(E)

# Population and Community Consequences of Spatial Subsidies Derived from Central-Place Foraging

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abstract: Central-place foragers, such as ants, beavers, and colonial seabirds, can act as biological conduits, subsidizing local communities with allochthonous resources. To explore the consequences of such biologically vectored resource redistribution, we draw on an example from cave ecology and develop a population-level model of central-place foraging based on the dispersal kernel framework. We explore how the size of the patch in which central-place foraging occurs and the spatial distribution of foragers within that patch feed back to influence the population dynamics of the central-place forager and the species richness of the associated recipient community. We demonstrate that the particular way in which a population of central-place foragers uses space has two important effects. First, space use determines the stability of the forager population and establishes patch size thresholds for persistence, stable equilibria, and limit cycles. Second, alternative foraging kernels lead to qualitatively different scaling relationships between the size of the foraging patch and species richness back at the central place. These analyses provide a new link among elements of ecology related to animal behavior, population dynamics, and species diversity while also providing a novel perspective on the utility of integrodifference equations for problems in spatial ecology.

*Keywords:* cave crickets, cave ecology, critical patch size, integrodifference equation, population cycles, spatial subsidies.

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Spatial subsidies, in which individuals or resources from one system move or are transferred into a neighboring system, have important effects on food web dynamics because they can change the relative strength of top-down and bottom-up control (Polis and Hurd 1996; Polis et al. 1997; Huxel and McCann 1998) and set conditions for species persistence or extinction (Fagan et al. 1999; Cantrell et al. 2001). Much effort has been devoted to characterizing inputs of allochthonous basal resources (e.g., sea wrack, dead leaves, salmon carcasses) and quantifying the importance of those subsidies relative to locally derived resources (e.g., Polis et al. 1997; Naiman et al. 2002). Clearly, a continuum of systems exists, ranging from those where spatial subsidies are of negligible importance to those where the quantity and quality of allochthonous resources are the primary determinants of local conditions. This latter extreme includes the communities of guanophilic species inhabiting rocky islands where seabirds nest (Sánchez-Piñero and Polis 2000; Ellis 2005), inquiline assemblages within ant or termite mounds (Aron et al. 1999; Ichinose et al. 2004), vast portions of the deep-sea floor that depend on marine snow (Herring 2002), and cave ecosystems where troglobitic species (obligate cave dwellers) depend on surface-derived productivity (Barr 1967).

One can classify subsidy-dependent communities in terms of the mechanism that affords the allochthonous inputs. For example, some subsidies, such as sea wrack and marine snow, are transported largely by physical processes, whereas in other cases, organisms themselves act as conduits for resource inputs into a local community (e.g., salmon, ants, seabirds). For both types of subsidies, it is important to consider the spatial domain from which those resources are drawn, and in the case of biologically vectored subsidies, it is possible to tie the extent and magnitude of spatial subsidies to the movement patterns of the animal vectors. The spatial extent of such effects can be substantial; for example, Naiman et al. (2002) have demonstrated that marine-derived nutrients (transported in the form of the bodies of migrating salmon) play critical roles in terrestrial ecosystems hundreds of kilometers from the coast. Of course, spatial subsidies occurring over much

smaller spatial scales may also help determine local conditions. For instance, seabirds foraging a few kilometers from their nest sites and ants foraging a few hundred meters from their colony both procure food in one area and transport those materials (or digesta and waste products thereof) to another, distant location. At the seabird and ant nesting areas, allochthonous resources contribute to successful reproduction, whereas the waste products from those species contribute to detritus pools (e.g., guano) on which other species depend (Haines 1978; Sánchez-Piñero and Polis 2000; Ellis 2005).

Seabirds, ants, and similar examples represent cases in which spatial subsidies are facilitated by so-called central-place foragers acting as biological conduits for allochthonous resources. Central-place-foraging theory (Orians and Pearson 1979; Schoener 1979; Elliott 1988) emerged as a branch of optimal-foraging theory designed to consider the many biological cases in which consumers restrict their resource acquisition activities to the general vicinity of some central place, such as a nest site or favored hunting perch. One theme, initiated by Orians and Pearson (1979), focused on consumers' decision-making among sets of randomly encountered, discrete patches that varied in quantity and quality of resources, whereas another theme, initiated by Schoener (1979), envisioned resources distributed continuously in space outward from the central place, with all of the resources being known to the consumer.

These classic studies, and indeed most subsequent work on central-place foraging, have focused on behavioral issues related to optimality in resource choice, such as how selective an individual consumer should be as a function of distance from its central place (Elliott 1988; Fryxell and Doucet 1991). Far less research has dealt with the ecological consequences of central-place foraging, such as the influences of foragers on community structure in the area surrounding the central place. Notable exceptions include studies of mammalian central-place foragers (e.g., beavers, pikas) that influence vegetation architecture (McGinley and Whitham 1985) or plant community composition (Huntly 1987). Birds, such as corvids (Weir 1969) and waders (Oliver and Legovic 1988), may nutritionally enrich local habitats through the spatial concentration of incompletely consumed meals and waste products. Likewise, central-place foraging by lizards may induce spatial patterning in the densities of their grasshopper prey and, indirectly, in the distribution of plants near lizard perch sites (Chase 1998).

Because of the long-standing focus on central-place foragers as individuals, studies linking central-place foraging to the population structure or dynamics of the foraging species are sorely lacking. We found only three exceptions. Getty (1981) outlined how simultaneous central-place foraging by several individuals may spatially subdivide a habitat. Wolff (1994) modeled a bird colony as a collection of individuals, each of which made its own foraging and movement decisions, to explore the effects of food availability and seasonal flooding on nestling survival. Finally, Buckley (1997) explored the role of central-place foraging in the evolution of coloniality. These three studies are especially noteworthy because together they provide a bridge between the "individual-forager" ideas inherent in the classical development of central-place foraging (Orians and Pearson 1979; Schoener 1979) and the ecological reality that many species that engage in central-place foraging behaviors, such as seabirds, bats, and ants, are often quite gregarious.

Here we draw some robust connections between spatial aspects of central-place-foraging behaviors and the population dynamics of the foraging species. We develop a theoretical model based on the dispersal kernel framework (Kot and Schaffer 1986; Neubert et al. 1995; Lutscher and Lewis 2004) to explore how the size of the spatial domain over which central-place foraging occurs and the spatial distribution of foragers within that domain feed back to influence key aspects of forager population dynamics, such as stability and patch size thresholds for persistence. Throughout our modeling, we take an explicitly population-level perspective of central-place foraging rather than the individual-level perspectives that have historically predominated in the field. Coupling this population-level perspective with "foraging kernels" in an integrodifference equation framework allows us to separate the domain over which foraging may occur from the patch size over which resources may be distributed and leads to situations in which population stability depends on how the central-place foragers use space.

To make our modeling more concrete, we organize our efforts around cave ecosystems in which cave crickets, like bats, shelter in caves but forage for resources aboveground in the area surrounding the cave entrance. Despite this focus, the modeling framework we develop is quite general, applying equally well to diverse species in terrestrial and marine environments where animals reside communally in central locations but forage in the surrounding area.

