

Territorial Defense, Territory Size, and Population Regulation

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ABSTRACT: The carrying capacity of an environment is determined partly by how individuals compete over the available resources. To territorial animals, space is an important resource, leading to conflict over its use. We build a model where the carrying capacity for an organism in a given environment results from the evolution of territorial defense effort and the consequent space use. The same evolutionary process can yield two completely different modes of population regulation. Density dependence arises through expanding and shrinking territories if fecundity is low, breeding success increases gradually with territory size, and/or defense is cheap. By contrast, when fecundity is high, breeding success sharply saturates with territory size, and/or defense is costly, we predict fixed territory sizes and regulation by floaters. These “surplus” individuals form a buffer against population fluctuations. Yet floaters can also harm breeder performance, and by comparing population growth of a territorial population to a nonterritorial (and individually suboptimal) alternative, we can quantify the harmful effect of evolutionary conflict on population performance. Territoriality has often been found to increase population stability, but this may come at a cost of reduced equilibrium densities.

Keywords: carrying capacity, evolutionarily stable strategy (ESS), floating, intruder pressure, population regulation, territoriality.

Many populations are ultimately limited by resources, and their abundance and distribution will determine the carrying capacity of an environment. Whenever a larger share

of resources leads to higher fitness, individuals should aim to secure resources for themselves, often excluding others through the defense of a territory (reviewed in Stamps 1994; Adams 2001).

What determines the carrying capacity for territorial populations? This question has, surprisingly, remained unanswered to date, despite the fundamental importance of the concept of carrying capacity in ecology and the large number of species that exhibit territorial behavior. One case that allows a fairly straightforward prediction is an environment that features a fixed, limited number of essential items needed for reproduction, such as nest cavities (Both and Visser 2003). In such a case territory sizes are relatively insensitive to the number of animals (von Haartman 1956; Dhondt et al. 1982), and the equilibrium number of breeders may simply equal the number of sites. The exclusive defense of such sites by some individuals forces the rest to form a population of nonbreeders, which are often called floaters (especially in bird studies; see, e.g., Smith and Arcese 1989; Zack and Stutchbury 1992).

However, in many cases potential habitat is more or less continuous, and it is less clear how the feedback between population numbers and space division should evolve. In such a case it is still possible that populations are regulated through the production of floaters. As early as a century ago, Moffat (1903) pointed out that an increasing population produces more floaters, and since these do not breed, the average per capita growth rate decreases. This results in density dependence (Hunt 1998). Floaters can further decrease population growth by interference, conflict, or direct disturbance, as shown, for example, in the ayu fish *Plecoglossus altivelis* (Iguchi and Hino 1996), red squirrels *Sciurus vulgaris* (Wauters and Lens 1995), and several species of birds (Hansen 1987; Arcese et al. 1992; Jenkins and Jackman 1993; Komdeur 1996). Aggressive behavior of breeders can also decrease the carrying capacity of the environment (Mougeot et al. 2003).

However, population regulation through “floating” is not necessarily the only option. In species such as the great tit *Parus major* and juvenile steelhead trout *Oncorhynchus mykiss*, it has been shown that increasing the number of competitors decreases the area that each individual occupies (Both and Visser 2000; Keeley 2000). This appears

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to be a general pattern in many taxa (Fryxell and Lundberg 1997; Adams 2001). Typically, space becomes divided as floaters establish new territories in the boundary zones of established breeders. For example, red-winged blackbirds *Agelaius phoeniceus* acquire territories by being attracted to areas in which current ownership is disputed (Beletsky 1992). Likewise, in oystercatchers *Haematopus ostralegus*, floaters can acquire territories by squeezing a small territory among the already existing territories and then expand their boundaries (Heg et al. 2000). Juvenile *Anolis aeneus* lizards win space by persisting in the occupation of areas that already belong to other territories (Stamps and Krishnan 1995). These examples illustrate the dynamic nature of territory boundaries in some species.

Thus, it is not straightforward to predict how population regulation will function in a territorial species. Given a homogeneous area of say, a forest, will a population consist of territories of fixed size, with surplus individuals being forced to remain as nonbreeders (as, e.g., in red squirrels *Tamiasciurus hudsonicus*; Boutin and Schweiger 1988)? Or, will territory boundaries be more flexible, so that in larger populations a surplus individual will be able “squeeze” its way to become a breeder by forcing others to occupy a new territory in the area (as in the red-winged blackbirds and the oystercatchers)? This can also regulate the population because diminishing average territory size must eventually lead to poorer reproduction for each breeder (Adams 2001).

The numbers of both breeders and floaters will depend on the number of territories and the reproductive output of the pairs defending them, and this is very likely to be influenced by territory size (either directly through resource availability or indirectly by the costs of defending the area against a particular intruder or neighbor pressure; Fryxell and Lundberg 1997; Adams 2001). Understanding the evolution of division of space in territorial species—which at the behavioral level means investigating the evolution of various defense strategies—is thus important for gaining insight into the regulation of their populations.

It is important to note that the payoffs of different defense strategies are dynamic; that is, they must change with the demographic structure of the population. For example, the costs of spending effort on defending a particular area will depend on the number of floaters attempting to acquire a territory (Chapman and Kramer 1996). Simultaneously, the production of floaters, and hence their equilibrium number, will be influenced by the size of the territory that breeders are able to defend, if breeding success depends on the resources available to a breeder (Adams 2001). Including the feedback between population structure and evolutionary payoffs is therefore crucial for understanding the evolution of territoriality.

Despite all this, most theoretical studies on territory size

are based on static optimality models and do not consider the interaction between behavior and population dynamics (review in Adams 2001). Although some models on the evolution of territorial and floating behavior have been produced by combining both evolutionary invasion criteria with the population-wide dynamics (Kokko and Sutherland 1998; Pen and Weissing 2000; Kokko et al. 2001), they have all assumed a given set of fixed territories and do not deal with the issue of division of space itself. Stamps and Krishnan (1999, 2001) modeled territories with flexible boundaries, but they did not consider the fitness consequences of spacing behavior. This gap was, in turn, filled by Morrell and Kokko (2003), but their study did not include the full dynamic feedback between individual resource use and population dynamics. Ridley et al. (2004) modeled a population of Seychelles warblers *Acrocephalus seychellensis* incorporating territory compression as an adaptive response to increasing population density. Our aim in this article is to produce a more simplified and general model that illustrates the evolution of territory size in a dynamic way and explores its consequences to population regulation, both in the case where floaters do not cause direct disturbance and in the case when they do.

Modeling Optimal Defense Effort and Territory Size

We consider a population living in a homogeneous habitat where individuals can either defend a territory and breed or float. This simplification excludes species with offspring retention (e.g., helping behavior). Some earlier models have shown that floating, instead of breeding, can be an adaptive decision if the available habitat is of low quality (Kokko and Sutherland 1998; Pen and Weissing 2000; Kokko et al. 2001). Our focus here is on a case where the population inhabits an area of continuous habitat that does not vary in quality, and consequently we do not expect floaters to appear in the population unless they have no possibility to get a territory of their own. That is to say, floating in this model is not an evolutionary decision (see Smith and Arcese 1989). Instead, to study the division of space into territories, we concentrate on the evolution of the defense effort of territory owners. We do not assume fixed territory sizes but let them evolve as a result of individual defense effort, denoted d , and the consequent dynamics of the population.

