

Socially Stable Territories: The Negotiation of Space by Interacting Foragers

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ABSTRACT: This article presents a theory of territoriality that integrates optimal foraging and conflict resolution through negotiation. Using a spatially explicit model of a sit-and-wait forager, we show that when resources are scarce, there is a conflict between foragers: there is not enough space for all individuals to have optimal home ranges. We propose that a division of space that solves this conflict over resources is the outcome of a negotiation between foragers. We name this outcome the socially stable territories (SST). Using game theory we show that in a homogenous patch occupied by two interacting foragers, both individuals receive identical energy yields at the socially stable territories; that is, there is economic equity. Economic inequity can arise in a heterogeneous patch or from asymmetries in fighting abilities between the foragers. Opportunity costs play a role in reducing economic inequity. When the asymmetry in fighting abilities is very large, a negotiated division of space is not possible and the forager with lowest fighting ability may be evicted from the habitat patch. A comparison between territories and overlapping home ranges shows that energy yields from territories are generally higher. We discuss why there are instances in which individuals nevertheless overlap home ranges.

Keywords: sit-and-wait predator, war of attrition, evolutionarily stable strategy (ESS), *Anolis*, prior residency, resource holding power (RHP).

How individual animals occupy and partition space has important consequences for the dynamics and distribution of populations on a larger scale (Gordon 1997). An un-

derstanding of territorial behavior, therefore, is valuable not only to the field of animal behavior but also has applications in ecology and conservation biology.

The first economic framework for the study of territoriality was proposed by J. L. Brown (1964). Brown suggested that for territorial behavior to evolve, the benefits of exclusive access to a resource should exceed the costs of territory defense. With the development of optimal foraging theory (Stephens and Krebs 1986), Brown's framework was used to make explicit predictions on optimal territory size (Schoener 1983) and on the conditions for territorial defense (Carpenter 1987).

Economic studies of territoriality look at territorial behavior from the point of view of a single territory owner (Adams 2001). However, we are often interested in the conflicts between interacting neighbors (Stamps and Krishnan 2001). The appropriate framework with which to model animal conflict is game theory (Dugatkin and Reeve 1998; Houston and McNamara 1999). Maynard Smith (1982) proposed a game in which competing owners agree on a division of space through negotiation. In Maynard Smith's game, the value of a piece of territory decreases in an ad hoc manner with the distance to the territory center. Each individual uses a negotiation strategy with different degrees of escalation. Strategies are played against each other, which produces a certain position for the territory edge, and the evolutionarily stable strategy (ESS) is determined. This game has been extended to asymmetric competitors (Parker 1985) and can explain some empirical patterns (Giraldeau and Ydenberg 1987; Ydenberg et al. 1988).

In this article we develop a theory of territoriality that uses optimal foraging to calculate the value of each piece of habitat to the competing individuals and game theory to find a negotiated division of space. Other studies have integrated optimal foraging and game theory to look at the distribution of nonterritorial foragers in space (Stephens and Stevens 2001) and to study habitat selection of nonterritorial foragers (Brown 1998), but to our knowledge, our work is the first to do so in the context of territoriality.

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We start by introducing an economic model of home-range size for a solitary forager. A conflict between foragers using a habitat patch arises when the patch is smaller than what would be optimal for each of the foragers if they were alone. Using game theory, we suggest that one solution to this conflict is a negotiated division of space in exclusive home ranges (i.e., territories). We study how the environment and forager asymmetries affect the negotiated territories. Finally, we compare the energy yields from a territorial division of space with the energy yields from overlapping home ranges.

Our models are specifically developed for feeding territories of *Anolis* lizards, which are sit-and-wait predators (Perry 1999). However, the theory and our results are applicable to other sit-and-wait predators, and the theoretical framework for conflict resolution through negotiation could be extended to other foraging strategies.

The Solitary Forager

Anolis lizards are food limited (Stamps and Tanaka 1981; Guyer 1988a) and have little predation pressure in the Lesser Antilles (Roughgarden 1995), which makes a good system for optimal foraging studies. Shafir and Roughgarden (1998) studied *Anolis gingivinus* on the island of Anguilla, the only anole on the island. In Anguilla, *A. gingivinus* density is low enough that the foraging decisions of an individual can be analyzed without considering interactions with neighbors. In one experiment, Shafir and Roughgarden (1998) showed that the probability of pursuing a prey of a given size approximates a step function: below a cutoff distance, every prey item is pursued, and beyond the cutoff distance, no prey item is pursued. In a second experiment, Shafir and Roughgarden found that cutoff distances were smaller in habitats with higher prey abundance.

These results support the solitary forager model developed by Roughgarden (1995). For simplicity we use a one-dimensional version of that model. Our forager preys along a line, between l and r , perching somewhere in between at x_0 . Let $a(x)$ be the point prey abundance in items/second/meter. The forager's mean waiting time for a prey item is

$$\tau = \frac{1}{\int_l^r a(x) dx}. \quad (1)$$

The mean pursuit time is the integral over the home range of the probability of a prey item appearing at a certain position x multiplied by the time the forager takes to get there and return to the perch:

$$\mu = \int_l^r \frac{a(x)}{\int_l^r a(y) dy} \frac{2|x_0 - x|}{v} dx, \quad (2)$$

where v is the sprint speed of the forager. Let e be the mean energetic content of a prey item, w the energy the forager spends per unit time while waiting for the prey, and p the energy spent per unit time while pursuing the prey. The forager's energy yield per unit time is the net energetic gain for each prey item captured divided by the mean time it takes to wait for and chase a prey:

$$E(l, x_0, r) = \frac{e - \tau \cdot w - \mu \cdot p}{\tau + \mu}. \quad (3)$$

The optimal home range for a solitary forager corresponds to the choice of l , x_0 , and r that maximizes E . Consider the case of a homogeneous environment with $a(x) = \alpha$. It is easy to see that the optimal perch x_0 is in the middle of the home range, and it does not matter where the forager places the home range; what is important is how large the home range is, $r - l$. Making $l = 0$, the optimal home-range size can be found by solving

$$\frac{\partial E}{\partial r} = 0. \quad (4)$$

The only solution is

$$r^* = \frac{-(p - w) + \sqrt{(p - w)^2 + 2\alpha e^2 v}}{\alpha e}. \quad (5)$$

Note that as expected from the experiments of Shafir and Roughgarden (1998), the optimal home-range size decreases when prey abundance increases.

