

Living in the city: Resource availability, predation, and bird population dynamics in urban areas

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Received 29 July 2006; received in revised form 28 November 2006; accepted 20 January 2007

Available online 20 February 2007

Abstract

This article explores factors that shape population structure in novel environments that have received scant theoretical attention: cities. Urban bird populations exhibit higher densities and lower diversity. Some work suggests this may result from lower predation pressure and more predictable and abundant resources. These factors may lead to populations with few winners and many losers regarding access to food, body condition, and reproductive success. We explore these hypotheses with an individual-energy-based competition model with two phenotypes of differing foraging ability. We show that low frequency resource fluctuations favor strong competitors and *vice versa*. We show that low predation skews equilibrium populations in favor of weak competitors and *vice versa*. Increasing the time between resource pulses can thus shift population structure from weak to strong competitor dominance. Given recent evidence for more constant resource input and lower predation in urban areas, the model helps understand observed urban bird population structure.

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Keywords: Resource dynamics; Predation; Population dynamics; Urban; Birds

1. Introduction

Rapid urbanization has become one of the major concerns in conservation ecology (Miller and Hobbs, 2002). Within 30 years, more than half of the world population is expected to live in cities (United Nations 2003). In recent years, urban ecology has received increasing attention from ecologists, anthropologists, and social scientists interested in understanding the influence of human activities on urban ecosystems and their biological communities (Grimm et al., 2000). Whereas urbanization normally leads to increasing population densities, species diversity is normally lower in cities than in adjacent wildlands (Marzluff, 2001). While these patterns are well documented, we know much less about the drivers of these patterns (Marzluff et al., 2001). Recently, Shochat et al. (2006) called for adopting a mechanistic approach to urban ecological

research. Although field experiments would comprise the main component of such an approach, theoretical and mathematical models will play important roles in helping frame and test new ideas in urban ecology. The work presented here focuses on the development of such theory.

Cities may represent an excellent laboratory for comparative studies on population dynamics as urban areas provide large-scale examples of changing environmental conditions (Grimm et al., 2000; Collins et al., 2000). Urban habitats (areas dominated by built structures, i.e. more than 10 buildings ha⁻¹ and at least 620 humans km⁻²) and suburban habitats (areas with 2.5–10 buildings ha⁻¹) (Marzluff, 2001) are normally characterized by extremely high food resource abundance. Indeed, despite high stress induced by a range of factors associated with urban life such as noise (Katti and Warren, 2004), chemical contaminants (Burger et al., 2004), and high densities of domestic predators (Sorace, 2002), urban habitats throughout the world are characterized by high population densities of different taxa (Marzluff et al., 2001; Beckmann and Berger, 2003a).

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These differences between population densities in urban and wild settings may simply reflect the predictions of the resource-matching rule (Parker, 1978) across large spatial scales, i.e. population density increases proportionately with resource density. However, based on results from field experiments on optimal foraging behavior (Bowers and Breland, 1996; Shochat et al., 2004a), Shochat (2004) suggested that, in terms of abundance, urban bird populations lay over the carrying capacity of the urban environment, resulting in lower average individual body condition. Thus, urban bird populations are relatively higher than the resource-matching rule would predict, and Shochat (2004) suggested this situation might persist as a long-term equilibrium. Our aim in this paper is to apply a mathematical model to explore potential factors that may facilitate persistent resource overmatching in urban areas.

Our investigation focuses on how changes in *population structure* (as defined by frequencies of phenotypes with differing competitive ability) induced by changes in resource dynamics and predation might potentially contribute to maintaining higher than expected population densities in urban areas. Specifically, temporal variation in urban environments may be low compared with wildlands (Beckmann and Berger, 2003a; Catterall et al., 1998; Shochat et al., 2004b). It has been suggested that this difference, that so far has been ignored, plays an important role in shaping urban population structure (Shochat, 2004). In what Shochat called the “Credit Card Hypothesis”, he suggested that low variability in resource abundance allows the persistence of many weak competitors who remain in poor body condition who are less reproductively successful and who would not otherwise survive. We develop and analyze a competition model to determine whether, and under what conditions, reducing variation in resource abundance can induce such a shift in population structure and, in turn, allow for sustained resource overmatching.