The effort d defines the defense effort against both neighbors and floaters. With respect to neighbors, the value of d (relative to that of the individual's neighbors) defines the pressure the owner exerts on its neighbors, such that an individual whose defense effort is, for example, 20% larger than that of its neighbors will maintain a 20% larger territory (see the appendix for a mechanistic

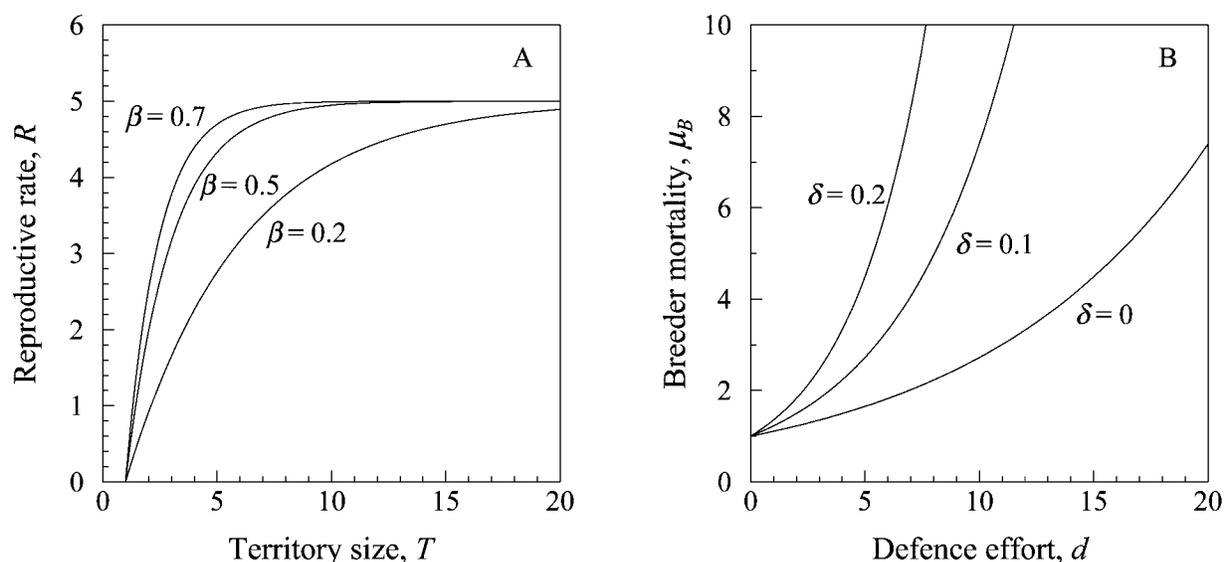


Figure 1: Model assumptions. A, Reproductive output R as a function of territory size T , from equation (1), with $\alpha = 5$ and $\beta = 0.2, 0.5$, and 0.7 . B, Mortality of breeders μ_B in relation to defence effort d , from equation (2), with $\gamma_0 = 0.1$ and $\delta = 0, 0.1$, and 0.2 .

justification). Simultaneously, d equals the minimum territory size defended against floaters: if its territory has size d , the owner is assumed to be able to exclude any intruders, and thus its territory cannot shrink below the size d .

Aggressiveness is often higher toward floating intruders than toward stable neighbors (Wilson 1975). Implicitly, our model includes this difference, as the effects of aggressiveness d are different toward neighbors (that are never driven away) than toward floaters. For simplicity, however, we exclude the evolution of aggression toward neighbors that is not accompanied by a corresponding change in aggression toward floaters (see “Discussion”).

We assume that floaters do not take over existing territories unless there is a vacancy after the death of the breeder. Instead, new territories can form when floaters “squeeze” themselves into the available habitat, thereby diminishing the space available for established breeders. This process, whereby floaters become breeders and territory sizes shrink, carries on until there are no floaters left in the population or territories reach the minimum size, determined by d , below which further intrusions are impossible. Thus, for a given population size n , territory sizes T will obey

$$T = \begin{cases} \frac{A}{n} & \text{if } \frac{A}{n} \geq d \\ d & \text{if } \frac{A}{n} < d \end{cases}, \quad (1)$$

where A is the total area of available habitat (the resource). We scale territory area such that $T = 1$ is the smallest area allowing any reproduction to occur. We model reproduction and death as continuous processes, so floaters may acquire territories and start breeding at any time.

To arrive at an equation for fitness of breeders, we must first specify the reproductive output of each breeder. In territorial animals, it is reasonable to assume that reproductive output R increases with territory size (Koenig 1990; Fryxell and Lundberg 1997; Both and Visser 2000) and that there is a minimum size (here $T = 1$) below which reproduction is impossible. Reproduction can thus be described by the following equation of diminishing returns:

$$R(T) = \begin{cases} \alpha[1 - e^{-\beta(1-T)}] & \text{for } T > 1 \\ 0 & \text{for } T \leq 1 \end{cases}. \quad (2)$$

Here, reproduction R increases asymptotically with territory size T toward a maximum value α . The parameter β describes how quickly reproduction saturates with increasing territory size (fig. 1A). At small values of β , reproductive output increases gradually with territory size. High values of β represent cases in which small territories are sufficient to yield high reproductive output, and thereafter increasing territory area yields little benefit (i.e., resources cannot be gathered from a large area even if this was available to a breeder).

We next need to define mortality rates of individuals.

Floaters do not make evolutionary decisions in our model, so their mortality rate μ_F can be assumed to be constant regardless of their behavior (in other words, μ_F includes any effects that competition for breeding sites has on floater mortality). For breeders, however, we assume that mortality depends on defense effort (Hammerstein and Riechert 1988):

$$\mu_B(d) = e^{\gamma(d)d}, \quad (3)$$

where μ_B is the instantaneous mortality rate of a territory owner (breeder), and $\gamma(d)$ describes the costs of defense (fig. 1B). Note that mortalities may exceed unity, which is simply a matter of scale: in a continuous time model, this means that the expected life span is <1 time unit long.

The total lifetime reproductive success (LRS) for an individual can be calculated by multiplying the reproductive rate by the expected life span. In a continuous-time model, life span equals the inverse of mortality. Therefore, combining equations (2) and (3), we get

$$\text{LRS}(T, d) = \frac{R(T)}{\mu_B(d)}. \quad (4)$$

According to equation (4), individuals would maximize their reproductive success by increasing territory size while spending the minimum defense effort. However, not every combination of T and d is possible since territory size is dependent on defense effort. Thus, below we will derive their relationship from the population dynamics.

To finish describing the model, we allow for the possibility that the costs of defense effort increase with the number of floaters (i.e., potential intruders) per territory, as has been shown to be the case in some empirical studies (e.g., Myers et al. 1979; Norton et al. 1982; Eberhard and Ewald 1994). We therefore assume the following relationship between the cost of defense $\gamma(d)$ and numbers of floaters and breeders:

$$\gamma(d) = \gamma_0[1 + \delta x(d)]. \quad (5)$$

Here γ_0 describes the baseline cost of defense, that is, the cost when there are no floaters in the population, and owners defend only against territorial neighbors. The parameter δ describes the effect of floaters on defense costs, and it scales how quickly defense costs increase with the number of potential intruders per breeder. The term $x(d)$ represents the ratio between the number of floaters n_F and the number of breeders n_B , which depends on defense effort d . Before we consider the evolutionary stability of particular values of d , we must specify the dynamics of a population in which a value of d is in use.

Population Equilibrium

Given a population with defense effort d , three scenarios are possible. (i) Breeder mortality μ_B falls clearly below per-breeder reproduction R , creating a population of surplus individuals. These individuals acquire territories by squeezing into the available space, until territory sizes decrease to the point where $T = d$, and no more “squeezing” is possible. The remaining surplus individuals cannot acquire territories and form a floating population. (ii) At relatively high values of μ_B , equilibrium population sizes are small and a newborn floater will always be able to form a new territory within the sparse network of existing territories. At equilibrium, territories are larger than the minimum dictated by the defense effort d and the equilibrium territory size is not determined by the presence of floaters, but by the size that balances death and recruitment. (iii) Breeder mortality μ_B is high, and therefore the population becomes extinct.