We begin our efforts with a brief overview of cave ecology and the biology of cave crickets in particular. The main body of the article is then devoted to development and analysis of a population-level central-place-foraging model. In our discussion of the model, we focus on the implications of patch size for the population dynamics of central-place foragers and the species richness of communities that are dependent on the allochthonous resources transported by the foragers. Additional analyses and details are provided in appendices A–F in the online edition of the *American Naturalist.*

## Cave Cricket Biology and the Spatial Ecology of Cave Ecosystems

Cave and camel crickets (Orthoptera: Rhaphidophoridae) are key elements of cave ecosystems. Ubiquitous inhabitants of cave walls and ceilings, cave crickets often reach high densities (effective trap density: 1–24 trap$^{-1}$ day$^{-1}$; Poulson and Culver 1969; Cokendolpher et al. 2001), with most individuals occurring in roost areas that are located tens to hundreds of meters interior from cave entrances (Reichle et al. 1965; Peck 1976; Taylor et al. 2005). Within a given cave, cricket populations may include many thousands of individuals (Culver 2005). Cave cricket densities and population sizes may thus reach levels that are one to two orders of magnitude higher than those of most other cave invertebrates (K. Schneider, personal observation).

The cave environment, which is relatively constant in temperature and limited in species richness (Culver 1982), offers crickets protection from heat and refuge from predators (Culver 2005). However, because all but a few cave interiors feature zero autochthonous primary productivity (Poulson and White 1969; Culver 1982), crickets must leave the caves to forage for food. In many, perhaps most, species of cave crickets, adults routinely exit their cave at night to forage on the surface (Culver 2001). In one study, marked individuals were recaptured up to 105 m from the cave entrance (Taylor et al. 2005). When foraging on the surface, cave crickets employ a highly omnivorous feeding strategy, scavenging for vegetation, fungi, fruits, insects, and detritus (Messana 2004; Taylor et al. 2005). Because cave crickets forage outside their caves but return to the cave for shelter and reproduction (Culver 2005), the crickets act as invaluable transporters of allochthonous energy and nutrients into ecosystems that are profoundly resource limited (Barr 1967; Poulson et al. 1995). In some cave cricket species (e.g., *Ceuthophilus secretus* [Taylor et al. 2005] and *Ceuthophilus conicaudus* [Campbell 1976]), these movements constitute diel migrations with several hours spent aboveground each day, whereas in other species, migrations into caves occur seasonally (e.g., *Ceuthophilus silvestris*; Hobbs 2005). In those populations with daily movements, individual crickets make the journey every week or so, depending on gut fullness (Reichle et al. 1965; Culver 2005; Poulson 2005; Taylor et al. 2005).

The crickets' contributions to cave ecosystems come in at least three forms: fecal material, cricket bodies, and cricket eggs (Taylor 2003; Taylor et al. 2005). After foraging, crickets return to the cave and digest food they have consumed outside; this food may weigh as much as 100%–200% of empty-gut body weight (Poulson 2005). Although crickets have very high assimilation efficiencies (Poulson 2005), their feces, which is often high in undigested veg-etable matter, is still resource rich and can provide food for a variety of consumers (Gnaspini 2005). Cricket defecation often occurs when crickets have moved away from their roost areas toward the back of their cave, thus providing an important, renewable source of resource transfer to the deep recesses of caves (Poulson 2005). This fecal material, which can accumulate into deposits of guano, constitutes a key resource for a community of generalized decomposer species (snails, millipedes, and springtails) and predatory species (catopid and pselaphid beetles, flies, mites, and worms) that exhibit increased densities in areas where cricket feces is most abundant (Peck 1976; Poulson 2005). Cricket bodies are also a rich resource, although in contrast to guano, bodies are sometimes quickly depleted and may not necessarily be replenished in the same localities (Poulson 2005). Cricket eggs are an unusually rich source of food in caves (Culver 2005; Poulson 2005), and their role as a unique resource has been extensively studied in diverse cave ecosystems (e.g., Barr 1967; Barr and Kuehne 1971; Kane and Poulson 1976; Taylor 2003). We discuss dynamic consequences of arthropod predation on cricket eggs in appendix C.

## Model Formulation and Analysis

We organize our presentation of the model into several subsections. These are (1) the baseline, nonspatial cave cricket–resource model, (2) the explicitly spatial model incorporating central-place foraging, (3) nondimensionalization of the spatial model, (4) calculation of the critical patch size, (5) investigation of steady states and their stability, focusing on the effect of patch size on consumer-resource dynamics, (6) extension of the spatial model to allow for "optimal foraging," and (7) explorations of how central-place foraging may influence biodiversity at the central place. Throughout, we focus on key qualitative results emerging from this model, saving technical details and formulas for a series of online appendices.

### Consumer-Resource Dynamics in the Nonspatial Case

Our model is based on the generalized schematic shown in figure 1. We use $C_t$ and $F_t$ to denote the density of the cave crickets and surface resources, respectively. Resources grow according to some function $G(F_t)$ and are consumed with probability $P(C_t)$ over the course of a year, yielding

$$F_{t+1} = G(F_t)[1 - P(C_t)]. \tag{1}$$

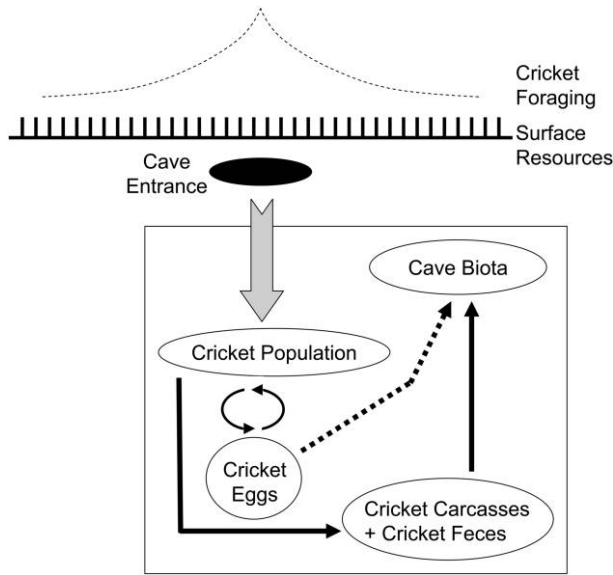We assume Beverton-Holt growth dynamics for the resource throughout; that is,

**Figure 1:** Schematic overview of our model linking central-place foraging by cave crickets to aboveground resource acquisition and the composition of the cave community that depends on those allochthonous resources.

$$G(F) = \frac{e^r K F}{K + (e^r - 1)F}. \tag{2}$$

Our choice of $G$ eliminates the strongly overcompensatory density dependence found in other candidate functions, such as Ricker growth, allowing us to focus on the effects of space and the dynamics of the within-cave community. We take $P(C)$ to be a negative exponential; that is,

$$P(C) = 1 - \exp(-a_F C), \tag{3}$$

where $a_F$ is the cricket's searching efficiency. The resources eaten during year $t$ are given by

$$E_t = G(F_t)P(C_t). \tag{4}$$

We assume that egg production of consumers is a linearly increasing function of resources consumed. Crickets survive from one year to the next with probability $s_c$, which we assume to be constant for simplicity. The cricket population follows the equation

$$C_{t+1} = s_c C_t + \tilde{\beta} E_t, \tag{5}$$

where $\tilde{\beta}$ is a conversion coefficient relating consumed biomass to new adult crickets, collapsing (for now) the cricket's entire developmental period into this single parameter. Note that $E$ is the total consumption, so that the

per capita consumption is $E/C$, and hence the total production is $\tilde{\beta}(E/C)C = \tilde{\beta}E$.