Predation, too, can have a strong effect on both inter- and intra-specific competition (Caswell, 1978; Mittelbach, 1986; Butler and Wolkowicz, 1986; Abramsky et al., 1998). While it is agreed that cities are richer in food resources than wildlands, there is still some debate whether predation decreases or increases in cities relative to wildlands (Gering and Blair, 1999; Thorington and Bowman, 2003; Blair, 2004). We believe that the weight of existing evidence suggests that predation pressure on adult birds is lower (see discussion below). Thus, since predation in urban environments is a key issue, we investigate how changes in predation pressure affect resource competition and population dynamics in general. Specifically, through the analysis of the model, we tease out the relative importance of competition for resources and predation on structuring urban populations and generate some specific predictions about population structure and individual body condition that may be tested through comparative studies of urban and non-urban populations.

2. Motivation for the model and scope of the analysis

Urbanization is a complex process that produces complex landscapes. There are thus many possible attributes to consider that may distinguish different types of urban areas from one another and from adjacent wildlands. The attributes of these different areas, in turn, may affect the population dynamics of organisms that inhabit them. Understanding the relationships between such attributes and the population dynamics of organisms that inhabit them is a core area of the rapidly developing field of urban ecology (Marzluff et al., 2001). There are many definitions of urban environments that focus on landcover, human population density, etc. (Marzluff et al., 2001; Hudson, 2001), all of which may affect population dynamics. Here we focus on two of the many factors hypothesized to drive urban populations: predation and food resource abundance. As we discuss below, urban (and suburban) areas may usefully be distinguished from wildlands along these two dimensions. Thus when we refer to “urban” or “wildlands” we refer to their associated predation and resource abundance characteristics rather than their physical characteristics (i.e. landcover types, edges, etc.). We recognize that this distinction is imperfect given such possibilities as wildlands (urban parks and open spaces) interspersed with urban (and suburban) areas. However, at sufficiently large scales, this distinction is reasonable and provides the basis for our investigation. Finally, we recognize that there are other potential factors suggested to affect bird populations such as toxins and disease. While these are often mentioned as important factors in urban settings, there is little research on urban bird ecotoxicology and disease. The scant research that has been done (Boal and Mannan, 1999; Burger et al., 2004) suggests that these factors probably play a negligible role in affecting population dynamics. Although the model is sufficiently general to be extended to explore these factors, we leave that for future work and focus on resource dynamics and predation.

Although the role resource abundance and predation in structuring urban populations is not fully understood, recent experimental studies on foraging behavior using the giving-up density (GUD) approach (sensu Brown, 1988) of urban squirrels (Bowers and Breland, 1996) and birds (Shochat et al., 2004a) sheds light on how these factors affect urban populations. The GUD is the leftover amount of food in a foraging patch determined by, among other factors, digestive costs, competition, the risk of predation, and the cost of missed opportunities (i.e. how rich is the rest of the environment in resources) (Brown, 1988). Shochat et al. (2004a) showed that in the case of birds, urban foragers decreased their GUDs compared with desert birds. Specifically, they found significant differences in GUDs between bush and open microhabitats in the desert, but none in the city. As bush microhabitat represents a safer habitat from predators (Kotler et al., 1991), the results described by Bowers and Breland (1996)

and by Shochat et al. (2004a) suggest that, at least for adult vertebrates, cities may be safer habitats than wildlands despite the higher abundance of domestic predators. Experiments with artificial nests, however, have produced conflicting results regarding the intensity of urban nest predation rates (Major et al., 1996; Gering and Blair, 1999; Matthews et al., 1999; Jokimaki and Huhta, 2000; Haskell et al., 2001; Blair, 2004).

Because urban ecology is a relatively new field, there is not a large body of empirical work on predation. Beyond the work cited above, we know of very few studies that have directly tested whether predation pressure on adult birds in urban settings is higher than in wildlands. Studies were either done in remnants of natural habitats in urban areas (e.g. Wilcove, 1985; Crooks and Soule, 1999; Matthews et al., 1999), were not comparative (Major et al., 1996; Matthews et al., 1999), or were done on nests only (Gering and Blair, 1999; Jokimaki and Huhta, 2000; Thorington and Bowman, 2003). Predation risk has been suggested to be higher in urban habitats than in wildlands, owing to the high density of domestic or feral predators (Sorace, 2002). If this is indeed the case, the extremely high urban bird densities and the overall tame behavior of urban birds are puzzling (Shochat, 2004). First, as suggested above, we need to distinguish between adult bird and nest predation. Furthermore, higher predation rates of artificial nests in urban areas than in wildlands may not necessarily indicate a higher predation risk in urban areas, especially when ground nests with quail eggs are used. When tested on wild birds, predation risk appears lower in urban areas than in wildlands. For example, in Darwin, Australia, high reproductive output of the Rufous-banded Honeyeater (*Conopophila albogularis*) has been explained by the scarcity of predators (Noske, 1998). The weight of evidence at present tends to support the claim that predation is lower in urban settings. Thus, although the role of predation in urban settings is yet to be resolved, in our model we investigate the outcomes of general changes in predation pressure and tentatively associate lower predation with urban settings.