We need to establish which of these states will be met when the population reaches equilibrium. At equilibrium, there is no net growth (dn/dt) of the population, so we can define the following equality:

$$\frac{dn}{dt} = R(T)n_B - \mu_B(d)n_B - \mu_F n_F = 0, \quad (6)$$

where n_B and n_F are the number of breeders and floaters at equilibrium, respectively, and μ_B and μ_F are their mortality rates.

Scenario (i), where population sizes are regulated by the existence of floaters and $T = d$, will be met whenever the number of floaters n_F is positive at equilibrium. This occurs when breeder mortality at $T = d$ is too low to allow for all new individuals to find space to breed:

$$\mu_B = e^{\gamma(d)d} \leq \alpha[1 - e^{\beta(1-d)}]. \quad (7)$$

If breeder mortality is higher, so that inequality (7) is not met, there will be no floaters (scenario [ii]) and therefore, T will exceed d . Setting $n_F = 0$ in equation (7),

$$\frac{dn}{dt} = R(T)n_B - \mu_B(d)n_B = 0, \quad (8)$$

and substituting $R(T)$ and $\mu_B(d)$ (eqq. [2], [3]) to obtain the equilibrium territory size T for the case without floaters:

$$T = 1 - \frac{\ln[1 - e^{\gamma(d)d/\alpha}]}{\beta}. \quad (9)$$

Density dependence in this case occurs through territorial

size adjustment: if the population grows, new recruits squeeze into the available space, thus decreasing reproductive success of all individuals by diminishing territory size. This process is possible if breeder mortality falls between $\alpha[1 - e^{\beta(1-d)}]$ and α . But if the condition

$$\mu_B = e^{\gamma(d)} \geq \alpha \quad (10)$$

applies, mortality exceeds highest possible reproduction α , and the population becomes extinct. In this case, territory size (eq. [9]) has no solution in the domain of real numbers.

To summarize our first result: when the mortality of breeders μ_B fulfills condition (7), populations are regulated by floaters, while territories stay fixed in terms of size and number. When breeder mortality lies between $\alpha[1 - e^{\beta(1-d)}]$ and α , density dependence operates by regulating the size and number of breeding territories. And if mortality is too high (condition [10]), the population is not viable.

The inequalities (7) and (10) include the defense effort d used by the population, which means that the mode of population regulation may be influenced by the evolution of defense strategies. These equations do not yet state, however, whether evolution can produce such a diversity of regulation patterns, that is, whether optimal values of d will fall into different regions described by inequalities (7) and (10) or maybe only one of them. We therefore next consider which values of d will be evolutionarily stable.

Evolutionary Stability

The reproductive value of a breeder v_B changes over time as

$$\frac{dv_B}{dt} = Rv_0 - \mu_B v_B, \quad (11)$$

where v_0 is the reproductive value of a newborn individual (for a justification of this method, see, e.g., Härdling et al. 2003). At equilibrium, $dv_B/dt = 0$; hence

$$v_B = \frac{R}{\mu_B} v_0. \quad (12)$$

A mutant can invade if its reproductive value exceeds that of a member of the resident population (Dieckmann 1997). Because a breeder is not assumed to be able to change its offspring's success (v_0) but it can change their number, mutants that produce higher values of R/μ_B can invade. Thus, this is our fitness measure (equivalent to $LRS[T, d]$; eq. [4]).

The evolutionarily stable defense effort $d^*(\alpha, \beta, \gamma_0, \delta, \mu_B)$ for a population with given mortalities and parameters for $LRS(T, d)$ can be calculated using pairwise invasibility plots (Dieckmann 1997; Geritz et al. 1998). These plots show whether a mutant individual that follows strategy d_m in a population of individuals that follow strategy d_p has higher fitness than the other individuals of the population. If it does, the mutant strategy can spread (indicated as a positive sign in the plot); if it does not, its strategy is selected against (negative sign). This is calculated for every possible combination of population and mutant strategies. The points where two zero contour lines intersect—one of them being the obvious 45° line, where mutant and residents use the same strategy—are singular points, that is, possible endpoints of evolution. For a singular point to be an evolutionarily stable strategy (ESS), any vertical derivation from it should give a lower fitness (i.e., negative sign). Figure 2 shows two examples of pairwise invasibility plots for our model and the resulting breeder and floater numbers for the different candidate strategies d .

Density Dependence and Equilibrium Population Sizes

One of the aims of this article is to evaluate the population consequences of individually optimal territorial behavior. We assess how territoriality influences the carrying capacity of an environment for a species by comparing the population dynamics of a territorial species to that of a hypothetical nonterritorial species. In this comparison, both species have an identical relationship between resource use and reproduction (i.e., equal values of α and β).

We assume that the territorial species divides space according to the evolutionarily stable defense effort d^* , using the same value at any population size (note that this may still lead to different territory sizes depending on the actual number of competitors, as shown in eq. [1]). This is a simplifying assumption, and one could argue that populations may have evolved a reaction norm to varying population densities (Clark and Yoshimura 1993), so that they adjust their defense effort to local circumstances. Despite this, the slope of density dependence around the equilibrium is likely to be similar under both scenarios.

In the territorial species, for each population size n , we first calculate the equilibrium defense effort d^* . Territory size T is then derived from equation (1) for each population size n . The number of breeders n_B (i.e., number of territories) will be the total available area A divided by the territory size T ($n_B = A/T$), and the number of floaters can easily be obtained by subtracting the number of breeders from the total population size n ($n_F = n - n_B$). The equilibrium population size is that at which net growth of the population is 0.