A Conflict between Neighbor Foragers

Consider now a group of N foragers inhabiting a homogeneous habitat patch of size z . If $z \geq Nr^*$, each forager can have its optimal solitary home range. Otherwise, if $z < Nr^*$, the foragers have a conflict of interest: there is not enough space for all individuals to have optimal home ranges. Note that when prey is scarce, a conflict between foragers can occur even in large habitat patches.

Empirical evidence for such conflicts in sit-and-wait predators comes from the inverse relationship between home-range size and female density in territorial Iguanids (Stamps 1983) and the higher frequency of space transfers in *Anolis aeneus* during territorial settlement at higher densities (Stamps and Krishnan 1995). Furthermore, studies with other types of foragers have shown experimentally that territory size is limited by competitor abundance

(Norton et al. 1982; Tricas 1989; Eberhard and Ewald 1994; Iguchi and Hino 1996).

We now turn our attention to finding a division of space in exclusive home ranges (i.e., territories) that would be acceptable for all individuals: the socially stable territories. Partial and complete home-range overlap is considered in a later section.

Socially Stable Territories

For simplicity we restrict ourselves to the case of two foragers in a patch perching at x_1 and x_2 , with $0 < x_1 < x_2 < z$. We assume that the territory border is the point that the two neighbors can reach at the same time. When both individuals have the same sprint speed, the border is at $(x_1 + x_2)/2$. The foragers negotiate the territory border through perch moves. The energy yield for each individual can be calculated from equation (3):

$$\begin{aligned} E_1(x_1, x_2) &= E\left(0, x_1, \frac{x_1 + x_2}{2}\right), \\ E_2(x_1, x_2) &= E\left(\frac{x_1 + x_2}{2}, x_2, z\right). \end{aligned} \quad (6)$$

Now suppose that forager 1 tries to move to $x_1 + \delta x_1$. This would change its energy to $E_1 + \delta x_1 \partial E_1 / \partial x_1$ and the energy yield of forager 2 to $E_2 + \delta x_1 \partial E_2 / \partial x_1$ (note that in most cases, $\partial E_2 / \partial x_1 < 0$). So the question is, will forager 2 accept this perch move?

The answer comes from game theoretical models of animal contests and, more specifically, from the asymmetric war of attrition (Parker and Rubenstein 1981). We need to know two types of information. First, we need to know how the opponents value the resource being contested. The resource is the difference in energy yields before and after the perch move. Thus, for forager 1 the resource value is $V_1 = (E_1 + \delta x_1 \partial E_1 / \partial x_1) - E_1 = \delta x_1 \partial E_1 / \partial x_1$, and for forager 2 the resource value is $V_2 = E_2 - (E_2 + \delta x_1 \partial E_2 / \partial x_1) = -\delta x_1 \partial E_2 / \partial x_1$. Second, we need to know at what rates the foragers incur costs during the contest. There are two types of costs: metabolic costs and opportunity costs. Metabolic costs correspond to the energy that a forager spends on displays and chases. Let d be the metabolic cost per unit time. While the animals are displaying and chasing each other, they are not foraging, and thus there are missed opportunity costs equal to the current energy yield. The total cost per unit time for forager i is

$$C_i(x_1, x_2) = d_i + E_i(x_1, x_2). \quad (7)$$

The ESS is for forager 2 to accept the move if it can assess that

$$\frac{1}{C_1(x_1, x_2)} \frac{\partial E_1(x_1, x_2)}{\partial x_1} > -\frac{1}{C_2(x_1, x_2)} \frac{\partial E_2(x_1, x_2)}{\partial x_1}. \quad (8)$$

That is, the yield gain of forager 1 weighted by the costs is larger than the yield loss of forager 2 weighted by the costs.

An intuitive explanation for this rule is as follows. Suppose that foragers accrue the resource over a time period T and that each individual is willing to display until paying a cost as high as the accrued value of the resource, $T \cdot V_i$. If forager i incurs costs C_i per unit time, then it should concede at time t_p given by $t_p \cdot C_i = T \cdot V_i$. The forager with higher t_i wins, leading us to the negotiation rule, (8). Note that Parker and Rubenstein (1981) have shown that the opponents should assess equation (8) as early as possible. Therefore, individuals do not need to estimate the accrual period T .

A rule for forager 1 to accept a perch move of forager 2 can be developed along the same lines. Thus, an equilibrium territorial configuration, x_1^* and x_2^* , would satisfy

$$\frac{1}{C_1(x_1, x_2)} \frac{\partial E_1(x_1, x_2)}{\partial x_1} = -\frac{1}{C_2(x_1, x_2)} \frac{\partial E_2(x_1, x_2)}{\partial x_1} \Bigg|_{(x_1^*, x_2^*)}, \quad (9a)$$

$$\frac{1}{C_1(x_1, x_2)} \frac{\partial E_1(x_1, x_2)}{\partial x_2} = -\frac{1}{C_2(x_1, x_2)} \frac{\partial E_2(x_1, x_2)}{\partial x_2} \Bigg|_{(x_1^*, x_2^*)}. \quad (9b)$$

Given that forager 2 is perching at x_2^* , if forager 1 is perching at the left of x_1^* , then equation (8) is true and forager 1 should move to the right. If forager 1 is perching to the right of x_1^* , then equation (8) is false and forager 1 would be compelled to move to the left. We name this equilibrium the socially stable territories (SST) because it is the only territorial division of space that is acceptable for the two interacting neighbors. While the SST result from both individuals using an ESS negotiation rule, the territories are not evolutionarily fixed but instead are the outcome of a negotiation. In the appendix we discuss algorithms that the foragers may use to negotiate the SST.