The overall lower GUDs in urban habitats indicate that urban foragers deplete food more efficiently than do wildland foragers. Given the high competition for resources (Shochat et al., 2004a), this is expected, as “urban life” probably selects for those species that specialize in acquiring food efficiently from patches with relatively low densities of food items. However, the extremely low urban GUDs suggest that the urban environment is unbalanced in terms of resource matching (*sensu* Parker, 1978). In other words, although the urban habitat probably has higher food resource densities, population density exceeds that expected under the resource-matching rule. A recent study of black bears in urbanizing areas in the south-western US found a similar overmatching deviation from an expected ideal-free distribution (Beckmann and Berger, 2003b): bear population density in urban-interface habitat was three times the pre-urbanization levels at the same

location, and 40 times that in adjacent wildland. Shochat (2004) suggested that to maintain overmatching over the long term, a cost to individuals in body condition and possibly life span must exist. He hypothesized that shifting the resource burden necessary to maintain larger population sizes to individuals in the form of reduced body condition may be facilitated by low resource variability lower predation risk. The daily routine of resource renewal in the city allows urban foragers to “live on their credit” and invest more in reproduction (Shochat, 2004). This credit card hypothesis predicts that urban populations should thus consist of a few winners and many losers with both bottom-up (resource variability) and top-down (lower predation) factors affecting urban population dynamics and composition.

Can such an overmatching situation hold over the long-term? Our model explores the credit card hypothesis, once by changing the resource renewal type from fluctuating inputs (e.g. wildland) to constant daily input, (e.g. urban) keeping predation pressure constant, and once by changing predation pressure from high to low, keeping resource input constant. This is important because the high urban population densities and the shift from small populations of mostly winners to large populations of mostly losers along the wildland-urban axis can result from both top-down and bottom-up effects. Our theoretical exploration is motivated by the desire to understand the relative importance of these factors and how they interact.

Finally, before describing the model, it is important to clearly specify the scope of the analysis. Differences between wildlands and urban areas can include many factors that structure ecological communities including interspecific competition, intraspecific competition, trophic interactions, and individual behavior. We cannot hope to address all these important issues in a modeling framework while at the same time retaining any analytical capacity. We thus choose to focus on two factors suggested by the credit card hypothesis to be especially important in urban settings: intraspecific competition and predation. The modeling effort is focused on understanding how changes in intraspecific competition for resources and predation affect the structure of a single population which, in turn, may affect the total number of individuals a particular environment can support. The model must thus include two basic components: (1) the ability of individuals to acquire resources and (2) the ability of individuals to reproduce and avoid predation given their “condition” (energy state).

3. A two-competitor, single resource model

Traditional competition models typically model growth rates as directly dependent on resource availability. These models provide a basis for our work, but do not capture the “condition” (e.g. energy state) of individuals. Models of individual foraging behavior typically link decisions to some internal state (McNamara and Houston, 1990a).

A commonly used state variable affecting survival and foraging decisions is energy reserves. Further, models often include constraints (morphological, physiological, genetic) such as metabolic rate, food handling time, and gut capacity. Our model considers an individual's energy state, metabolic rate (using standard forms of these physiological functions), and energy storage capacity. This approach allows us to extend simple aggregate models of population dynamics to incorporate (indirectly) individual foraging behavior, physiological constraints, and competitive interactions.