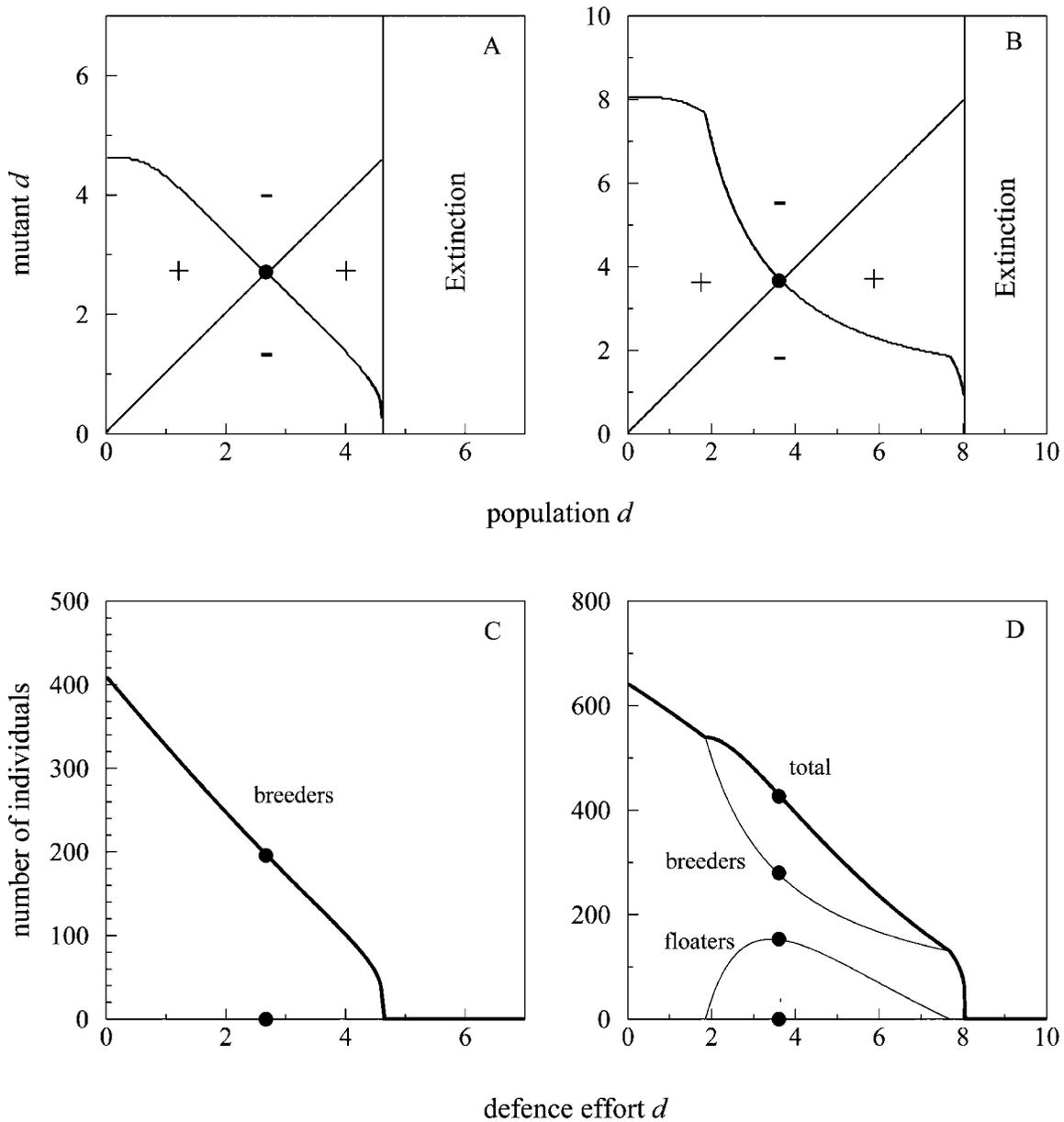


Figure 2: A, B, Two examples of pairwise invasibility plots that yield the ESS defense effort d^* . C, D, The corresponding equilibrium population sizes that result from a range of values of d . In A and C, the ESS strategy $d^* = 2.67$ produces no floaters, and territory size is determined by breeder-breeder interactions only (in this case, $T^* = A/n_b = 5.07$). In B and D, floaters are produced, and territory size $T^* = d^* = 3.65$ is limited by floater pressure to acquire a territory. The dots indicate the ESS defense effort d^* (A, B) and its population consequences (C, D). Note that the resulting ESS does not maximize the carrying capacity (equilibrium number of individuals), which would instead occur if territory defense was absent ($d = 0$). Parameters used are as follows: in A and C, $\alpha = 4$, $\beta = 0.2$, $\gamma_0 = 0.3$, $\delta = 0.1$, and $\mu_F = 2$; in B and D, $\alpha = 5$, $\beta = 0.4$, $\gamma_0 = 0.2$, $\delta = 0.1$, and $\mu_F = 2$. In all cases, $A = 1,000$.

In the nonterritorial species, we assume that a population size of n individuals simply leads to each individual gaining access to resources that occur in a fraction A/n of the total area A , and reproduction then follows according

to equation (2). We call this the “equal-share scenario” and note that it does not describe individually optimal behavior. We are interested in this scenario simply to quantify the effect of territorial behavior on population dy-

namics. In the equal-share scenario, individuals obviously do not pay any costs of territorial defense, nor do they gain any of its benefits.

Results

Evolutionarily Stable Territory Size

High reproductive rates (α and β) and high costs of defense (γ_0 and δ) result in small defense effort, yielding small equilibrium territory sizes (fig. 3). This makes intuitive sense: costs of defense influence the trade-off between the benefits of obtaining a larger territory, and the negative relationship between γ (or δ) and territory size is particularly easy to explain. With the reproductive parameters α and β , a negative relationship may appear less intuitive, since high α and β both increase the reproductive benefits of occupying a territory of a given size. This highlights the importance of population dynamics as a determinant of fitness payoffs: if populations grow faster when territory sizes are big, territory defense becomes more costly because of stronger competition, while simultaneously a small territory becomes sufficient to yield adequate reproductive output. Furthermore, high values of the parameter β imply a steep relationship between territory size and reproductive rate (fig. 1A); thus, claiming an ever-larger territory is of little benefit. Likewise, low mortality of floaters (small μ_F) increases the number of floaters in the population (not shown). This causes a re-

duction in evolutionarily stable territory sizes when floaters influence defense costs ($\delta > 0$; eq. [5]).

Population Regulation

Interestingly, the same process of optimal territory defense (fig. 3) can create two completely different types of population regulation. For example, when α and β are high and small territory sizes are sufficient to yield high numbers of individuals, the evolutionarily stable defense equilibrium describes individuals occupying small territories at high population density. At this density, not all individuals can obtain a territory. The surplus individuals remain floaters that attempt to gain a breeding area. The larger the surplus, the more individuals remain nonbreeding, and the population obeys regulation by floaters while territory size remains fixed.

Alternatively, if reproduction is low and/or is not rapidly enhanced by increasing territory size (low α , low β), the total breeding space (A) becomes divided among all individuals, and equilibrium population sizes are smaller. In this case, territory size and, therefore, population growth are limited only by breeder-breeder interactions: small population sizes yield large territories and good per capita reproductive output, which then results in the new recruits squeezing into the available space. This process balances when territory size has shrunk to a point where reproduction exactly balances mortality. Floaters do not appear during this process, as territory size has not diminished to the

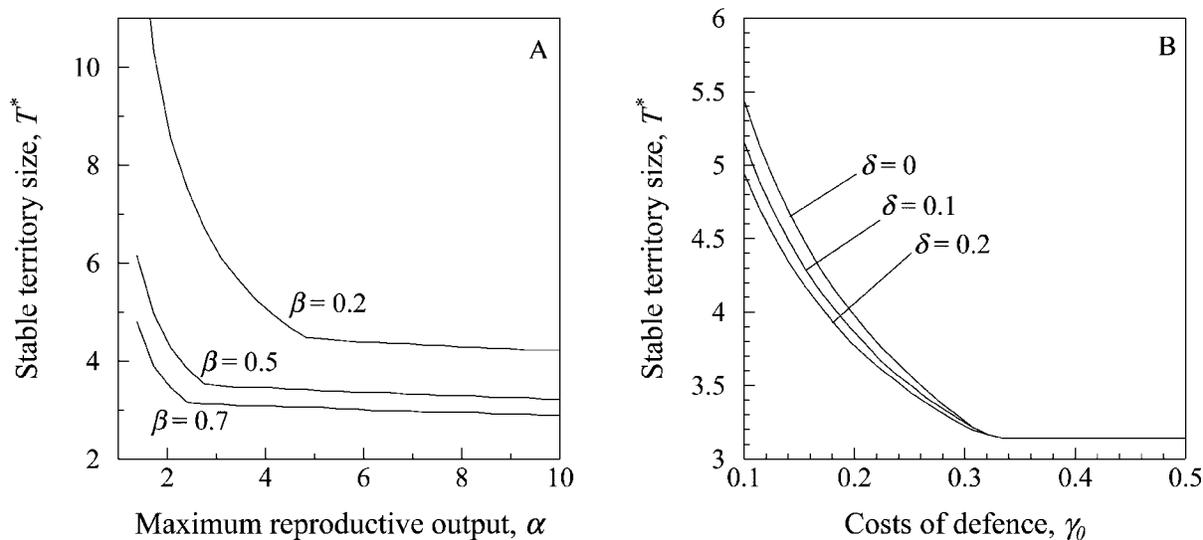


Figure 3: Evolutionarily stable territory sizes T^* resulting from the ESS defense effort d^* for different parameter values. A, Maximum reproductive output α for $\beta = 0.2, 0.5$, and 0.7 , $\gamma_0 = 0.2$, $\delta = 0.1$, and $\mu_F = 2$. B, Costs of territory defense γ_0 for $\alpha = 6$, $\beta = 0.3$, $\delta = 0, 0.1$, and 0.2 , and $\mu_F = 2$.

minimum dictated by evolutionarily stable territorial defense. We call this alternative regulation by breeders.