Symmetric Foragers

We now analyze the division of space at the SST when foragers are symmetric (v , p , w , and d are identical for both individuals) and how the SST are affected by the prey distribution.

Homogeneous Habitat

Let the prey abundance be uniformly distributed ($a(x) = \alpha$) in the suitable habitat between 0 and z . The following perches then obey equations (9) and are an SST equilibrium:

$$\begin{aligned} x_1^* &= \frac{1}{4}z, \\ x_2^* &= \frac{3}{4}z. \end{aligned} \quad (10)$$

This SST equilibrium is very intuitive: each forager gets half of the habitat and perches in the middle of its half. A numerical study suggests that this is the only SST equilibrium. The SST correspond to an even distribution of resources, a situation of economic equity, with

$$E_{\text{SST}}^* = E_1^* = E_2^* = \frac{4v(\alpha ze - 2w) - \alpha z^2 p}{8v + \alpha z^2}. \quad (11)$$

This expression assumes a peaceful coexistence of both foragers after the territory negotiation. However, there may be instances where postnegotiation costs of territorial defense are significant, such as territorial defense against floaters. Expression (11) could then be modified by subtracting the defense costs per unit time.

Figure 1 gives some more insight into the equations for the SST (eqq. [9]). Forager 2 is perching at the SST equilibrium while forager 1 is allowed to perch anywhere in the left half of the habitat patch. The further to the right forager 1 perches, the greater its energy yield and the smaller is the energy yield of forager 2. On the other hand, the further to the right forager 1 perches, the less valuable a perch move to the right is for forager 1 ($\partial E_1/\partial x_1$) and the greater is the loss of energy yield of forager 2 from such perch move ($-\partial E_2/\partial x_1$). Therefore, the further to the right forager 1 perches, the lower is the gains-to-costs ratio of a further move to the right and the higher is the losses-to-costs ratio of forager 2. The SST perch of forager 1 corresponds to the point where those ratios are equalized (eqq. [9]). In a homogeneous environment with symmetric foragers, both the marginal yields and the energy yields cross at the SST ($x_1^* = 3.75$ in fig. 1), but this is not generally the case. It is also interesting to note that when

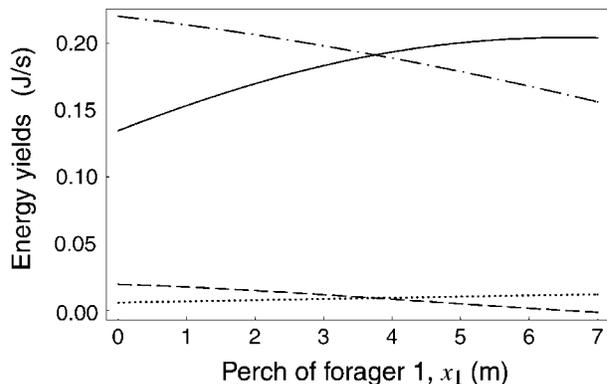


Figure 1: Energy yields and marginal yields in a homogeneous environment, as a function of the perch of forager 1. Forager 2 is perching at $x_2^* = 11.25$, and the territory of forager 1 extends from 0 to $(x_1 + 11.25)/2$. E_1 = solid line; E_2 = alternating dot-dash line; $\partial E_1/\partial x_1$ = dashed line; $-\partial E_2/\partial x_1$ = dotted line. Parameters given in table 1.

the metabolic costs are negligible ($C_i \approx E_i$), what is equalized are proportional gains, that is, the marginal yields relative to the territories the foragers already have.

Heterogeneous Habitat

We now consider a habitat patch in which there is a linear gradient of prey abundance. We keep the total prey abundance in the patch constant and independent of the gradient. The distribution of prey between 0 and z is

$$a(x) = \alpha \left(1 + \gamma - 2\gamma \frac{x}{z} \right), \quad (12)$$

where γ measures the steepness of the gradient and can vary from 0 (homogeneous habitat) to 1 (maximum heterogeneity).

Forager 1 should place the left border of its territory at 0 so that it gets the best portion of the habitat, but it is

Table 1: Typical parameter values

Symbol	Description	Value
w	Energy spent while waiting	.006 J/s
p	Energy spent while pursuing prey	.14 J/s
d	Energy spent while displaying	.08 J/s
v	Sprint speed of the forager	1.2 m/s
e	Caloric content of a prey item	6 J
z	Habitat patch size	15 m
α	Point prey abundance	.005 insects/m/s

Note: Values for w , p , v , and e are based on empirical relationships (Roughgarden 1995) and correspond to a lizard with snout-to-vent length of 50 mm and a prey size of 3 mm.

not clear that forager 2 will want to have its right border at z because there may not be enough prey there. Therefore, we need to add a third equation to equations (9):

$$\frac{\partial E_2(x_1, x_2, r_2)}{\partial r_2} = 0 \bigg|_{(x_1^*, x_2^*, r_2^*)}, \quad (13)$$

where r_2 is the right border of the territory of forager 2. If there is a combined solution to equations (9) and (13) with $0 < x_1^* < x_2^* < r_2^* < z$, then at the SST, forager 2 does not extend its territory all the way into the edge of the habitat. Otherwise, $r_2^* = z$, and the SST are given as before by equations (9).