Given our focus on the effect of changing predation and resource dynamics on the distribution of individuals within a population, we must allow for heterogeneity within the population. We focus on the simplest case possible with intraspecific heterogeneity: two phenotypes defined by their ability to forage and access good quality food. This simple characterization has empirical support in some recent urban studies showing that urban populations consist of winners and losers, that winners forage on food of higher quality than losers, and that this may affect their fitness in the long term (Pierotti and Annett, 2001; Sol et al., 1998). We define the better foragers as type 1 (“strong competitors” or “winners”) and the poorer foragers as type 2 (“weak competitors” or “losers”). The population size of each type of individual at time t is denoted by $n_1(t)$ and $n_2(t)$, respectively. The two populations are not distinct species, can interbreed, and produce offspring of both types. The foragers compete for a common resource denoted by $s(t)$. Assuming that resources enter the system at a rate $I(t)$, the populations evolve over time according to the following differential equations:

$$\frac{ds}{dt} = I(t) - C_1(n_1, s(t)) - C_2(n_2(t), s(t)), \quad (1a)$$

$$\frac{dn_1}{dt} = b_1(n_1(t), s(t)) - d_1(n_1(t), s(t)), \quad (1b)$$

$$\frac{dn_2}{dt} = b_2(n_2(t), s(t)) - d_2(n_2(t), s(t)), \quad (1c)$$

where $C_i(\cdot)$, $b_i(\cdot)$, and $d_i(\cdot)$ are the resource consumption, birth, and death rates for each type, respectively. This basic formulation has been used extensively to study competition in fluctuating environments (Grover, 1990; Hale and Somolinos, 1983; Hsu, 1980; Smith, 1981), but we are interested in describing more than whether the two populations can coexist. Our goal is to also compare the body condition of each type. The condition of each type at time t is measured by its energy state, $e_i(t)$. The energy state changes over time based on foraging activity and metabolic rate. The energy state, in turn, influences birth and death rates. Thus, we extend the basic formulation in (1a)–(1c) as follows:

$$\frac{ds}{dt} = I(t) - c_1(s(t), e_1(t))n_1 - c_2(s(t), e_2(t))n_2 - Ds, \quad (2a)$$

$$\frac{dn_1}{dt} = b_1(n_1(t), e_1(t), n_2(t), e_2(t)) - d_1(n_1(t), e_1(t)), \quad (2b)$$

$$\frac{dn_2}{dt} = b_2(n_2(t), e_2(t), n_1(t), e_1(t)) - d_2(n_2(t), e_2(t)), \quad (2c)$$

$$\frac{de_1}{dt} = c_1(s(t), e_1(t)) - m_r(e_1(t)), \quad (2d)$$

$$\frac{de_2}{dt} = c_2(s(t), e_2(t)) - m_r(e_2(t)), \quad (2e)$$

where $c_i(s(t))$ is consumption as a function of resource availability, and $m_r(\cdot)$ is the metabolic expenditure, or energy usage rate per unit time. We also add the term Ds to the resource dynamics to incorporate the fact that if not consumed, resources will degrade over time (be consumed by other organisms). The expressions (rate functions) that make up the right-hand sides of Eqs. 2(a)–(e) are chosen to be as simple as possible and yet capture the basic relationship between energy state, resource availability and birth, death, consumption, and metabolic rates. A common feature of these relationships is a saturation effect. For example, at low resource densities, resource uptake increases with increasing resource density. However, at very high resource densities, increasing resource density has no effect on resource uptake because some other limiting factor (handling time or gut capacity) comes into play (e.g. Michaelis–Menton-type growth curves). A second important feature is the existence of thresholds. For example until a certain threshold energy reserve level is surpassed, birds will not reproduce. In fact, all of the rate functions in the model have three common features: a ceiling at a maximal rate (saturation), a floor at zero, and a sigmoidal transition from floor to ceiling (threshold). Thus, for all the rate functions in the model we use a simple, general function that captures these three common features:

$$f(x; \gamma, \rho, x_h) = \frac{\gamma x^\rho}{x_h^\rho + x^\rho}, \quad \rho \geq 1, \quad (3)$$

where γ is maximum value (ceiling) of $f(\cdot)$, x_h is the half saturation constant (location of the threshold), and ρ controls the sharpness of the threshold. Fig. 1(A) shows three examples to illustrate the various possible behavior of $f(\cdot)$ as it depends on parameter choices. With this function now defined, we can provide the rationale behind each of the rate-functions in (2a)–(2e):