When costs of defense γ_0 are high, the parameter region where regulation occurs by breeders increases; that is, larger values of α and/or β are required to cause the switch to regulation by floaters (fig. 4). This is because higher costs result in higher mortality of breeders μ_B (eq. [3]), and therefore, territory vacancies occur more frequently and floaters can obtain breeding positions faster; thus this process more easily leads to a situation where the population runs out of floaters.

Carrying Capacity as an Outcome of Territorial Conflict

When comparing a territorial system resulting from optimization of individual behavior with an individually suboptimal equal-share scenario, equilibrium population sizes differ. Thus, territoriality has an effect on the carrying capacity of an environment. Interestingly, in most cases territoriality yields lower population sizes than a nonterritorial system (see fig. 5 for examples). This shows that conflict over space use often leads to suboptimal performance of a population, even though we do not consider

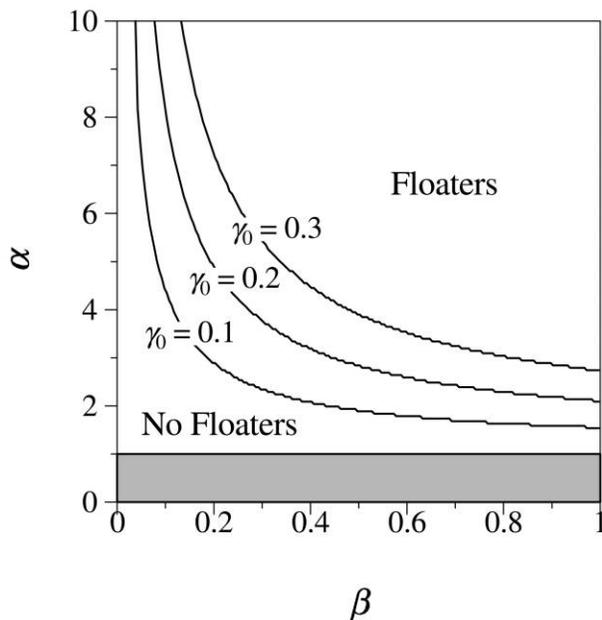


Figure 4: Two modes of population regulation can result, depending on parameters α , β , and γ_0 . High values of the three parameters produce floaters that limit population growth by attempting to obtain a territory. Where parameter values are low, no floaters are produced, and territory sizes and population growth are limited only by breeder-breeder competition. The solid lines indicate the transition between two modes of regulation for three values of γ_0 (0.1, 0.2, and 0.3). The shaded area indicates extinction.

spiteful “superterritoriality” (Knowlton and Parker 1979). Territoriality benefits the fraction of the population that manages to secure a breeding position, but overall population growth is reduced (fig. 5). However, this is not a universal truth. For highly fertile populations (high values of α , β) where territory defense is cheap (low values of γ_0), a territorial system may produce larger populations than a nonterritorial one (fig. 5C).

The equilibrium population size of a territorial species also depends on the effect of floaters on defense costs δ , while there is no such relationship in a nonterritorial species (that obviously does not pay such costs; fig. 6). When floaters exist and decrease breeder survival through interference or aggressive interactions (large δ), population sizes often reduce further, indicating that competition for territories and the consequent evolutionary conflict can hamper population performance (fig. 6A). This decrease in equilibrium population numbers is due to a decrease in the number of floaters. As mortality of breeders increases due to disturbance by floaters δ , territory vacancies occur more often and are filled by floaters, creating a higher turnover of territory ownership and a low overall population size. However, this is not necessarily reflected in the number of breeding individuals. Since optimal territory sizes decrease with increasing defense costs (fig. 3B), more breeding individuals can fit in a given area (fig. 6).

More complicated relationships between defense costs and population sizes are possible, too. For high values of α and β and low values of γ_0 , population size increases initially and then decreases with the effect of floaters on breeders δ (fig. 6B). This is because the higher number of breeders that can exist in an area when territory size is small (as predicted by high costs δ) will produce a large absolute number of floaters in cases where reproduction is efficient despite small territory size (as is the case for high α and β ; fig. 6B). This produces the initial increase in population size in figure 6B. Eventually, however, the turnover effect on mortality becomes the more important process, and population sizes decline again with increasing costs (fig. 6B).

Discussion

Since Gilbert White’s seminal observations on swifts *Apus apus* (White 1789), territoriality has been proposed and shown to regulate animal populations in different taxa including spiders (Riechert 1981), insects (Baker 1983), fish (Titus 1990; Barlow 1993; Balshine et al. 2001), reptiles (Philibosian 1975), birds (Brown 1969; Newton 1992, 1998), and mammals (Wolff 1997). Until now, however, our understanding of exactly how space gets divided among individuals has been lacking a full integration of individual- and population-level phenomena.

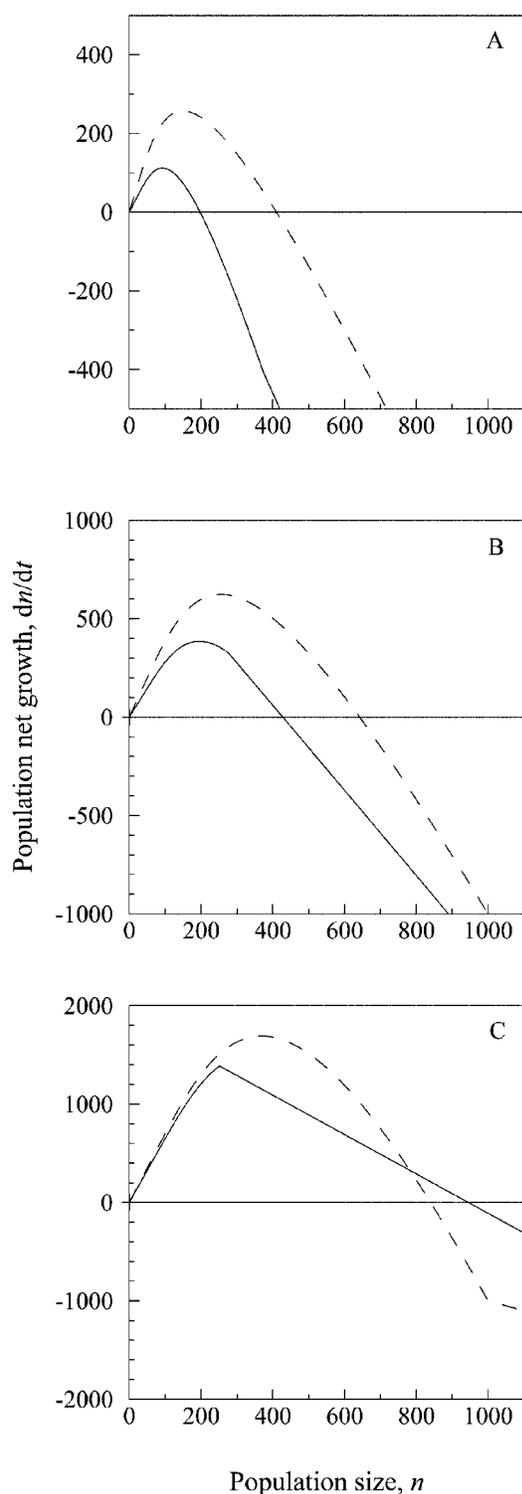


Figure 5: Net population growth resulting from the ESS defense effort d^* (solid line) compared with a nonterritorial equal-share scenario (dashed line). Population equilibrium is reached when net growth is 0. A, There are no floaters, and territoriality decreases population growth and

Our most fundamental result is that different modes of population regulation in territorial species can be derived from first principles of costs and benefits of space use. We predict populations to be more likely to be regulated by floaters with fixed territory sizes if fecundity is high, breeding success saturates quickly with territory size, and/or territory defense is relatively costly. On the other hand, any of the opposite assumptions—that is, low fecundity and a slowly saturating relationship between territory size and reproductive output, together with relatively cheap territory defense—is likely to favor regulation by breeders, where territories expand and shrink (and therefore reproductive output increases and diminishes) as populations decline or increase. Floaters do not occur in this mode of regulation, as they can always become breeders by squeezing in a territory between existing boundaries.