Note that in the case of the homogeneous habitat, checking for the existence of a solution to equations (9) and (13) is equivalent to checking for the existence of a conflict between neighbor foragers. If there is a solution, then there is no conflict ($z > 2r^*$), and each forager can have an optimal home range (e.g., 0 to r^* and r^* to $2r^*$). In a heterogeneous habitat, even if there is a solution, there is a conflict of where to place the border between the two foragers because forager 2 wants to perch as far to the left as it can.

Figure 2 shows a numerical solution of the SST for a range of gradients. Note that for these parameters, forager 2 always places the right border of its territory at z . As the prey gradient increases, the foragers go from a situation of economic equity to one of economic inequity (fig. 2b): forager 1 gets an increasingly better territory and forager 2 gets an increasingly worse territory. This is an interesting result, because the foragers are symmetric in all respects but their initial residences in the patch: one forager perches in the prey-rich side of the habitat and the other in the prey-poor side. This difference in initial residences could be a consequence of forager 1 having a prior residency in the patch and forager 2 being a newcomer. Note that even for the steepest gradient, it would be possible to have a territorial configuration in which forager 2 would get an equal or higher energy yield than forager 1 by making the territory of forager 1 small enough. That, however, does not happen at the SST. The territory of forager 2 does increase as the gradient increases (fig. 2a), but the increase is not fast enough to compensate for the gradient.

Figure 2 also examines the effect of opportunity costs. The economic inequity is larger when opportunity costs are ignored (*filled squares*, fig. 2): forager 2 receives a smaller territory and a smaller energy yield than when opportunity costs are not ignored. This means that opportunity costs reduce part of the prior residency advantage. This reduction happens because forager 1 pays higher opportunity costs than forager 2.

A numerical study of the parameter space suggests that there is always one and only one SST equilibrium.

Asymmetric Foragers

We now show that in a homogeneous environment, there can be economic inequity if the foragers incur metabolic costs at different rates during contests. Define the metabolic costs asymmetry between two foragers as $\delta = \log(d_2/d_1)$. Higher metabolic costs may be due to a reduced ability to engage in displays or a higher rate of injury during fights. We assume that the foragers are similar in all other respects: v , p , and w are the same for both individuals.

Homogeneous Habitat

The SST can be obtained by solving equations (9) numerically for uniform prey abundance subject to the constraints $0 < x_1 < x_2 < z$. Figure 3 shows the SST for a range of asymmetries, from identical metabolic costs ($\delta = 0$) to increasing metabolic costs for forager 2. As would be expected, the forager that has the highest costs (i.e., lowest fighting ability) gets the smallest territory and therefore a low energy yield. If the asymmetry is very large ($\delta > 2.2$), there is no solution to equations (9) that obeys the constraints: there is a maximum asymmetry for which the SST exist. This result contrasts with our analysis of environmental heterogeneities where we always find an SST equilibrium.

When the SST break down, foragers are no longer able to negotiate small changes in perches. Two situations can then occur: the forager with lowest fighting ability is evicted, or alternatively, both foragers remain in the patch in a situation of permanent conflict. Eviction is likely to occur when the forager with lowest fighting ability can move to a different patch without great loss of fitness. If fitness on other habitat patches is extremely low, the forager perching at the patch edge will try to remain in the current patch at any cost, and in some cases escalation to fatal fighting may occur (Enquist and Leimar 1990).

Opportunity costs play a role in diminishing the effects of the asymmetry in fighting abilities. If the foragers ignore opportunity costs ($C_i = d_i$), the SST break down when the asymmetry is smaller (*filled square*, fig. 3). Interestingly, if the prey are scarce, then the maximum asymmetry for which SST exist is also smaller (*open circle*, fig. 3). Thus, if there are fewer resources, cohabitation of two asymmetric foragers becomes less likely.

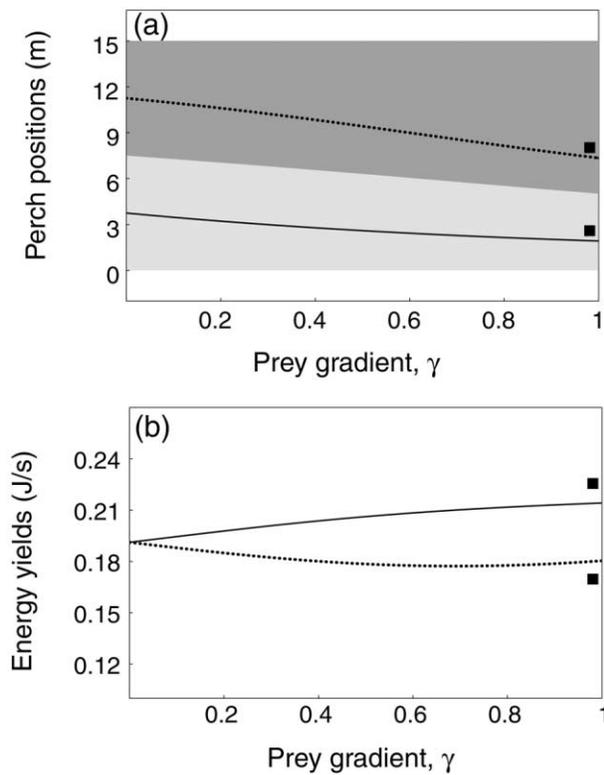


Figure 2: Socially stable territories for symmetric foragers as a function of habitat heterogeneity (parameters given in table 1). *a*, Perch positions: x_1 (solid line) and x_2 (dotted line). The habitat patch extends from 0 to 15 on the vertical axis. The territory of forager 1 corresponds to the light gray region, and the territory of forager 2 to the dark gray region. *b*, Energy yields: E_1 (solid line) and E_2 (dotted line). The filled squares show the foragers' perches and energy yields when opportunity costs are ignored ($C_i = d$) and the prey gradient is maximum.