3.1. Birth and death rates

We assume that an individual's energy state affects its ability to forage, reproduce, avoid predators, and maintain metabolic processes. As the energy reserve level increases, birth rates increase. Beyond a certain threshold, however, the energy reserve level no longer impacts birth rates. This is represented by a curve of type B or C in Fig. 1(A). In the model, we define the *per-capita* birth rate as $b(e_i(t)) = f(e_i(t), \bar{b}, b_T, \tilde{b})$ where \bar{b} is the maximum birth rate, \tilde{b} is the energy level at which the birth rate is half the maximum, and b_T is the sharpness of the increase in birth rates as the energy level increases past \tilde{b} . Further, individuals of each

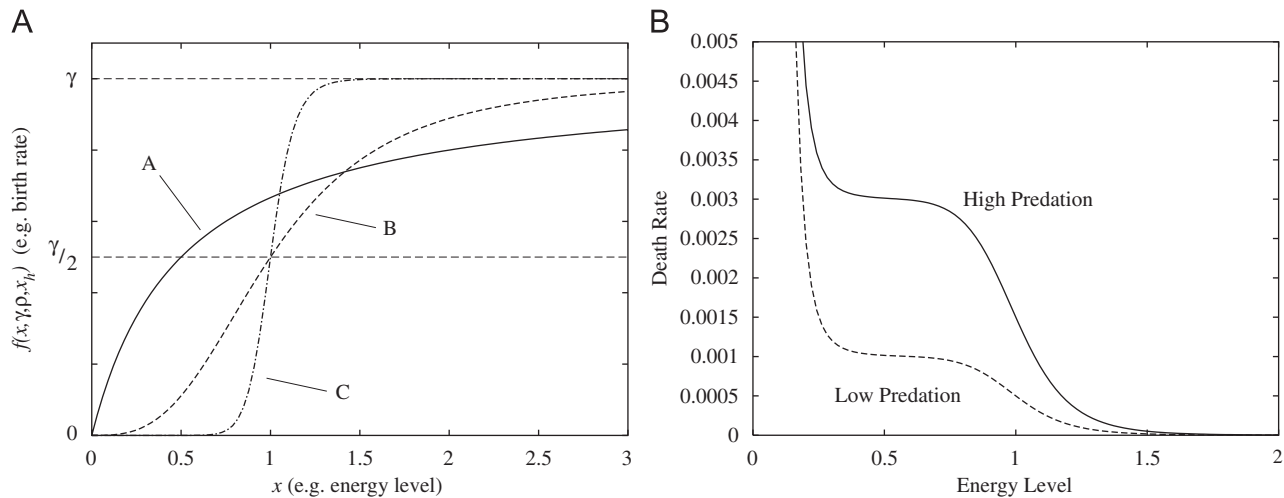


Fig. 1. (A) Shows various possible forms of $f(\cdot)$. Curve A corresponds to $f(x; \gamma, 1, 0.5)$, B to $f(x; \gamma, 3, 1)$ and C to $f(x; \gamma, 12, 1)$. The parameter γ has been left unspecified, as it merely scales the y-axis. The horizontal line at $\gamma/2$ is shown to highlight the role of x_h , the x-coordinate at which $f(\cdot)$ is one half its maximum value. Increasing x_h shifts the threshold to the right. In curve A, $\rho = 1$ in which case $f(\cdot)$ is convex. In curves B and C, $\rho > 1$ in which case $f(\cdot)$ is sigmoidal. The larger ρ , the sharper the transition (cf. curves B and C); (B) shows death rates under two predation scenarios: the solid curve represents high predation while the dashed curve represents lower predation.

type can produce offspring of their own and the other type (interbreeding genotypes). We assume that type j individuals produce type i individuals at the rate α_{ij} where i and j can take on values of 1 or 2. Thus, the total birth rates of each type are

$$b_1(n_1, e_1, n_2, e_2) = \alpha_{11}b(e_1)n_1 + \alpha_{12}b(e_2)n_2, \quad (4)$$

$$b_2(n_2, e_2, n_1, e_1) = \alpha_{21}b(e_1)n_1 + \alpha_{22}b(e_2)n_2. \quad (5)$$

