, Residency distinguishes the resident strategy from the invading strategy, Severity3 and Severity4 distinguish three levels of stochastic mortality (2%, 3%, and 4%), **bold font** = selected model.

DISCUSSION

Our simulations reveal several interesting outcomes. First, despotic and pre-emptive strategies co-existed across a broad range of parameter values. Second, respect for property rights (pre-emptive habitat selection) persisted more often, and at higher densities, than did territorial defence and aggression (despotic habitat selection). Third, the relative success (rank density) of each strategy was higher when it was the resident than when it was the

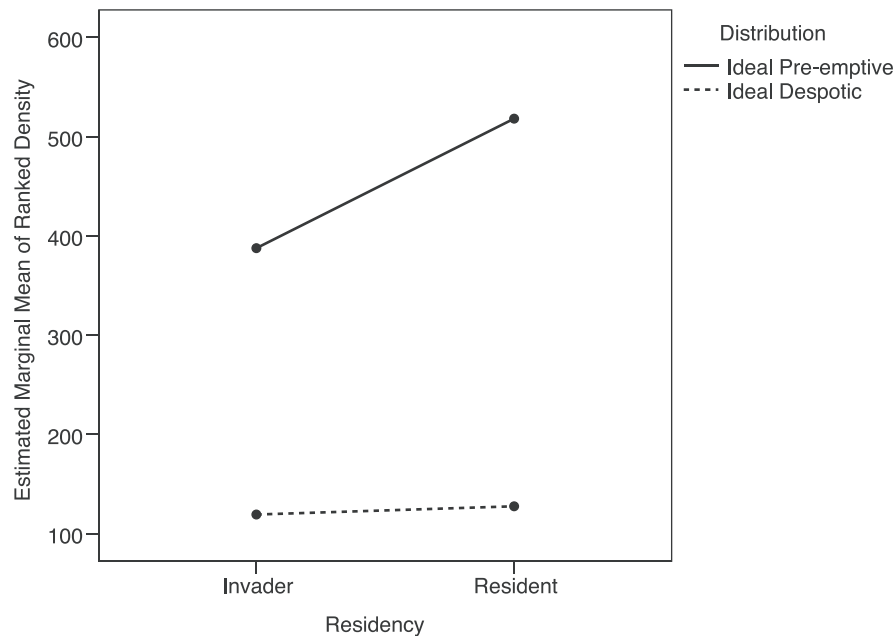


Fig. 2. Interaction profiles illustrating differences in mean ranked density between ideal despotic and pre-emptive habitat selectors when resident and invader.

invader. Fourth, the premium paid by being resident was greater for the pre-emptive strategy than it was for the despotic one. Fifth, the success of each strategy increased as the environment became more 'stable' (lower frequency of mortality). Finally, stochastic differences in the distribution of territorial quality in association with stochastic sampling by individuals can cause populations to fail (or to remain at very low density) even if the mean and variance of territory quality are held constant.

The implications for our collective understanding of territoriality, and its role in habitat selection and population dynamics, are rather profound. Although the strategies can co-exist, pre-emptive habitat selection appears capable of yielding substantially higher population size. Behavioural differences associated with habitat selection should thus be prominent additions to our increasing understanding of the interaction between behaviour and population dynamics (Pelletier and Garant, 2012; see also Morris, 1988, 1994). Differences among individuals in such traits as aggression, as well as tenacity to challenge for and defend sites, are likely to represent substantive differences in the way that individuals search for, and occupy, habitat. Site occupation may thereby often emerge through respect for property rights rather than through assessments of resident versus invader quality and 'power' (see also Kokko *et al.*, 2006).

Our results reinforce a variety of empirical studies documenting, in various ways, respect for territory ownership. Respect for ownership can be inferred, for example, when reproductive success depends on site, rather than on interference with neighbours. Such an effect is apparent from studies on goshawks (*Accipiter gentilis*) in Germany where fecundity was closely linked to territory quality rather than to density (Krüger and Lindström, 2001).

Respect for ownership can also be reinforced through cooperative defence. Neighbouring male African fiddler crabs (*Uca annulipes*) occasionally cooperate to repel floater males prospecting for territory (Detto *et al.*, 2010). Allies are much more likely when intruding floaters are smaller than the ally, and hence more likely to lose the contest. Benefit to allies appears to emerge as a by-product of reduced expectations of conflict with ‘the enemy you know’ rather than renegotiating territorial boundaries with a new adversary (Detto *et al.*, 2010). The way in which such coalitions yield respect for ownership has been well documented in the related Australian fiddler crab (*Uca mjoebergi*). Attempts by floaters to usurp existing territories are far more frequent when nearest neighbours of opponents are smaller than the floater than when they are larger (Milner *et al.*, 2011).