## *The Spatial Model and Its Analysis*

In the nonspatial form (eqq. [1], [5]), this resource-consumer system has been studied widely, most prominently in host-parasitoid systems with $s_c = 0$, Ricker or Hassell dynamics for the resource, and various forms for $P(C_t)$ (e.g., Hassell 2000; Kot 2001; Murdoch et al. 2003 and references therein). Since cave crickets, like other central-place foragers, must leave their central place to forage on spatially distributed food resources in the vicinity of the cave, we now modify the model to take space into account. We assume that foraging distances of the crickets are given by a certain probability density function $k(x)$, similar to a dispersal kernel (Neubert et al. 1995; Kot et al. 1996); see figure 2 for examples. Then the density of crickets foraging on the surface is simply $C_t k(x)$. With these modifications, equations (1) and (4), respectively, change to

$$F_{t+1}(x) = G(F_t(x))[1 - P(C_t k(x))], \tag{6}$$

$$E_t = \int G(F_t(x))P(C_t k(x)) \, dx, \tag{7}$$

while equation (5) remains unchanged, if we assume that no crickets die while foraging. (We discuss foraging-related death below.) For simplicity, we assume that resource growth is spatially homogeneous, that is, that $G$ does not explicitly depend on spatial location. We always assume that the central place is located at $x = 0$ and that the foraging kernel $k(x)$ is a nonnegative symmetric function whose integral over the entire real line is 1.

To study the effects of habitat size, we assume a habitat of size $L$ symmetric around the cave; that is, we choose the interval $[-L/2, L/2]$ as the domain of integration in equation (7). We assume that the resource $F$ recruits locally and does not undergo spatial redistribution. Note that this model development allows the crickets to act as central-place foragers in the spatial sense only. Aside from the movement behaviors captured via alternative dispersal kernels, we are not yet including any details concerning behavioral rules related to resource choices available to individual foragers. However, we emphasize that all the kernels we consider (except the top-hat kernel) reflect a requirement that Chase (1998) derived from behavioral considerations, namely, that "optimal foragers should concentrate efforts near refugia and decrease efforts with increasing distance from refugia" (p. 1236). Note also that our view of how resources are distributed on the surface follows the continuum-of-resources perspective of central-

place foraging (Schoener 1979) rather than the patches-of-resources perspective (Orians and Pearson 1979).

### *Nondimensionalization*

We start the analysis of the model by introducing the nondimensional quantities $F_t = Kf_t$, $a_F C_t = c_t$, and $\beta = \tilde{\beta} K a_F$, allowing us to rewrite equations (5)–(7) as

$$f_{t+1}(x) = \frac{e^r f_t(x)}{1 + (e^r - 1)f_t(x)} \exp[-c_t k(x)], \tag{8}$$

$$c_{t+1} = s_c c_t + \beta$$

$$\times \int_{-L/2}^{L/2} \frac{e^r f_t(x)}{1 + (e^r - 1)f_t(x)} [1 - \exp(-c_t k(x))] \, dx, \tag{9}$$

where we may assume that $x$ has been scaled such that the average dispersal distance is unity—that is, $\int |x|k(x)\,dx = 1$—and $L$ measures multiples of this quantity.

### *The Critical Patch Size*

Linearizing equation (9) at the steady state ($f^* = 1$, $c^* = 0$) yields the persistence condition for the crickets,

$$\int_{-L/2}^{L/2} k(x)dx > \frac{1 - s_c}{\beta}. \tag{10}$$

The critical patch size $L^*$ for persistence of the crickets is given when equation (10) is an equality. In appendix A, we give explicit critical patch sizes for a variety of alternative dispersal kernels. Since the integral on the left-hand side of equation (10) does not exceed 1, the cricket population cannot persist if $s_c + \beta < 1$.

Our assumption that cave crickets do not die while foraging implies that crickets foraging outside the habitat patch do not contribute to offspring production, but they do return to the cave. However, crickets must contend with a variety of mortality agents while above ground, such as nocturnal insectivorous mammals and road traffic (Taylor et al. 2005). Even though different types of foraging-related mortality will enter the equations in different ways, they share a common qualitative result, regardless of source or spatial location: they all increase the critical patch size for persistence of the cricket population. Precise expressions for the critical patch sizes in the presence of alternative forms of foraging-related mortality are given in appendix B. In appendix C, we consider how critical patch size effects are modified by the presence of a cave-dwelling specialist predator that preys on cricket eggs.

### *Steady States and Their Stability*

When surface-foraging crickets are uniformly distributed inside the patch (see the top-hat kernel in fig. 2*A*), equations (8) and (9) reduce to a nonspatial model, which we analyze in appendix D. For other kernels, the analysis of positive steady states is much harder because the distributions are not homogeneous in space, and the resulting linear operators have continuous spectra. We relied on extensive numerical simulation in those cases. Analysis and numerics combined demonstrate the intriguing result that the size of the patch in which the crickets forage controls the stability and dynamics of their population.

One of our most important findings is that the effects of patch size on cricket population dynamics are qualitatively different for different dispersal kernels (fig. 3). For example, for all four kernels, as the patch size $L$ increases beyond the critical size $L^*$, a stable equilibrium density for the crickets, $c^* > 0$, emerges. As has been observed for a variety of central-place-foraging species (e.g., Huntly 1987; Chase 1998), resources are depleted in the immediate vicinity of the central place when the consumer population is at this stable equilibrium, provided that foraging is not uniform. Here, resource depletion means that the equilibrium density is held far below its carrying capacity and may be 0. The steady state distributions $f(x)$ for three different kernels are given in figure 4.

The crickets' equilibrium density increases as patch size increases, indicating that enhanced foraging opportunities will sustain a larger population of crickets. However, depending on the values of other parameters and the dispersal kernel involved, this equilibrium may eventually become unstable via a Hopf bifurcation, leading to cyclical population dynamics. For instance, for $e^r = 2$, $s_c = 0.5$, and $\beta = 4$, there is a Hopf bifurcation for the top-hat kernel at some patch size $L^{**}$, and there are limit cycles for all $L > L^{**}$. None of the other kernels (tent, Laplace, and Gaussian) shows a Hopf bifurcation for $\beta \leq 4$ and $0 \leq s_c \leq 1$. However, if we increase $\beta$ to 6, we see Hopf bifurcations for all kernels except the Laplace kernel (fig. 3). To obtain limit cycles with the Laplace kernel (as well as the other three kernels) requires increasing $\beta$ even further, for example, to 12 (results not shown). In appendix E, we demonstrate that the relationship between the parameters $\beta$ and $s_c$ and the Hopf bifurcations differ markedly between the spatially uniform top-hat kernel and the other kernels we consider; those results clarify that the loss of stability of the cricket population is truly a spatial effect.