Individuals die as a result of either starvation or predation. The *per-capita* death rate function is therefore a combination of these two factors. Predation risk is lower at high energy levels, and increases as energy state decreases; the shape of this component can vary depending on other factors such as habitat and specific predators. Note that the effect of energy level on death rates is opposite to its effect on birth rates. This “opposite” behavior can be easily generated using the function $\gamma - f(x; \gamma, \rho, x_h)$. Starvation is modeled as a lower energy threshold below which basic metabolism ceases, and the death rate escalates. This is accomplished with a function of the form $\gamma - f(x; \gamma, \rho, x_h)$ as well, but with γ and ρ chosen much larger than for predation-induced mortality and x_h chosen much lower (ability to avoid predators drops off before starvation sets in). Combining these factors yields the *per capita* death rate given by

$$d(e_i(t)) = d_b + \bar{d}_p - f(e_i; \bar{d}_p, d_{T_p}, \tilde{d}_p) + \bar{d}_s - f(e_i; \bar{d}_s, d_{T_s}, \tilde{d}_s), \quad i = 1, 2, \quad (6)$$

where \bar{d}_p and \bar{d}_s are the maximum death rates due to predation and starvation when energy stores are low, respectively; \tilde{d}_p and \tilde{d}_s are the energy levels at which these death rates are half their maxima; and d_{T_s} and d_{T_p} characterize the “sharpness” of the energy threshold below which the ability of individuals to avoid predation and

starvation drops off. Finally, d_b is the background death rate independent of energy state. Fig. 1(B) shows examples of the death rate function for $d_b = 0$, $\bar{d}_p = 0.003$ (high predation), $\bar{d}_p = 0.001$ (low predation), $\tilde{d}_p = 1$. The total death rate for each type is then simply the product of *per capita* death rate and the population size, i.e. $d_i(n_i(t), e_i(t)) = d(e_i(t))n_i(t)$.

3.2. Resource uptake and energy state

Birds increase their energy store by consuming the resource and decrease it through activity (metabolic expenditure rate). The foraging ability of each of the competitors is a simple Michaelis–Menton (Holling type II) functional form (type A curve in Fig. 1(A)). The energy uptake depends on the available resources, and the competitive abilities of each forager. By assumption, type 1 individuals always out-compete type 2 individuals. To accomplish this, we define

$$c_i(s, e_i) = f(s; \bar{c}_i, 1, \tilde{c}_i) \left(1 - \frac{e_i}{\bar{e}}\right), \quad i = 1, 2, \quad (7)$$

where \bar{c}_i and \tilde{c}_i are the maximum uptake rate and resource level at which the uptake rate is one half of the maximum, respectively, and \bar{e} is the maximum energy storage capacity. Without loss of generality we assume $\tilde{c}_1 < \tilde{c}_2$ (better competitors are labeled as type 1). Fig. 2(B) shows representative examples of the resource uptake functions with $\bar{c}_1 = \bar{c}_2 = 1$, $\tilde{c}_1 = 1$, and $\tilde{c}_2 = 2$. The term $(1 - e_i/\bar{e})$ captures the fact that there is a physiological limit to the amount of resources each individual can consume and store. The capacity to store resources affects the extent to which a population can cope with variations in resource input, and potential time-lags between changes in resource input levels and the population response. It is important