Heterogeneous Habitat

Figure 4 analyzes the effect of a metabolic costs asymmetry when the environment is heterogeneous. The SST exist when the forager with greatest fighting ability, forager 2, is on the prey-rich side of the habitat (*bottom triangle*, fig. 4) but not when forager 2 is on the prey-poor side (*top triangle*, fig. 4). When forager 2 is on the prey-rich side of the habitat, it does not mind losing a portion of the prey-poor part of the habitat. However, when forager 2 is on the prey-poor side, it wants to move into the prey-rich side as much as possible, and because forager 2 incurs lower costs during contests, it may end up evicting forager 1. Thus, figure 4 suggests that an SST equilibrium is more likely when the forager with lower fighting ability gets the prey-poor side of the habitat. Note that the forager with lower fighting ability gets not only the prey-poor side of the habitat but also a very small portion of the habitat

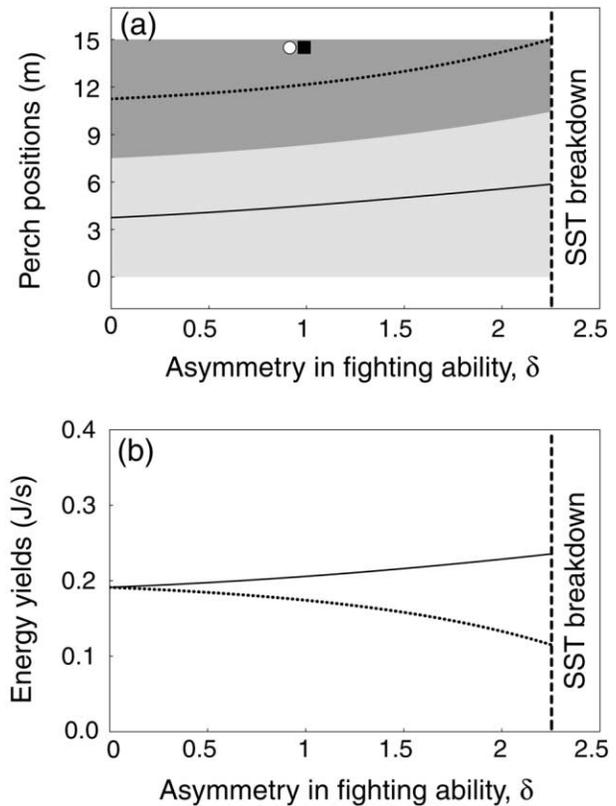


Figure 3: Socially stable territories as a function of asymmetry in fighting ability ranging from equal fighting abilities ($\delta = 0$) to a fighting ability 12 times lower for forager 2 relative to forager 1 ($\delta = 2.5$). *a*, Perch positions: x_1 (solid line) and x_2 (dotted line). The habitat patch extends from 0 to 15 on the vertical axis. The territory of forager 1 corresponds to the light gray region, and the territory of forager 2 to the dark gray region. The open circle marks where the SST break down for a prey abundance four times lower. The filled square marks where the SST break down when opportunity costs are ignored ($C_i = d_i$). *b*, Energy yields: E_1 (solid line) and E_2 (dotted line). Parameters: $d_1 = 0.08$ J/s, $d_2 = d_1 e^{\delta}$ J/s, others as in table 1.

(compare this perch configuration to the one in fig. 2*a*) and consequently a low energy yield.

Overlapping Home Ranges

An alternative solution to a territorial division of space would be to overlap home ranges. In this section we compare the energy yields at the SST with the energy yields from overlapping home ranges. We examine symmetric foragers in a homogeneous environment only.

Consider first complete home-range overlap: the two individuals perch at $z/2$ and forage from 0 to z . Assume that both individuals forage at the same time of the day and that each individual chases and captures 50% of the

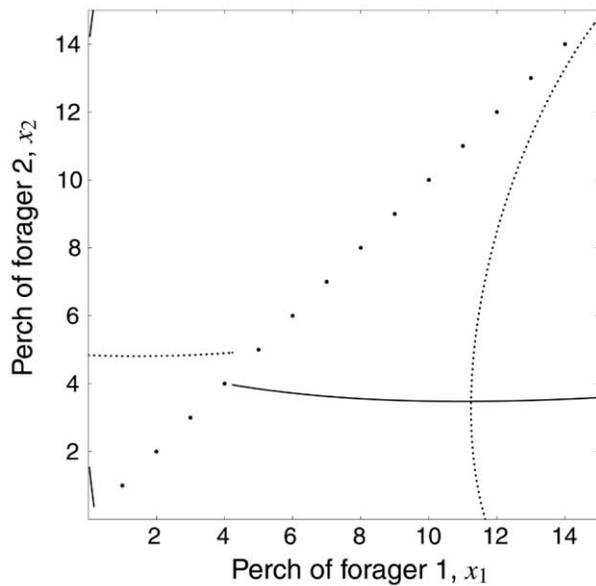


Figure 4: Feasible solutions to equations (9; *solid line*) and (10; *dotted line*) for asymmetric foragers when the habitat is heterogeneous ($\gamma = 1$). Forager 2 has greater fighting ability than forager 1 ($\delta = -0.81$). In the top triangle, forager 1 is on the left and forager 2 is on the right, as usual. In the bottom triangle, the positions are reversed. The socially stable territories correspond to the point where both curves cross. Parameters: $\alpha = 0.0012$ items/m/s, $d_1 = 0.18$ J/s, $d_2 = 0.08$ J/s, others as in table 1.