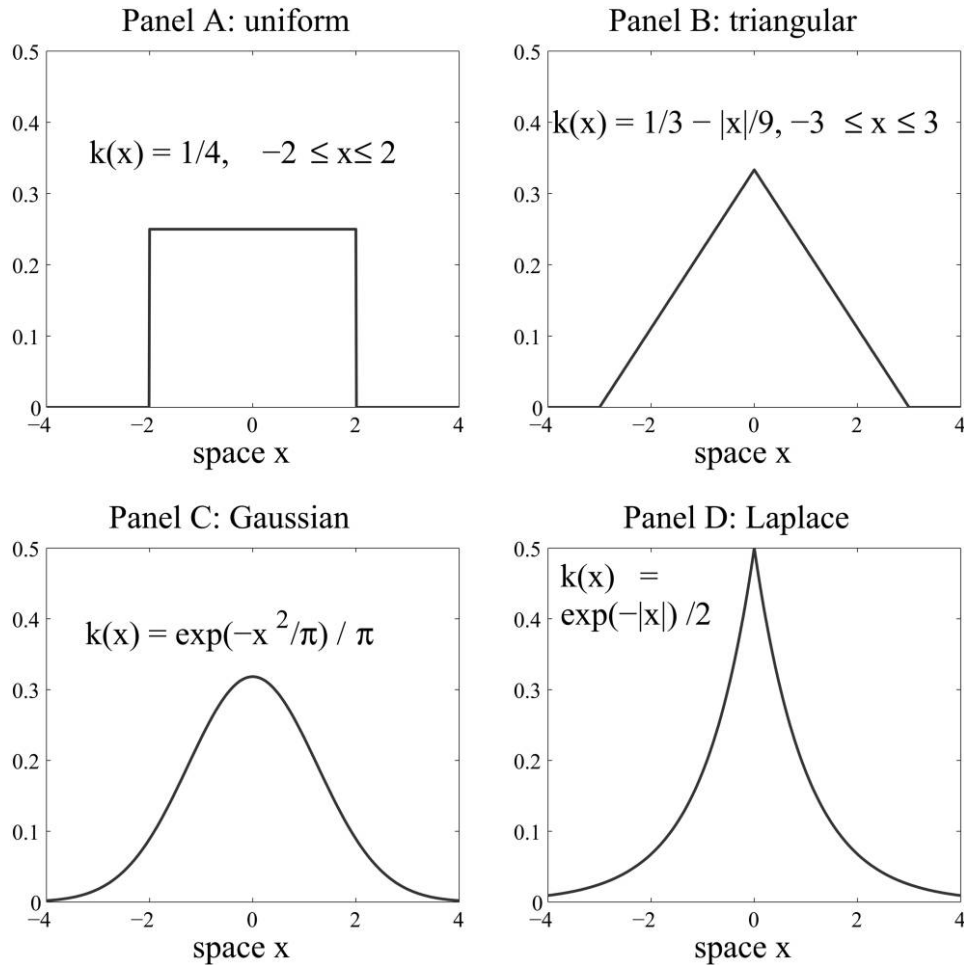Interestingly, increasing patch size still further may restabilize previously unstable steady states (fig. 3). Specif-

## Panel A: uniform

$$k(x) = 1/4, \quad -2 \leq x \leq 2$$

space x

## Panel B: triangular

$$k(x) = 1/3 - |x|/9, \ -3 \ \leq x \leq 3$$

space x

## Panel C: Gaussian

$$k(x) = \exp(-x^2/\pi) \, / \, \pi$$

space x

## Panel D: Laplace

$$k(x) = \exp(-|x|) \, /2$$

space x

**Figure 2:** Alternative foraging kernels characterizing the aboveground spatial distributions of central-place-foraging cave crickets: top-hat (or uniform) kernel (*A*), tent (or triangular) kernel (*B*), Gaussian kernel (*C*), and Laplace kernel (*D*). The equations governing each kernel's probability density function are given in the respective panels.

ically, in all kernels except the top-hat kernel, if the parameters are chosen such that there is a Hopf bifurcation leading to limit cycles for certain values of *L*, then those cycles tend to disappear again for larger values of *L*.

### Increasing Model Realism via the Use of "Adaptive" Foraging Kernels

Until now, we have assumed that the shape of the crickets' foraging kernel is constant over time. This assumption is typically made in integrodifference equations, and it seems reasonable for certain species (e.g., seeds of plants) and certain, typically large, spatial scales. In the present context, however, the assumption seems rather restrictive and departs substantially from the classical framework for central-place foragers, in which individual foragers make

different decisions about foraging for resources, depending on the spatial distribution of those resources. In this section, we incorporate certain aspects of classical central-place-foraging theory by allowing the foraging kernel to depend on the resource distribution at each time step.