There are, of course, many processes important to population regulation that are not included in our model. For instance, population dynamics are often strongly dependent on stochastic events; factors such as high winter mortality could then lead to a scenario in which territories in the following year expand, lessening the need to defend core areas and improving breeding success. Other factors that could be included in future models include variable defense efforts toward particular types of intruders (Ydenberg et al. 1988; Temeles 1994), variable habitat quality (Kokko and Sutherland 1998; Pen and Weissing 2000; Kokko et al. 2001), or adaptively variable behavior that depends on the current size or density of the population (Clark and Yoshimura 1993).

Whether our study provides a necessary deterministic backbone for more inclusive models depends on the validity of its assumptions, which should be subject to empirical scrutiny in the future. Fruitful ways to test these assumptions include relating occupancy of a larger area to reproductive output in varying densities, examining whether better reproduction in larger territories (in species with regulation by breeders) is sufficient to contribute to significant variations in population growth rate, and detecting a trade-off between the effort spent in territorial defense and reproductive output. Evidence for high floater pressure having negative consequences for breeders would further strengthen the case, although it should be noted that the

carrying capacity; $\alpha = 4$, $\beta = 0.2$, $\gamma_0 = 0.3$, $\delta = 0$, $\mu_F = 2$. B, Floaters are produced, and territoriality still yields lower population growth than a nonterritorial system; $\alpha = 5$, $\beta = 0.4$, $\gamma_0 = 0.2$, $\delta = 0.1$, $\mu_F = 2$. C, Floaters are produced, and the evolutionarily stable territorial system produces more individuals than a nonterritorial system; $\alpha = 8$, $\beta = 0.7$, $\gamma_0 = 0.1$, $\delta = 0$, $\mu_F = 2$. In all cases, $A = 1,000$.

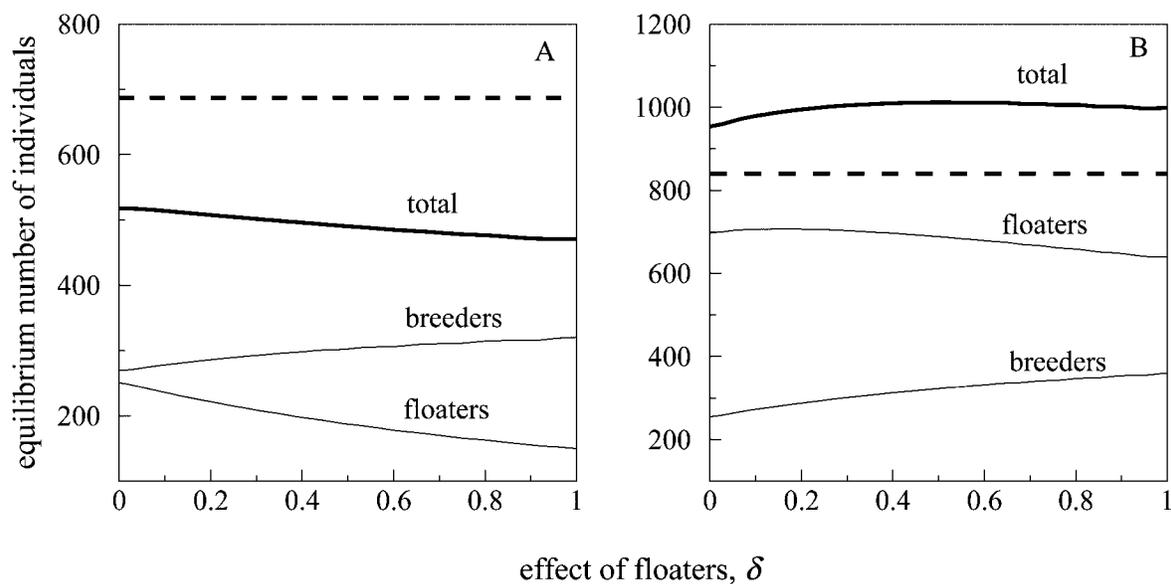


Figure 6: Equilibrium population numbers for different degrees of floaters' effect on territory defense costs δ . *A*, As the effect gets stronger, territory sizes decrease (fig. 3*B*), resulting in a higher number of territories (i.e., breeders) and increasing breeder mortality (eq. [4]), which in turn yields a higher rate of turnover and, therefore, a smaller number of floaters. Parameter values are $\alpha = 6$, $\beta = 0.4$, $\gamma_0 = 0.2$, $A = 1,000$, and $\mu_F = 2$. *B*, For high values of α and β and low values of γ_0 , however, floater numbers may increase initially with δ , and territoriality yields higher population sizes than no territoriality. Parameter values are $\alpha = 8$, $\beta = 0.7$, $\gamma_0 = 0.1$, $A = 1,000$, and $\mu_F = 2$. The dashed line indicates the equilibrium population size for a nonterritorial system (the "equal-share scenario").

model considers such effects as an option rather than a necessary condition for the regulatory process to work.

Finally, a comparative analysis that investigated whether our predicted life-history factors correlate with the ways populations are regulated could be worthwhile, although we acknowledge the difficulties of measuring factors such as "speed saturation of area benefits" and the diverse ways in which species differ in other reproductive parameters. One way to overcome much of this confounding diversity is to compare populations of the same species: one of our central predictions is that the type of population regulation may change as a result of rather minor variations in the cost and benefit curves of area occupancy; thus one should expect "borderline species," in which populations occupying high-quality areas end up with floater populations, while poorer quality habitats become regulated by territory size adjustment.

To theoreticians, our main message is to highlight that feedback between individual payoffs and population density is essential for deriving predictions on territorial behavior. In other contexts, such as in the evolution of parental care (Houston et al. 2005) and dispersal (Heino and Hanski 2001), it is increasingly recognized that evolutionary decisions will be influenced by the numbers of individuals one interacts with and that these numbers in turn

evolve according to the evolution of strategies in the population. Similarly, in our context, territory size cannot be evaluated as a simple optimization problem. Consider the prediction that high reproductive output decreases territory sizes. This occurs through two distinct mechanisms: the environment becomes more competitive because of more frequent territory intrusions, and the costs of defense therefore increase. Meanwhile, "sufficient" reproduction (in the sense of overcoming the costs) can be achieved with less effort when small territories are sufficient to yield good reproductive output (Morrell 2004). The former effect is consistent with empirical studies that describe smaller territories when the population density is high (associated with high reproductive values α and β and low mortalities of floaters μ_F in our model) and the consequent increase in the number of competitors increases the costs of defense (Myers et al. 1979; Iguchi and Hino 1996).