prey. The average prey abundance for each forager is then $\alpha/2$. The energy yields are given by equation (3):

$$E_{\text{overlap}}^*(z) = E\left(0, \frac{z}{2}, z\right) = \frac{2v(\alpha z e - 2w) - \alpha z^2 p}{4v + \alpha z^2}. \quad (14)$$

Are territories more advantageous for the foragers? Subtracting equation (14) from equation (11) yields

$$E_{\text{SST}}^*(z) - E_{\text{overlap}}^*(z) = \frac{2v\alpha z^2[\alpha z e + 2(p - w)]}{(8v + \alpha z^2)(4v + \alpha z^2)}. \quad (15)$$

Note that $p > w$, and therefore $E_{\text{SST}}^*(z) > E_{\text{overlap}}^*(z)$; that is, the territorial division is more advantageous. However, it is worth noting that the difference between overlapping home ranges and territories diminishes as the resources get less abundant (as α or z approaches 0).

A territorial division of space yields higher energy intakes than a complete overlap of home ranges. What happens if foragers overlap only partially? For instance, the foragers could overlap home ranges around the territorial border, for example, between $(x_1 + x_2)/2 - \Delta x$ and $(x_1 + x_2)/2 + \Delta x$. In this case, for each forager, the waiting

time for a prey item (eq. [1]) is the same, but the mean pursuit time (eq. [2]) increases. The energy yield (eq. [3]) is a monotonic decreasing function of pursuit time. Therefore, partial overlap also yields a lower energy intake than a sharp border and exclusive home ranges.

Discussion

Our theory provides an integrated view of territoriality in sit-and-wait predators. If prey abundance is very high or suitable habitat is abundant, foragers should settle in exclusive home ranges in a solitary context, that is, with little or no interaction between neighbors. As the resources get more scarce, the foragers need to negotiate territories, and eventually they settle to the socially stable territories (SST). As resources get even more scarce, cohabitation of two asymmetric individuals in the same habitat patch gets less likely, and the forager with greatest fighting ability may get a territory encompassing the entire patch.

We now suggest how the main predictions from our theory could be tested and discuss relevant empirical work.

Economic Equity

We predict a situation of economic equity in a homogeneous habitat when foragers are of similar sizes and incur the same metabolic costs during contests. In the case of sequential territorial settlement, this prediction is particularly interesting because a homogeneous patch will be divided equally between residents and newcomers, provided they have similar physiological states. Stamps (1992) found in a study with *Anolis aeneus* that the number of individuals settling territories does not differ when individuals arrive simultaneously or sequentially to the patch. Nevertheless, we cautiously remark that in some instances, residents have accumulated significant amounts of energy (Riechert 1998), causing an asymmetry in fighting ability between residents and newcomers.

Economic Inequity

We predict that in a heterogeneous habitat, there may be economic inequity between foragers. This has two consequences. First, individuals arriving at the same time at a heterogeneous patch may obtain territories associated with different fitnesses. Second, in a heterogeneous habitat, residents should obtain better territories than newcomers, as in the ideal despotic distribution of Fretwell (1972). We do not know of any controlled experiments to test these patterns with sit-and-wait predators. However, studies with birds and mammals hint at the generality of economic inequity and first settler's advantage in heterogeneous environments (Nolet and Rosell 1994; Hasselquist 1998;

Turner and McCarty 1998). For instance, red squirrel (*Sciurus vulgaris*) females shift territories from areas of low food abundance to areas of high food abundance when high food abundance territories are vacated by the death of previous owners (Wauters et al. 1995). Furthermore, female reproductive output is correlated with the food abundance in the territory (Wauters et al. 1995). A more direct test of our models could be performed by manipulating the prey gradient with food supplementation and tracking the changes in territory borders.

Forager Asymmetries

Much of the work on territorial contests focuses on winner-take-all contests (Riechert 1998), in which resource holding power (RHP) asymmetries play a decisive role in the contest outcome. In our theory, a winner-take-all contest arises when fighting abilities, the main factor affecting RHP, are very asymmetric between individuals. However, there is a wide range of asymmetries for which space is effectively a divisible resource. In this more general situation, foragers with greater fighting ability obtain territories with higher fitness even in homogeneous environments. In agreement with our results, Civantos (2000) showed that, for the lizard *Psammotrogon algirus*, home-range size is correlated with the degree of aggressiveness and that individuals with larger home ranges have higher survival rates.

Opportunity Costs

Opportunity costs minimize economic inequity when there are prior residence differences in a heterogeneous environment or when the foragers have asymmetric fighting abilities. At anytime during a territory negotiation, the forager that holds the best territory pays the highest opportunity cost and is willing to concede slightly more to shorten the negotiation. Whether foragers usually take into account opportunity costs is an open question. For instance, if the time allocated to foraging does not depend on the time allocated to territory negotiation, then the opportunity costs are null. Therefore, a test of our predictions could be performed by manipulating time budgets in an experimental setting. One such test could use two time-budget scenarios: most food provided during territory negotiation periods and most food provided outside negotiation periods. Habitat configuration would be changed daily in order to make the animals renegotiate territories. If foragers have asymmetric fighting abilities, our model predicts that when opportunity costs are high, the first scenario results in a more equitable distribution of resources than the second scenario.