More specifically, we choose a family of foraging kernels with a single parameter, for example, the variance or average dispersal distance. At each time step, we consider the scaled resource distribution $f_t$ and choose the parameter of the kernel to optimize population-level food intake, $E_t$ (eq. [7]). Using this parameter value and the resulting kernel, we then calculate the resource distribution and consumer density for the next time step. Hence, we fix a domain size *L*, and the foraging behavior of the population is "adapted" to the resource distribution at each time step. This adaptation has several interesting consequences. First
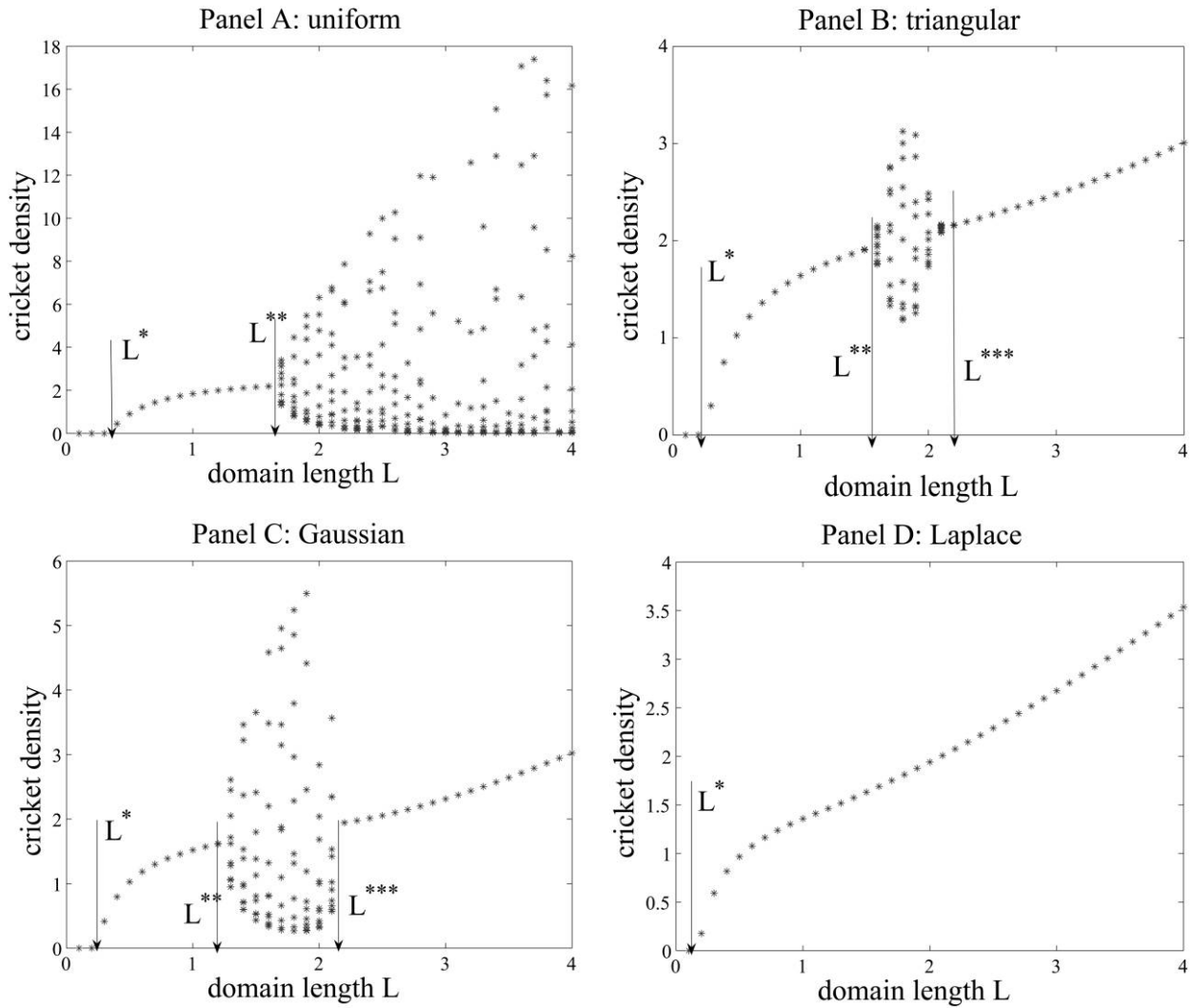
**Figure 3:** Stable equilibria and population cycles for the cave cricket population as a function of patch size *L*. Panels differ with respect to which foraging kernel the crickets employ (fig. 2): uniform (*A*), tent (*B*), Gaussian (*C*), or Laplace (*D*). Parameters in all four panels are $e^r = 2$, $s_c = 0.5$, and $\beta = 6$. Hopf bifurcations and limit cycles occur for all kernels except the Laplace, which has a stable equilibrium under these conditions. The critical patch size $L^*$ and the Hopf bifurcation point $L^{**}$ are indicated as in "Steady States and Their Stability." The size at which the limit cycles disappear (for the triangular and Gaussian kernels) is indicated by $L^{***}$. The plots are obtained as follows. The equations are solved numerically for 2,000 generations; then the values for the last 10 generations are plotted. If the system is at steady state, then all 10 points are on top of each other. If the system is at a limit cycle, then the points fall on a vertical line above the corresponding value for *L*.

of all, the critical domain size with maximizing food intake through changing foraging pattern now reads

$$\sup_{a>0}\left\{\int_{-L/2}^{L/2} k_a(x)\,dx\right\} > \frac{1 - s_c}{\beta}. \qquad (11)$$

If we think of the parameter *a* as a variance, then the integral on the left approaches unity as *a* approaches 0.

Hence, the supremum on the left-hand side has a value of 1 independent of the patch size; that is, the population can persist on arbitrarily small domains, provided that $\beta > 1$ and $0 \le s_c \le 1$. Note, however, that the population size will become arbitrarily small at small domain sizes; hence, the population will be prone to extinction through stochastic effects that we are not modeling here. In the following, we report and contrast numerical results on the stability of steady states and bifurcations for two different families of kernels.
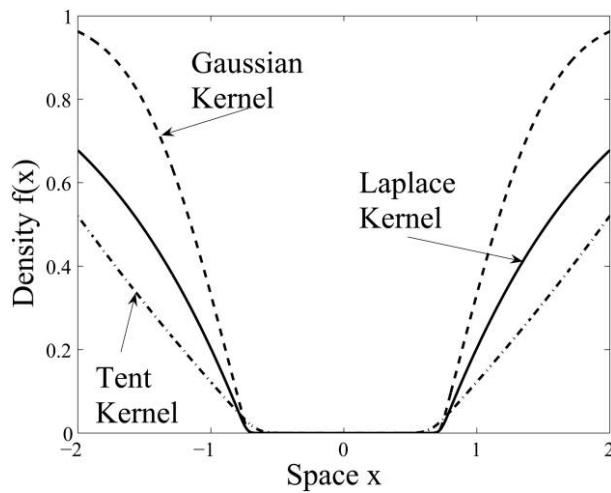
**Figure 4:** Steady state resource distribution ($F(x)$) with positive cricket density. The parameters are $e^r = 1.5$, $\beta = 4$, $s_c = 0.5$, and $L = 4$. The different lines represent different foraging kernels for the crickets: Gaussian (*dashed line*), Laplace (*solid line*), and tent (*dash-dotted line*). The central place is at $x = 0$. Maximum resource density is scaled to unity.

We start with the Laplace kernel (fig. 2*D*), where the variance is the free parameter used to adapt the kernel to the resource distribution. It turns out that the effect of optimizing population-level food intake at every time step is to stabilize the steady state of the consumer-resource model in the following sense. For a fixed domain size and fixed values of $r$ and $s_c$, the value of $\beta$ for which the Hopf bifurcation occurs is larger with optimization than without. (Specifically, the bifurcation line in fig. D1*C* in the online edition of the *American Naturalist* is shifted upward; results not shown.) The Laplace kernel (and many others) has its maximum at $x = 0$; that is, foragers are concentrated near the central place, even if the resource is depleted there. In the next paragraph, we introduce a novel kernel that allows foragers to be concentrated away from the central place.

Specifically, we explore adaptive central-place foraging via the "gamma kernel,"

$$k_a(x) = \frac{|x|^{a-1}e^{-|x|}}{2\Gamma(a)}. \tag{12}$$

The gamma kernel (fig. 5*A*) is obtained from the standard form of the gamma probability density function by reflection at $x = 0$ and normalization by a factor of $1/2$. The variance of $k_a$ is $a(a + 1)$. For $0 < a < 1$, this kernel has a singularity at $x = 0$, whereas for $a = 1$, we have the Laplace kernel with a variance of 2. For $a > 1$, the gamma kernel is 0 at $x = 0$, meaning that, unlike the other

kernels considered thus far, the gamma kernel with $a > 1$ peaks away from the center.