We found that while the total population size is not maximized by evolutionarily stable strategies, such behavior often produces a large floating population (fig. 2*D*; see also Kokko and Sutherland 1998; Pen and Weissing 2000; Kokko et al. 2001). The remarkable stability of territorial populations over time is often attributed to floaters, which are seen as a reserve that buffers population changes in the breeding population (Hunt 1998). The mechanism for

the operation of the buffer is that any decrease (e.g., sudden mortality) in the breeder population will be compensated by floaters moving to breeder positions (Newton 1992, 1998). Floaters can, however, influence population dynamics in many ways (Ridley et al. 2003), and their effects on breeder fitness include decreased feeding rates as a result of floaters feeding in breeders' territories (Davies and Houston 1981; Iguchi and Hino 1996), increased stress (Matter et al. 1998; Praw and Grant 1999), increased exposure to predators (Diaz-Uriarte 1999), nest disturbance (Komdeur 1996), extrapair copulations (Kempnaers et al. 2001), and intraspecific brood parasitism (Sandell and Dieemer 1999). This list of negative fitness consequences for breeders could potentially form a serious threat to population persistence. As an anecdotal example, in the late 1980s the world population of Seychelles magpie robins *Copsychus sechellarum* was just over 20 individuals, yet several individuals spent their time harassing breeders who occupied the best habitats instead of attempting to produce offspring of their own (Komdeur 1996). Our results show that a floater buffer is not required for population persistence (as in the alternative of regulation by breeders), and thus the role of floaters in shaping population dynamics requires much more scrutiny.

Another interesting outcome of our model relates to the well-known fact that solutions of conflicts, in general, rarely produce an outcome that is good from the species' point of view (Haldane 1932; Huxley 1938; Lande 1976). In our model, a hypothetical nonterritorial species that divides resources equally would typically perform better, in the sense that it maintained a higher growth rate at a given size and a higher equilibrium population size. However, this result was not uniformly true: in some cases the opposite was found, and territoriality could "manage" the resources of the environment in a way that increased the carrying capacity. Together with our results on floating, this means that population regulation through territoriality is a double-edged sword. The population stability-enhancing effects of territoriality (Southern 1970; Watson and Moss 1970; Nilsson 1987; Newton 1988; Smith et al. 1991) will often link with negative consequences of "selfish" use of resources, including competition by floaters for available space. The net effect can be negative on population performance. 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.

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APPENDIX

Mechanistic Definition of Territory Defense Effort d

Consider an individual i that defends a territory with effort E_i . Territorial pressure from neighbors p increases with distance l_i from center (Giraldeau and Ydenberg 1987). We can express this relationship as

$$p_i = p_0 + r \frac{E_i}{l_i}, \quad (\text{A1})$$

where p_0 and r are constants. If we assume that the boundary between the territories of two animals 1 and 2 falls where pressures are equal (Maynard Smith 1974), the boundary will fall where

$$p_0 + r \frac{E_1}{l_1} = p_0 + r \frac{E_2}{l_2} \Leftrightarrow \frac{E_1}{E_2} = \frac{l_1}{l_2}. \quad (\text{A2})$$

Moreover, if p_c denotes a critical pressure just large enough to exclude any floating intruders, then the minimum territory size is related to the effort required to maintain it by $p = p_c$, or

$$l = \frac{rE}{p_c - p_0}. \quad (\text{A3})$$

This minimum defendable distance can be understood as an indicator of defense effort because it is proportional to E . The measure of defense effort d used in this article is the two-dimensional equivalent to l .

Literature Cited

- Adams, E. S. 2001. Approaches to the study of territory size and shape. *Annual Review of Ecology and Systematics* 32:277–303.
- Arcese, P., J. N. M. Smith, W. M. Hochachka, C. M. Rogers, and D. Ludwig. 1992. Stability, regulation, and the determination of abundance in an insular song sparrow population. *Ecology* 73:805–822.
- Baker, R. R. 1983. Insect territoriality. *Annual Review of Entomology* 28:65–89.
- Balshine, S., B. Leach, F. Neat, H. Reid, M. Taborsky, and N. Werner. 2001. Correlates of group size in a cooperatively breeding cichlid fish (*Neolamprologus pulcher*). *Behavioral Ecology and Sociobiology* 50:134–140.