Overlapping Home Ranges versus Territories

Our results suggest that exclusive home ranges are the best energetic choice for sit-and-wait predators. A similar advantage of exclusive home ranges over overlapping home ranges was found by Smith (1968) using a simple model of central-place foraging. In agreement with these theoretical predictions, lizards from the family Iguanidae, mostly sit-and-wait predators, have territorial divisions of space (Stamps 1977). Moreover, studies of juveniles of *A. aeneus* (Stamps 1984) have shown that growth rates are negatively correlated with the degree of home-range overlap. Nevertheless, there are instances in which individuals overlap home ranges. For example, in *Anolis pogus* there is no territorial overlap among males or among females, but each male overlaps extensively with one female (Pereira et al. 2002), which suggests that the male-female overlap is related to reproduction.

Some studies have reported increased home-range overlap as a response to food supplementation (Stamps and Tanaka 1981; Ferguson et al. 1983; Guyer 1988b). Under food supplementation, one of our assumptions may not be satisfied: prey is abundant enough that neighbors will not want to pursue every prey item. Instead, individuals may become satiated and ignore prey items or forage at different times of the day. At the other extreme, we showed that when resources are very scarce, the difference in energy yields between overlapping home ranges and a territorial division of space is small. In this case the costs accumulated during a negotiation to settle territories may not be compensated by the small benefits of exclusive home ranges. An explicit calculation of the negotiation costs would require a model of the negotiation process such as the one in the appendix. Negotiation costs are particularly important if there are frequent environmental changes requiring a renegotiation of the territories. Finally, postnegotiation costs of territorial defense, not incorporated in our model, may also play a role in a decision to overlap home ranges.

Multiple Habitat Patches

Habitat selection theory gives insights into how multiple patches could be incorporated into our theory (Fretwell 1972; Rosenzweig 1991; Weber 1998). The availability of other patches for territory settlement adds an option to the foragers. If they can get a better territory somewhere else, they should leave the current patch. This is of special relevance in situations of economic inequity: the forager that is worse off may leave even when SST exist because the mean energy yield at other patches is higher than the yield at the current patch. Learning rules for a decision

of when to leave a patch have been explored by Ruxton et al. (1999) and Bernstein et al. (1991).

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APPENDIX

A Model of the Negotiation Process

There has been little empirical work on how individuals settle territories (Stamps and Krishnan 1999). We conjecture the following negotiation dynamics. From initial perch positions $x_1(0)$ and $x_2(0)$, each individual moves in the direction allowed by equation (8). The greater the difference between the weighted marginal energy yields, the larger the move is. The foragers then reestimate their own and their opponents' marginal yields and move again. After a series of moves, the foragers are expected to settle at the SST. A continuous time model of this process is

$$\frac{dx_1}{dt} = \eta \left(\frac{1}{C_1(x_1, x_2)} \frac{\partial E_1(x_1, x_2)}{\partial x_1} + \frac{1}{C_2(x_1, x_2)} \frac{\partial E_2(x_1, x_2)}{\partial x_1} \right), \quad (\text{A1a})$$

$$\frac{dx_2}{dt} = \eta \left(\frac{1}{C_1(x_1, x_2)} \frac{\partial E_1(x_1, x_2)}{\partial x_2} + \frac{1}{C_2(x_1, x_2)} \frac{\partial E_2(x_1, x_2)}{\partial x_2} \right), \quad (\text{A1b})$$

where η is a parameter that measures how large the perch moves are. It is easy to see that the SST configuration (eq. [9]) is the only equilibrium of equations (A1). It can be shown that the real part of the eigenvalues of equations (A1) at the SST are negative, implying that the SST equilibrium is locally stable.

It is interesting to note that the quantity

$$L(x_1, x_2) = \ln \left(\frac{E_1(x_1, x_2) E_2(x_1, x_2)}{d} + \frac{E_1(x_1, x_2) + E_2(x_1, x_2)}{d} + 1 \right) \quad (\text{A2})$$

is maximized during the negotiation and is a Lyapunov function of equations (A1) with time; that is, $dL(x_1, x_2)/dt > 0$, except at the SST where it equals 0. This result suggests that the SST are globally stable (i.e., the SST equilibrium is reached from any initial perches), but a complete proof is not pursued here.

This Lyapunov function has an interesting interpretation. Consider first the case where opportunity costs are negligible relative to metabolic costs. Then the first term inside the logarithm can be ignored, and maximizing $L(x_1, x_2)$ is equivalent to maximizing the sum of the energy

yields, or productivity, of both foragers. Therefore, maximum productivity is achieved by perfect competition (for a similar result in a nonterritorial context, see Brew 1984).

When opportunity costs cannot be ignored, the sum of the productivity and $E_1(x_1, x_2)E_2(x_1, x_2)$ is maximized. This term is a measure of economic equity in the territorial configuration (note that $[E + \delta][E - \delta] < E^2$). Therefore, a combination of economic equity and productivity is maximized.

Literature Cited

- Adams, E. S. 2001. Approaches to the study of territory size and shape. *Annual Review of Ecology and Systematics* 32:277–303.
- Bernstein, C., A. Kacelnik, and J. R. Krebs. 1991. Individual decisions and the distribution of predators in a patchy environment. II. The influence of travel costs and structure of the environment. *Journal of Animal Ecology* 60: 205–226.
- Brew, J. S. 1984. An alternative to Lotka-Volterra competition in coarse-grained environments. *Theoretical Population Biology* 25:265–288.
- Brown, J. L. 1964. The evolution of diversity in avian territorial systems. *Wilson Bulletin* 76:160–169.
- Brown, J. S. 1998. Game theory and habitat selection. Pages 188–220 in L. A. Dugatkin and H. K. Reeve, eds. *Game theory and animal behavior*. Oxford University Press, New York.
- Carpenter, F. L. 1987. Food abundance and territoriality: to defend or not to defend? *American Zoologist* 27:387–400.
- Civantos, E. 2000. Home-range ecology, aggressive behaviour, and survival in juvenile lizards *Psammmodromus algirus*. *Canadian Journal of Zoology* 78:1681–1685.
- Dugatkin, L. A., and H. K. Reeve. 1998. *Game theory and animal behavior*. Oxford University Press, New York.
- 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.
- Enquist, M., and O. Leimar. 1990. The evolution of fatal fighting. *Animal Behaviour* 39:1–9.
- Ferguson, G. W., J. L. Hughes, and K. L. Brown. 1983. Food availability and territorial establishment of juvenile *Sceloporus undulatus*. Pages 135–148 in R. Huey, E. Pianka, and T. Schoener, eds. *Lizard ecology*. Harvard University Press, Cambridge, Mass.
- Fretwell, S. D. 1972. *Populations in a seasonal environment*. Princeton University Press, Princeton, N.J.
- 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.
- Gordon, D. M. 1997. The population consequences of ter-