Using this kernel in the adaptive model described above, we report the numerical results in two cases: first, we fix all parameters except for $\beta$, and second, we fix all parameters except for $L$. We are particularly interested in whether the resulting optimal kernel has a maximum at 0 or away from 0, that is, whether $a < 1$ or $a > 1$.

For small values of $\beta$, we observe a stable positive steady state at which the corresponding scale parameter $a$ of the optimal foraging kernel is less than 1; that is, the kernel has its maximum at 0, and peak forager densities are close to the central place. As $\beta$ increases, the scale parameter of the kernel increases, too, and eventually, the scale parameter exceeds unity, such that the kernel now has a maximum away from 0 and peak foraging occurs some distance away from the central place. Increasing $\beta$ even further, we observe a Hopf bifurcation (cf. fig. D1), where initially the scale parameter of the kernel stays above 1 for the whole cycle. As $\beta$ increases even more, the cycles remain, but now the scale parameter drops below 1 for some of the time steps during a complete cycle. What happens is that while foraging is concentrated away from the central place, the resource can grow near the central place. At some point, there is so much resource near the central place that the optimal food intake occurs near the central place, and the shape of the foraging kernel changes qualitatively. By the time these nearby resources are depleted, resources farther away have replenished, and optimal foraging leads the population to forage farther away from the central place (fig. 5*B*).

For small $L$, there is a positive stable steady state at which the scale parameter of the kernel increases from below unity to above unity; that is, there is a patch size at which the cricket population's optimal foraging switches from nearby to farther away. As patch size increases further, a bifurcation occurs. Unlike the Hopf bifurcations observed for static kernels, this bifurcation for adaptive kernels is a flip bifurcation. The best strategy is now to alternate between foraging nearby and farther away. As patch size increases still further, another bifurcation turns the preexisting two-cycle process into a three-cycle process, where over four successive time steps, the optimal strategy is to forage far away, at an intermediate distance, close by, and then far away again (fig. 5*C*). The resulting sequence of kernels for one example of the three-cycle case is given in figure 5*D*.

Note that while we continue to eschew modeling the decision-making of individual-level foragers in favor of a population-level perspective, we can nevertheless capture some key elements of classical central-place-foraging theory via the use of foraging kernels that differ among time steps as a function of the distributions of available re-
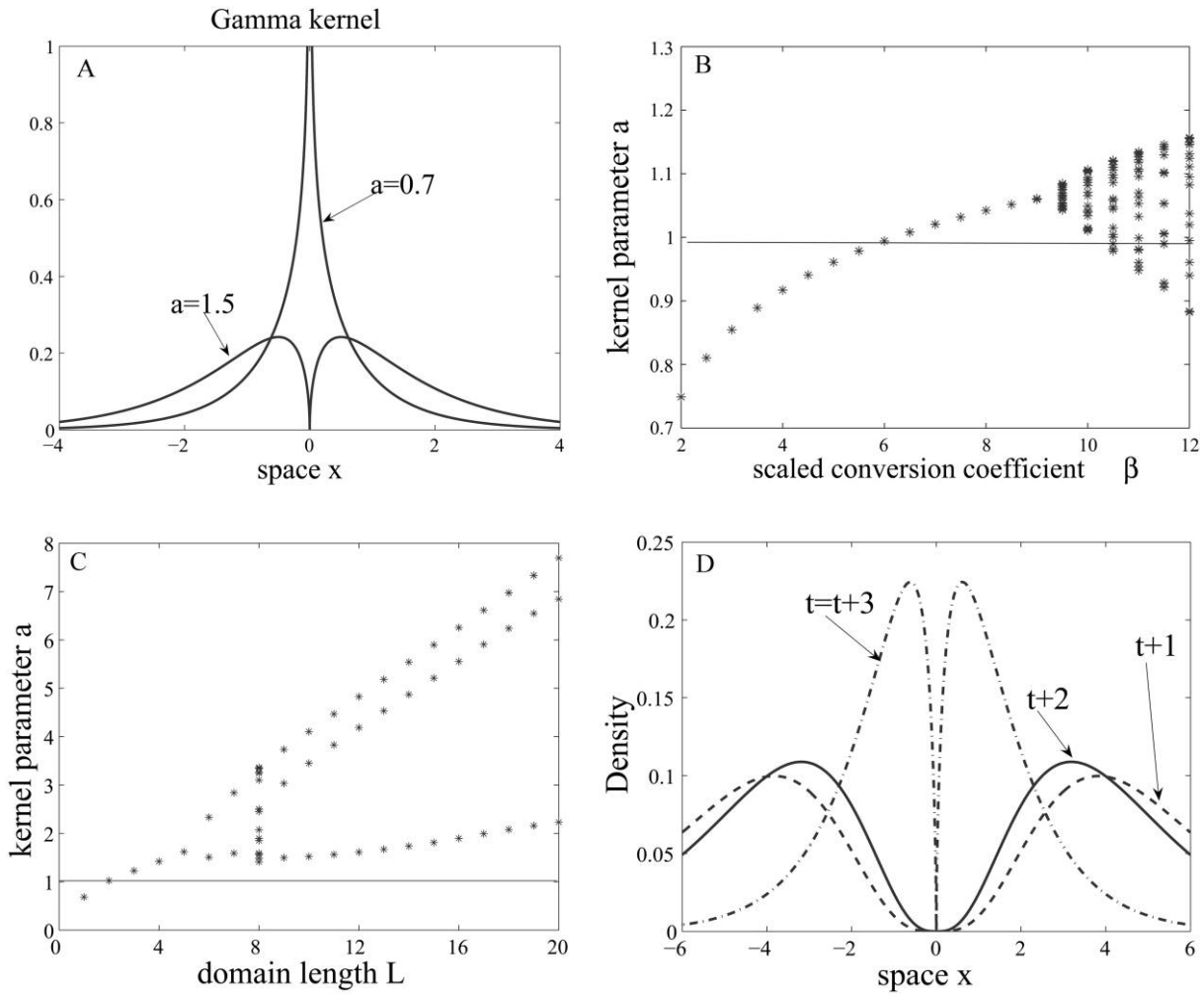
**Figure 5:** Results from our investigations of adaptive kernel dynamics. *A,* Symmetric gamma kernels ($k(x) = |x|^{a-1}\exp(-|x|)/2\Gamma(a)$) with $a = 0.7$ and 1.5. *B,* Bifurcation diagram for parameters $r = \ln(3)$, $L = 1.8$, and $s_c = 0.2$, illustrating how an increase in consumptive efficiency causes the crickets' optimal foraging kernel to vary among time steps. Points below the line $y = 1$ involve kernels that have a maximum at the central place, whereas those above the line have symmetric maxima away from the central place. Thus, for $\beta \geq 10$, the cricket population will cycle through a sequence of foraging kernels, one for each of several consecutive time steps. *C,* Bifurcation diagram for parameters illustrating the existence of stable periodic solutions in which, for large patch sizes, the crickets' optimal foraging kernels oscillate among two or three alternative kernels as the resource regrows. Parameters are $r = \ln(3)$, $s_c = 0.2$, and $\beta = 5$. *D,* The three optimal foraging kernels through which the cricket population cycles in *C* for $L = 12$.

sources. The scenario we present is admittedly more appropriate for social species (e.g., ants, termites), in which there are opportunities for colony-level decision-making about resource acquisition, than it is for colonial (but not social) cave crickets. Nevertheless, our exploration of adaptive foraging kernels does strengthen the connections between our model and classical models of central-place-foraging theory while also identifying opportunities for additional research.