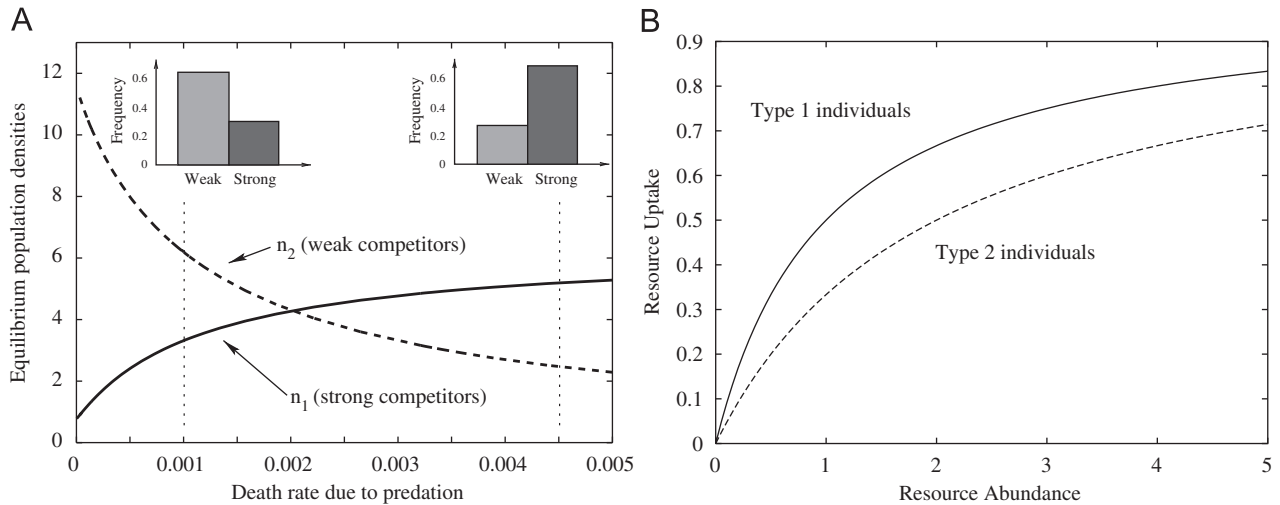


Fig. 2. (A) Shows the equilibrium population densities for each competitor as a function of predation pressure; (B) shows resource uptake ability as a function of resource abundance in the two types of individuals.

for our study because we want to compare stable (urban) versus fluctuating (wildland) environments and assess the relative importance of the effect of predation and fluctuating resources on population structure.

3.3. Metabolic expenditure rate

We model metabolic expenditure rate, $m_r(e_i)$, in the same way as we model the uptake (type A curve in Fig. 1(A)), i.e. $m_r(e_i) = f(e_i; \bar{m}_r, 1, \tilde{m}_r)$ where \bar{m}_r and \tilde{m}_r are the maximum metabolic rate and energy level at which the metabolic rate is one half of the maximum. Above a certain threshold, the basal metabolic rate is constant. When an individual's energy level falls below the threshold, activity levels necessarily decrease, and with them, the basal metabolic rate.

3.4. Resource input rates

The last element of the model is that the populations compete for a single resource with a given input rate, I , which is either constant (urban) or fluctuating (non-urban). In the case of a constant input rate, it can be shown that I merely scales the population sizes (and is thus consistent with what would be expected from the resource matching rule), and we thus set it equal to 1 in the analysis that follows.

4. Analysis and results

Our goal in developing the model was to investigate the predictions of the credit card hypothesis (Shochat, 2004) concerning the effect of changing resource input dynamics and predation regimes on population structure. We thus focus our attention on three parameters in the model: the death rate due to predation, d_p , the maximum energy storage capacity, \bar{e} , and the periodicity of resource input, ω . All the other parameters in the model were held

constant at the levels shown in Table 1 throughout the analysis. Before turning our attention to the analysis, we first provide the rationale for our parameter choices.

Because the model is focused solely on the outcome of competition between two competitors, it is “closed” to the outside world other than through the resource input rate, $I(t)$. As such, only the *relative magnitudes* of the parameters are important. For example, for a bird it is not the absolute magnitude of its energy state (other than being sufficient for staying alive), its birth, death, or resource uptake rates, but rather the magnitude of these quantities relative to its *competitors* that is important. Given this, two factors drive our parameter selection: (1) parameter values match intuitive sensibilities; (2) parameter values are chosen to be “order 1” were possible to ease the numerical analysis and the interpretation of the results.

For example, the resource input and degradation rates do nothing other than scale the equilibrium population sizes. Thus, the resource input rate is scaled to 1 unit per unit time. Since the only important feature of an individual's energy level is its effect on birth and death rates, we are free to choose its units, e.g. as $e_i(t)$ ranges from 0 to some upper bound, the birth rate ranges from 0 to its maximum. Parameter values have been chosen so that birth and death rates span their ranges as $e_i(t)$ ranges from 0 to around 5. This is done by choosing $\tilde{b} = 1$ so that the birth rate rises from 0 to half its maximum as $e_i(t)$ increases from 0 to 1 and from half its maximum to its maximum value as $e_i(t)$ increases from 1 to roughly 5. Likewise, \tilde{d}_p is set to 1. Next we set the sharpness of the thresholds when $e_i(t)$ passes through $\tilde{b} = 1$ and $\tilde{d}_p = 1$ to $b_T = 3$ (similar to curve B in Fig. 1(A)) and $d_T = 10$ (similar to curve C in Fig. 1(A)), respectively. The model results are qualitatively the same for a wide range of choices for b_T and d_T as long as they are both larger than 1. Note that the threshold for the death rate function is more sharp than for the birth rate function ($d_T > b_T$). This is due to the fact that at low energy levels, death is guaranteed, and is therefore necessarily