- ritorial behavior. *Trends in Ecology & Evolution* 12: 63–66.
- Guyer, C. 1988a. Food supplementation in a tropical mainland anole, *Norops humilis*: demographic effects. *Ecology* 69:350–361.
- . 1988b. Food supplementation in a tropical mainland anole, *Norops humilis*: effects on individuals. *Ecology* 69:362–369.
- Hasselquist, D. 1998. Polygyny in great reed warblers: a long-term study of factors contributing to male fitness. *Ecology* 79:2376–2390.
- Houston, A., and J. McNamara. 1999. *Models of adaptive behaviour*. Cambridge University Press, Cambridge.
- 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.
- Maynard Smith, J. 1982. *Evolution and the theory of games*. Cambridge University Press, Cambridge.
- Nolet, B. A., and F. Rosell. 1994. Territoriality and time budgets in beavers during sequential settlement. *Canadian Journal of Zoology* 72:1227–1237.
- 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.
- Parker, G. A. 1985. Population consequences of evolutionarily stable strategies. *British Ecological Society Symposium* 25:33–58.
- Parker, G. A., and D. I. Rubenstein. 1981. Role assessment, reserve strategy and acquisition of information in asymmetric animal conflicts. *Animal Behaviour* 29:221–240.
- Pereira, H. M., S. Loarie, and J. Roughgarden. 2002. Monogamy, polygyny and interspecific territoriality in two coexisting *Anolis* species. *Caribbean Journal of Science* 38:132–136.
- Perry, G. 1999. The evolution of search modes: ecological versus phylogenetic perspectives. *American Naturalist* 153:98–109.
- Riechert, S. E. 1998. Game theory and animal contests. Pages 64–93 in L. A. Dugatkin and H. K. Reeve, eds. *Game theory and animal behavior*. Oxford University Press, New York.
- Rosenzweig, M. L. 1991. Habitat selection and population interactions: the search for mechanism. *American Naturalist* 137(suppl.):S5–S28.
- Roughgarden, J. 1995. *Anolis lizards of the Caribbean: ecology, evolution, and plate tectonics*. Oxford University Press, New York.
- Ruxton, G. D., J. D. Armstrong, and S. Humphries. 1999. Modelling territorial behaviour of animals in variable environments. *Animal Behaviour* 58:113–120.
- Schoener, T. W. 1983. Simple models of optimal feeding-territory size: a reconciliation. *American Naturalist* 121: 608–629.
- Shafir, S., and J. Roughgarden. 1998. Testing predictions of foraging theory for a sit-and-wait forager, *Anolis gingivinus*. *Behavioral Ecology* 9:74–84.
- Smith, C. C. 1968. The adaptive nature of social organization in the genus of three squirrels *tamiasciurus*. *Ecological Monographs* 38:31–64.
- Stamps, J. A. 1977. Social behavior and spacing patterns in lizards. Pages 265–334 in C. Gans and D. W. Tinkle, eds. *Biology of the reptilia*. Vol. 7. Ecology and behavior. Academic Press, London.
- . 1983. Sexual selection, sexual dimorphism and territoriality. Pages 169–204 in R. Huey, E. Pianka, and T. Schoener, eds. *Lizard ecology*. Harvard University Press, Cambridge, Mass.
- . 1984. Growth costs of territorial overlap: experiments with juvenile lizards (*Anolis aeneus*). *Behavioral Ecology and Sociobiology* 15:115–120.
- . 1992. Simultaneous versus sequential settlement in territorial species. *American Naturalist* 139:1070–1088.
- 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.
- Stamps, J. A., and S. Tanaka. 1981. The influence of food and water on growth rates in a tropical lizard (*Anolis aeneus*). *Ecology* 62:33–40.
- Stephens, D. W., and J. R. Krebs. 1986. *Foraging theory: monographs in behavior and ecology*. Princeton University Press, Princeton, N.J.
- Stephens, D. W., and J. R. Stevens. 2001. A simple spatially explicit ideal-free distribution: a model and an experiment. *Behavioral Ecology and Sociobiology* 49:220–234.
- Tricas, T. C. 1989. Determinants of feeding territory size in the corallivorous butterflyfish, *Chaetodon multicinctus*. *Animal Behaviour* 37:830–841.
- Turner, A. M., and J. P. McCarty. 1998. Resource availability, breeding site selection, and reproductive success of red-winged blackbirds. *Oecologia (Berlin)* 113:140–146.
- Wauters, L. A., L. Lens, and A. A. Dhondt. 1995. Variation in territory fidelity and territory shifts among red-squirrel, *Sciurus vulgaris*, females. *Animal Behaviour* 49: 187–193.
- Weber, T. P. 1998. News from the realm of the ideal free distribution. *Trends in Ecology & Evolution* 13:89–90.
- Ydenberg, R. C., L. A. Giraldeau, and J. B. Falls. 1988. Neighbors, strangers, and the asymmetric war of attrition. *Animal Behaviour* 36:343–347.