## Allochthonous Resources and Community-Level Critical Patch Size Effects

Most troglobitic species feed on allochthonous detritus that finds its way into a cave. As is true in some cave systems (Taylor et al. 2005), we assume here that cave crickets are the primary conduits for these resources from outside the cave and that the detrital resources themselves consist solely of cricket carcasses and feces. This would be

especially true in caves lacking bat colonies or flowing water and in those parts of a cave remote from the entrance, where other sources of surface productivity, such as falling leaves or the decomposing bodies of wayward raccoons, would make negligible contributions. Relaxing this assumption to consider other sources of allochthonous productivity in caves (e.g., leaves or animals that fall, wash, or wander into caves) requires only straightforward changes to the model below.

To this end, we model a single pool of detrital biomass inside the cave by $B_t$. This biomass decays at a certain rate, so that the biomass equation reads

$$B_{t+1} = s_b B_t + \gamma_1 C_t + \gamma_2 (1 - s_c) C_\rho, \tag{13}$$

where $s_b$ denotes the fraction of biomass persisting to the next year, $\gamma_2$ is the conversion factor of dead crickets into biomass, and $\gamma_1$ is the rate at which crickets produce feces.

Because there is no productivity within the cave, the species richness of the troglobitic community will depend entirely on the amount of allochthonous biomass transferred into the cave by crickets that have been foraging above ground. We use

$$S_t = g \ln (B_t + 1). \tag{14}$$

This submodel for species richness is clearly a phenomenological approach, but the notion that there exists a positive, curvilinear, and decelerating relationship between the productivity of a community and the richness of species it harbors has been borne out by a variety of empirical studies (reviewed by Mittelbach et al. [2001]; Chase and Ryberg [2004]), and we use a logarithmic function to capture the shape of this relationship. Collectively, these studies suggest that this type of productivity-richness relationship holds for reasonably large spatial scales, especially when one considers the full range of trophic levels present, rather than just a suite of competitors (Mittelbach et al. 2001).

If we do not consider any feedbacks from $S_t$ to either $B_t$ or $C_\rho$, we can simply compute and plot the steady state value $S^*$ in the case when the steady state $(F^*(x), C^*)$ is stable with $C^* > 0$. The expressions are given by the system

$$B^* = \frac{\gamma_1 + \gamma_2 (1 - s_c) c^*}{a_B (1 - s_F)},$$

$$S^* = g \ln (B^* + 1). \tag{15}$$

In figure 6, we plot $S^*$ in the $\exp(r) \times L$ plane for two different kernels, demonstrating how aboveground cricket foraging sustains the belowground community and how this effect of the allochthonous subsidy depends on the
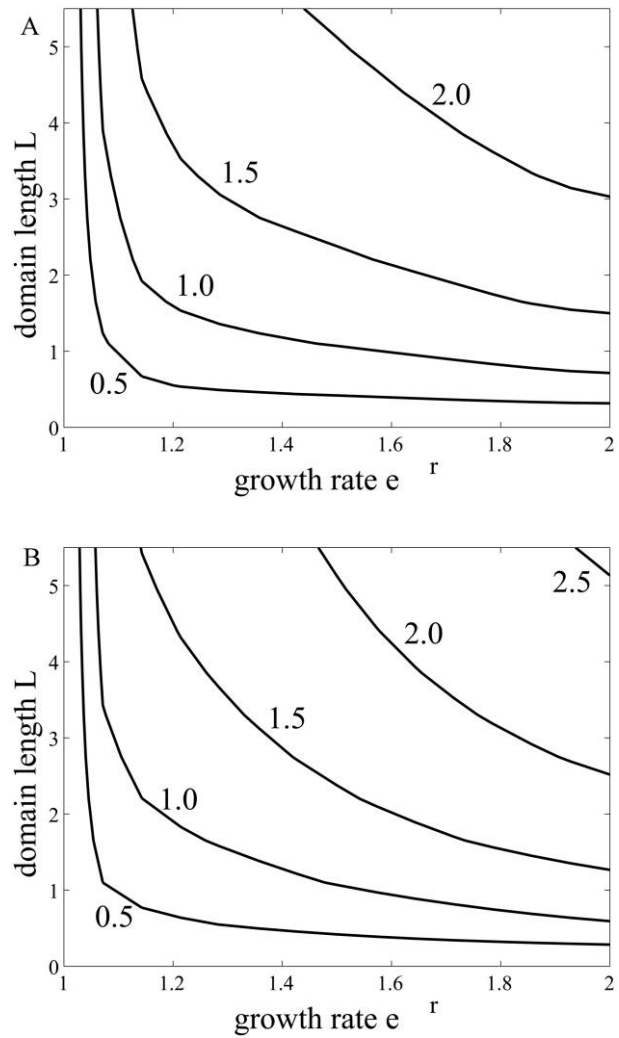


**Figure 6:** Contour lines for the steady state value $S^*$ in the $e^r \times L$ plane quantifying species richness as a function of allochthonous detritus present in the cave. *A*, Results for the tent kernel; *B*, results for the Laplace kernel. The horizontal axis is the growth rate of the aboveground resource, $e^r$; the vertical axis is the patch size $L$.

spatial distribution of foraging crickets. The Laplace kernel has a smaller critical patch size than the tent kernel, and indeed when either $\exp(r)$ or $L$ is small, within-cave diversity is higher for the Laplace kernel than for the tent kernel. However, for somewhat higher values of $L$, the situation reverses, with the tent kernel affording higher levels of species richness in the cave (i.e., for a fixed $\exp(r)$, a larger patch size is necessary to attain a given high level of species richness with the Laplace kernel). This reversal occurs because the Laplace kernel has a larger fraction of the dispersers concentrated around the central place (fig. 2), leading to a large increase in food intake

with increasing patch size when patch size is small but diminishing returns as patch size increases. However, as patch size increases still further, another reversal occurs, and foraging via the Laplace kernel leads to higher species richness back at the central place. This is because the Laplace kernel also has far more probability mass far from $x = 0$ than does the tent kernel (which actually goes to 0 for large $x$; see fig. 2). Thus, species richness is higher for the Laplace kernel at very small and very large $L$, but in between, the tent kernel leads to higher richness.