Perhaps the most important outcome from our simulations is the likelihood that territoriality exists as a mixed strategy that varies with the severity and frequency of stochastic events. Differences between male and female fiddler crabs in burrow acquisition (Milner *et al.*, 2010) may represent such a mixed strategy. Male fiddler crabs typically challenged residents for burrows whereas females acquired empty ones. Despite different strategies for acquiring burrows, there was no difference between the sexes in the distance travelled, time taken to acquire a burrow, or the number of burrows visited. Although these results are from only a single study on one species, it is somewhat intriguing that the two sexes (and strategies) appear to possess equal sampling effort as assumed in our simulations.

Mixed strategies are predicted by extensions of hawk–dove games with population-dynamic feedback where ‘floaters’ can either contest territory or wait for new territories to become available (Kokko *et al.*, 2006). Mixed strategies can emerge, for example, through negative frequency-dependent selection on floaters. If mortality increases with aggression in floaters, then queues for vacant territories are shortened for non-aggressive individuals (Kokko *et al.*, 2006).

By way of comparison, our modelling approach may appear, superficially, to yield mixed strategies only because it contrasts two fundamentally different mechanisms of habitat selection. More appropriately, one should view the pre-emptive strategy as one end of a continuum of territorial behaviour (respect ownership) that grades into various degrees of despotism (increasing challenge and defence costs). Indeed, many assessments of site-dependent population regulation mention, or imply, only the despotic strategy (Kokko *et al.*, 2004; Ridley *et al.*, 2004; Nevoux *et al.*, 2011). What is most important, however, is that both approaches predict respect for ownership.

The clear priority effect associated with being the resident strategy is non-intuitive and interesting. We suspect that it is associated almost entirely with pre-emption. When the despotic strategy is resident, the population stops growing at a relatively small size because the cumulative sampling and challenges for territory exhaust the potential to find the few remaining sites of superior quality. Invading pre-emptive individuals are faced with a landscape where the best territories are mostly occupied and thus unavailable (and not invasible). Nevertheless, invaders occupy a large number of lower-quality breeding sites, which allows their population to increase. Despotic individuals retain their population size because each individual can, on average, attain a site where it replaces itself.

When the pre-emptive strategy is resident, the population grows to a higher density because individuals can occupy the highest quality sites that would otherwise be usurped by despots. The pre-emptive strategy can then maintain its relative numerical advantage by occupying many sites with low quality ($1 < R_i < 2$). But why cannot the invading despotic strategy increase to the same density as it did when resident? Recall that the simulation

provides an equal and rotating opportunity to each strategy during the invasion phase. When invading the pre-emptive strategy, despots are forced, on average, to mount twice as many potential challenges for territory as they did when resident at the same density. Challenge exhausts their ability to search for more productive sites and similarly reduces recruitment from the territories they currently hold. The end result is somewhat lower recruitment and reduced population size at equilibrium.

Our simulations highlight that population success is itself very much a stochastic process that can result in failure to invade or occupy otherwise highly suitable environments that yield large and persistent populations for the same distributions of territory quality. This final point may help to explain why populations of some species fail to recover from low density, and why species re-introductions either fail or succeed (Griffith *et al.*, 1989; Fischer and Lindenmayer, 2000), often under apparently similar conditions.

We echo López-Sepulcre and Kokko's (2005) prescient call for further theory on the connection between conflicts over space and population dynamics. We also believe that there is high potential to further explore the consequences with existing theory. We do not yet know, for example, how different distributions of site quality might influence the relative success of despotic versus pre-emptive strategies, or how those distributions might interact with the intensity and frequency of stochastic variation in mortality. We also need to explore more deeply the parameter space that underlies models of site selection. Although we have much more to learn, and more difficult models to explore, we are encouraged that at least one other research team has used simulation and experiment to confirm ideal pre-emptive habitat selection [in mottled sculpins (Petty and Grossman, 2009)]. We are even more encouraged to know that relatively simple models of habitat selection can yield rather substantial insights into the joint stability of conflicts for space and population dynamics.

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