- Barlow, G. W. 1993. The puzzling paucity of feeding territories among fresh-water fishes. *Marine Behaviour and Physiology* 23:155–174.
- Beletsky, L. D. 1992. Social stability and territory acquisition in birds. *Behaviour* 123:290–313.
- Both, C., and M. E. Visser. 2000. Breeding territory size affects fitness: an experimental study on competition at the individual level. *Journal of Animal Ecology* 69:1021–1030.
- . 2003. Density dependence, territoriality, and divisibility of resources: from optimality models to population processes. *American Naturalist* 161:326–336.
- Boutin, S., and S. Schweiger. 1988. Manipulation of intruder pressure in red squirrels (*Tamiasciurus hudsonicus*): effects on territory size and acquisition. *Canadian Journal of Zoology* 66:2270–2274.
- Brown, J. L. 1969. Territorial behavior and population regulation in birds. *Wilson Bulletin* 81:293–329.
- Chapman, M. R., and D. L. Kramer. 1996. Guarded resources: the effect of intruder number on the tactics and success of defenders and intruders. *Animal Behaviour* 52:83–94.
- Clark, C. W., and J. Yoshimura. 1993. Behavioral responses to variations in population size: a stochastic evolutionary game. *Behavioral Ecology* 4:282–288.
- Davies, N. B., and A. I. Houston. 1981. Owners and satellites: the economics of territory defence in the pied wagtail, *Motacilla alba*. *Journal of Animal Ecology* 50:157–180.
- Dhondt, A. A., J. Schillemans, and J. Delaet. 1982. Blue tit territories in populations at different density levels. *Ardea* 70:185–188.
- Diaz-Uriarte, R. 1999. Anti-predator behaviour changes following an aggressive encounter in the lizard *Tropidurus hispidus*. *Proceedings of the Royal Society of London B* 266:2457–2464.
- Dieckmann, U. 1997. Can adaptive dynamics invade? *Trends in Ecology & Evolution* 12:128–131.
- Eberhard, J. R., and P. W. Ewald. 1994. Food availability, intrusion pressure and territory size: an experimental study of Anna's hummingbirds (*Calypte anna*). *Behavioral Ecology and Sociobiology* 34:11–18.
- Fryxell, J. M., and P. Lundberg. 1997. Individual behavior and community dynamics. Chapman & Hall, New York.
- Geritz, S. A. H., E. Kisdi, G. Meszina, and J. A. J. Metz. 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evolutionary Ecology* 12:35–57.
- Giraldeau, L. A., and R. Ydenberg. 1987. The center-edge effect: the result of a war of attrition between territorial contestants. *Auk* 104:535–538.
- Haldane, J. B. S. 1932. *The causes of evolution*. Harper, London.
- Hammerstein, P., and S. E. Riechert. 1988. Payoffs and strategies in territorial contests: ESS analyses of two ecotypes of the spider *Agelenopsis aperta*. *Evolutionary Ecology* 2:115–138.
- Hansen, A. J. 1987. Regulation of bald eagle reproductive rates in southeast Alaska. *Ecology* 68:1387–1392.
- Hårdling, R., H. Kokko, and K. E. Arnold. 2003. Dynamics of the caring family. *American Naturalist* 161:395–412.
- Heg, D., B. J. Ens, H. P. Van der Jeugd, and L. W. Bruinzeel. 2000. Local dominance and territorial settlement of nonbreeding oystercatchers. *Behaviour* 137:473–530.
- Heino, M., and I. Hanski. 2001. Evolution of migration rate in a spatially realistic metapopulation model. *American Naturalist* 157:495–511.
- Houston, A. I., T. Szekely, and J. M. McNamara. 2005. Conflict between parents over care. *Trends in Ecology & Evolution* 20:33–38.
- Hunt, W. G. 1998. Raptor floaters at Moffat's equilibrium. *Oikos* 82:191–197.
- Huxley, J. S. 1938. The present standing of the theory of sexual selection. Pages 11–42 in G. R. de Beer, ed. *Evolution*. Clarendon, Oxford.
- Iguchi, K., and T. Hino. 1996. Effect of competitor abundance on feeding territoriality in a grazing fish, the ayu *Plecoglossus altivelis*. *Ecological Research* 11:165–173.
- Jenkins, J. M., and R. E. Jackman. 1993. Mate and nest-site fidelity in a resident population of bald eagles. *Condor* 95:1053–1056.
- Keeley, E. R. 2000. An experimental analysis of territory size in juvenile steelhead trout. *Animal Behaviour* 59:477–490.
- Kempnaers, B., S. Everding, C. Bishop, P. Boag, and R. J. Robertson. 2001. Extra-pair paternity and the reproductive role of male floaters in the tree swallow (*Tachycineta bicolor*). *Behavioral Ecology and Sociobiology* 49:251–259.
- Knowlton, N., and G. A. Parker. 1979. Evolutionarily stable strategy approach to indiscriminate spite. *Nature* 279:419–421.
- Koenig, W. D. 1990. Territory size and duration in the white-tailed skimmer *Plathemis lydia* (Odonata, Libellulidae). *Journal of Animal Ecology* 59:317–333.
- Kokko, H., and W. J. Sutherland. 1998. Optimal floating and queuing strategies: consequences for density dependence and habitat loss. *American Naturalist* 152:354–366.
- Kokko, H., W. J. Sutherland, and R. A. Johnstone. 2001. The logic of territory choice: implications for conservation and source-sink dynamics. *American Naturalist* 157:459–463.
- Komdeur, J. 1996. Breeding of the Seychelles magpie robin *Copsychus sechellarum* and implications for its conservation. *Ibis* 138:485–498.
- Lande, R. 1976. Natural selection and random genetic drift in phenotypic evolution. *Evolution* 30:314–334.
- Matter, J. M., P. J. Ronan, and C. H. Summers. 1998. Central monoamines in free-ranging lizards: differences associated with social roles and territoriality. *Brain, Behavior and Evolution* 51:23–32.
- Maynard Smith, J. 1974. *Models in ecology*. Cambridge University Press, Cambridge.
- Moffat, C. B. 1903. The spring rivalry of birds: some views on the limit to multiplication. *Irish Naturalist* 12:152–166.
- Morrell, L. J. 2004. Are behavioural trade-offs all they seem? counter-intuitive resolution of the conflict between two behaviours. *Behavioral Ecology and Sociobiology* 56:539–545.
- Morrell, L. J., and H. Kokko. 2003. Adaptive strategies of territory formation. *Behavioral Ecology and Sociobiology* 54:385–395.
- Mougeot, F., S. M. Redpath, F. Leckie, and P. J. Hudson. 2003. The effect of aggressiveness on the population dynamics of a territorial bird. *Nature* 421:737–739.
- Myers, J. P., P. G. Connors, and F. A. Pitelka. 1979. Territory size in wintering sanderlings: effects of prey abundance and intruder density. *Auk* 96:551–561.
- Newton, I. 1988. A key factor-analysis of a sparrowhawk population. *Oecologia* (Berlin) 76:588–596.
- . 1992. Experiments on the limitation of bird numbers by territorial behavior. *Biological Reviews of the Cambridge Philosophical Society* 67:129–173.
- . 1998. *Population limitation in birds*. Academic Press, San Diego, CA.
- Nilsson, S. G. 1987. Limitation and regulation of population density

- in the nuthatch *Sitta europaea* (Aves) breeding in natural cavities. *Journal of Animal Ecology* 56:921–937.
- Norton, M. E., P. Arcese, and P. W. Ewald. 1982. Effect of intrusion pressure on territory size in black-chinned hummingbirds (*Archilochus alexandri*). *Auk* 99:761–764.
- Pen, I., and F. J. Weissing. 2000. Optimal floating and queuing strategies: the logic of territory choice. *American Naturalist* 155:512–526.
- Philibosian, R. 1975. Territorial behavior and population regulation in lizards, *Anolis acutus* and *Anolis cristatellus*. *Copeia* 3:428–444.
- Praw, J. C., and J. W. A. Grant. 1999. Optimal territory size in the convict cichlid. *Behaviour* 136:1347–1363.
- Ridley, J., J. Komdeur, and W. J. Sutherland. 2003. Population regulation in group-living birds: predictive models of the Seychelles warbler. *Journal of Animal Ecology* 72:588–598.
- . 2004. Incorporating territory compression into population models. *Oikos* 105:101–108.
- Riechert, S. E. 1981. The consequences of being territorial: spiders, a case study. *American Naturalist* 117:871–892.
- Sandell, M. I., and M. Diemer. 1999. Intraspecific brood parasitism: a strategy for floating females in the European starling. *Animal Behaviour* 57:197–202.
- Smith, J. N. M., and P. Arcese. 1989. How fit are floaters? consequences of alternative territorial behaviors in a nonmigratory sparrow. *American Naturalist* 133:830–845.
- Smith, J. N. M., P. Arcese, and W. M. Hochachka. 1991. Social behavior and population regulation in insular bird populations: implications for conservation. Pages 148–167 in C. M. Perrins, J. D. Lebreton, and G. J. M. Hiron, eds. *Bird population studies*. Oxford University Press, Oxford.
- Southern, H. N. 1970. Natural control of a population of tawny owls (*Strix aluco*). *Journal of Zoology (London)* 162:197–285.
- Stamps, J. 1994. Territorial behavior: testing the assumptions. *Advances in the Study of Behavior* 23:173–232.
- Stamps, J. A., and V. V. Krishnan. 1995. Territory acquisition in lizards. III. Competing for space. *Animal Behaviour* 49:679–693.
- . 1999. A learning-based model of territory establishment. *Quarterly Review of Biology* 74:291–318.
- . 2001. How territorial animals compete for divisible space: a learning-based model with unequal competitors. *American Naturalist* 157:154–169.
- Temeles, E. J. 1994. The role of neighbors in territorial systems: when are they “dear enemies”? *Animal Behaviour* 47:339–350.
- Titus, R. G. 1990. Territorial behavior and its role in population regulation of young brown trout (*Salmo trutta*): new perspectives. *Annales Zoologici Fennici* 27:119–130.
- von Haartman, L. 1956. Territory in the pied flycatcher. *Ibis* 98:460–475.
- Watson, A., and R. Moss. 1970. Dominance spacing behaviour and aggression in relation to population limitation in vertebrates. Pages 167–223 in A. Watson, ed. *Animal populations in relation to their food resources*. Blackwell, Oxford.
- Wauters, L. A., and L. Lens. 1995. Effects of food availability and density on red squirrel (*Sciurus vulgaris*) reproduction. *Ecology* 76:2460–2469.
- White, G. 1789. *The natural history of Selborne*. Benjamin White, London.
- Wilson, E. O. 1975. *Sociobiology: the new synthesis*. Harvard University Press, Cambridge, MA.
- Wolff, J. O. 1997. Population regulation in mammals: an evolutionary perspective. *Journal of Animal Ecology* 66:1–13.
- Ydenberg, R. C., L. A. Giraldeau, and J. B. Falls. 1988. Neighbors, strangers, and the asymmetric war of attrition. *Animal Behaviour* 36:343–347.
- Zack, S., and B. J. Stutchbury. 1992. Delayed breeding in avian social systems: the role of territory quality and floater tactics. *Behaviour* 123:194–219.

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