Because the cave-dwelling species actively consume the detrital biomass, the fraction of detrital biomass persisting to the next year should become a decreasing function of $S_t$; thus, $s_b = s_b(S_t)$. The exact shape of this relationship is currently under debate (reviewed by Mittelbach et al. [2001]; Chase and Ryberg [2004]), but we use the same functional form as for the probability of finding a resource above, yielding

$$s_b(S) = s_b^* \exp(-a_B S). \tag{16}$$

In any case, since the relationship should be a decreasing function of $S$, if we set $s_b = s_b(0)$ in the above formulas for constant $s_b$, we obtain an upper bound for species richness. The $F$-$C$ system is unaffected by $S$. In appendix C, we consider a possible feedback from $S$ on $C$ that may alter the dynamics of the $F$-$C$ system. Furthermore, in appendix F, we discuss a variety of possible extensions to the model, such as the addition of resource recruitment and redistribution, resource-dependent cricket mortality, and other complications.

## Discussion

Here we have developed a spatial model that links central-place foraging to population dynamics and community diversity. By translocating resources (or their derivatives) from the surrounding region to local habitats, central-place foragers act as biological conduits, subsidizing local communities with allochthonous materials. We have framed our efforts in the context of certain cave ecosystems, where cave crickets and other species constitute biological conduits providing a critical source of energy and nutrients in otherwise productivity-free cave interiors (e.g., Poulson 2005; Taylor et al. 2005). Despite this focus on caves, our modeling framework is quite general and appears relevant to a wide variety of systems where central-place foragers are important conduits for resource subsidies.

Our analyses predict that the particular way in which central-place foragers use space (i.e., which kernel governs how the foragers obtain resources) can affect both the population dynamics of the forager (fig. 3) and the species richness of the community back at the central place (fig. 6). These population- and community-level results are clearly spatial effects, rather than, say, emerging as consequences of overcompensatory density dependence in the forager (see apps. D, E). As a result, we can interpret many of the changes in population dynamics and species richness in terms of the interplay between patch size and patterns of foraging.

For a given foraging kernel, we observed several different threshold patch sizes (eq. [10]; app. D), including thresholds separating persistence from population extinction, thresholds governing the onset—and later, the cessation—of population cycling, and threshold patch sizes necessary for the stable maintenance of particular levels of species richness back at the central place. All of these thresholds could be termed "critical patch sizes"; however, only the first of these fits the traditional definition of a critical patch size in mathematical ecology (e.g., Kierstead and Slobodkin 1953; Ludwig et al. 1979). The specific patch sizes necessary for these various phenomena can depend sensitively on which kernel the central-place foragers employ, with predictions for the Laplace kernel deviating most strongly from those of other kernels (figs. 3, 5).

Our model setup is sufficiently close to the biology of a range of ecological systems that, given appropriate parameterization, this framework may afford insights relevant to specific questions in resource management. For example, the work of Taylor et al. (2005), which provided some empirical motivation for our study, involved mark-recapture efforts designed to quantify how crickets emerging from a particular Texas cave moved about above ground to feed. Such spatial data were important as a source of guidance on the elimination of nonnative predators (fire ants) from near cave entrances and the delineation of development-free buffer zones around caves. Buffer zones, which are conceptually similar to the critical patch sizes provided by our modeling efforts (eq. [10]; figs. 3, 6), were of interest to resource managers because similar caves harbor a suite of federally listed species that may largely depend on cricket-derived resources. Likewise, one could modify our modeling framework to fit scenarios in which human fishing pressures were believed linked to declines of particular seabird colonies (Bertram 1995; Arnold et al. 2006). Note that additional sources of mortality for the central-place foragers while they were acquiring resources result in a (nonlinear) increase in the size of the buffer zone necessary for population persistence (app. B). Similar increases in buffer zone size would be necessary if, instead of mere persistence, one were interested in particular population sizes for the forager or levels of species richness back at the central place (figs. 3, 6).

Our findings suggest several hypotheses that could be

tested in the field or via comparisons among different central-place-foraging species. First, at the population level, one clear prediction is that the population dynamics of central-place foragers will tend to be more stable when the exploitable resources are confined to a small patch. This is because with a small patch, fewer opportunities exist for nonlinear interactions between resource growth and the spatial distribution of foragers (figs. 3, 5*C*). Second, our results suggest that population sizes of central-place foragers will vary more over time in those species with low year-to-year survival but high resource conversion efficiency. This prediction, which holds regardless of the foraging kernel employed (fig. 5*B*; app. E), emerges because the combination of low survival and high conversion efficiency tends to decouple resource acquisition from population change. Third, when central-place foragers can optimize the shape of their foraging kernels to maximize population-level resource intake, species with higher resource conversion efficiencies should forage more widely, such that at equilibrium, peak foraging activity will occur farther away from the central place (fig. 5*B*). Additional theoretical investigations are necessary to characterize the generality of this prediction, but it can nonetheless be explored empirically. For example, one could evaluate this prediction by comparing, across ant species, the relationship between spatial foraging strategies and resource conversion efficiencies.

Our model also makes predictions at the community level. For example, our assumed relationship between allochthonous productivity and diversity is a sufficient basis for expecting a positive relationship between the number of individuals in a population of central-place foragers and the number of resident species supported by the allochthonous resources back at the central place (i.e., more foragers should lead to greater spatial subsidies). However, our model also makes the not necessarily obvious prediction that the size of the habitat patch over which a population forages will be strongly linked to species richness only in productive environments. This is because species richness back at the central place scales with patch size only when the surrounding resources have a high recruitment rate (fig. 6). We would thus expect, for example, more–species rich guanophilic communities at those seabird rookeries that are surrounded by highly productive oceanic waters. A more intuitive corollary is that subsidies garnered from a small patch will support few species regardless of the patch's productivity (fig. 6).

As a final point of discussion, we note that a conceptual link exists between the spatial distribution of resources, as we have considered it here, and distributions of heterogeneous resources more generally. For example, in our model, a foraging kernel can be interpreted as a probability density function characterizing the consumers' relative use of resources as a function of spatial position. In a nonspatial case, a similar kernel-type formulation could be used to characterize how a population of consumers differentially selects among a suite of resources distributed along some other axis, such as body size or stoichiometric quality, while also allowing for variation among resources in terms of relative abundance and intake efficiency. We are not aware of nonspatial, continuum-type models of consumers foraging on heterogeneous resources that would mirror the ecological situation we considered here, but we suggest that this perspective is worth considering in models of diet choice. Indeed, models involving a continuum-of-resources approach are starting to appear in the speciation literature (e.g., Ackermann and Doebeli 2004).

The analyses we present here provide a new link among elements of ecology related to animal behavior, population dynamics, and species diversity. Our modeling approach differs from other approaches to central-place foraging by explicitly considering alternative ways in which populations of consumers may use space but excluding individual-level behavioral optimizations based on the distribution of resources. Our efforts also differ from the well-developed body of spatially explicit consumer-resource models (e.g., reaction-diffusion or integrodifference models; reviewed by Briggs and Hoopes [2004]) that have included more or less random dispersal but have not considered the effects of a central place. By focusing on that part of central-place-foraging behavior related to the spatial distribution of populations of consumers, our efforts provide a novel perspective on the utility of integrodifference equations in spatial ecology. Further explorations should allow for additional insights into the effects that different types of spatial subsidies have on population dynamics and community structure.

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