Table 1
Parameter definitions and default values

Symbol	Description	Default value
α_{11}	Probability that a type 1 individual has type 1 offspring	0.1, 0.2
α_{12}	Probability that a type 2 individual has type 1 offspring	0.1
α_{21}	Probability that a type 1 individual has type 2 offspring	0.9, 0.8
α_{22}	Probability that a type 2 individual has type 2 offspring	0.9
\bar{b}	Maximum birth rate	0.003
\tilde{b}	Energy level at which birth rate is half the maximum	1
b_T	Sharpness of the energy threshold for successful reproduction	3
\bar{d}_p	Maximum death rate due to predation	Varies
\tilde{d}_p	Energy level at which death rate due to predation is half the maximum	1
d_T	Sharpness of the energy threshold for successful predator avoidance	10
d_s	Death rate due to starvation	20
d_b	Background death rate	0.0002
\bar{e}	Maximum energy storage capacity	Varies
\bar{c}_i	Maximum resource consumption rate	$\bar{c}_1 = \bar{c}_2 = 1$
\tilde{c}_i	Resource level at which resource consumption is half of the maximum	$\tilde{c}_1 = 1$ $\tilde{c}_2 = 2$
\bar{m}_r	Maximum metabolic rate	0.2
\tilde{m}_r	Energy level at which the metabolic rate is one half of the maximum	0.5
ω	Resource pulse period	Varies
β	Resource pulse sharpness	30
Θ	Resource pulse amplitude	13.6

a threshold or step-function. Birth, on the other hand, is more probabilistic, and reproductive output increases more gradually with energy levels.

With the relationships between birth and death rates and energy state now set, we turn our attention to the relationship between energy state and resource uptake. It turns out that the choice of the maximum resource uptake rate relative to demographic rates is a very important aspect of the model. Setting $\bar{c}_1 = \bar{c}_2 = 1$ and $\bar{m}_r = 0.2$ means that with abundant resources, the time required to replenish 1 unit of energy reserves (that required to move from a completely depleted energy state to one sufficient for a positive growth rate) is on the order of 1 time unit (e.g. a day or hour depending on the organism). The choice of this time unit then sets what choices are reasonable for the birth and death rates. For example, if metabolic and demographic processes occur roughly on the same time scales, then a reasonable choice for birth and death rates

would be order 1 (e.g. $\bar{b} = 0.3$). In the case of birds, it is reasonable to assume that demographic processes are 2 orders of magnitude slower than metabolic processes (e.g. the former occur on a yearly time scale while the latter occur on a daily time scale). In this case, reasonable choices for birth and death rates are order 10^{-2} (e.g. $\bar{b} = 0.003$). Finally, the difference in resource uptake abilities between competitors is captured by choosing $\tilde{c}_1 = 1$, and $\tilde{c}_2 = 2$ (Fig. 2(B)).

The analysis is comprised of studying the long-run behavior of model equilibria as the remaining free parameters (shown in bold Table 1) are varied. It is shown in Appendix A that there exists an equilibrium which supports positive population densities. However, there do not exist closed form general expressions for the equilibrium values of each of the state variables. Thus, numerical techniques based on pseudo-arclength continuation (Doedel, 1981) as implemented in *XPPAUT* (Ermentrout, 2002) are used to explore the properties of this fixed point as parameters are varied. A complete analysis was conducted for the three primary parameters of interest (d_p , \bar{e} , and ω) for two different choices of important secondary parameters, (\bar{b} and α_{ij}) as described below. For clarity of presentation, we first analyze the behavior of the model with constant resource input and focus on predation and storage capacity. We then address the more challenging case with fluctuating resources.

4.1. Predation

We begin the analysis by studying the effect of changing predation on population structure. Fig. 2(A) shows the population structure as a function of the death rate due to predation. At low levels of predation (city), the weak competitors dominate the population. As predation increases, the dominance of the poorer competitors weakens. When the death rate due to predation reaches approximately 0.002, the stronger competitors begin to dominate (the solid and dashed lines cross). The reason for this reversal is due to the body condition of individuals. Because the strong competitors can acquire more resources, they can always maintain a higher energy state at the *individual level* than the weaker competitor. The inset bar graphs show the frequency distribution of the two types of individuals for the value of \bar{d}_p shown by the vertical dotted line (cf. Shochat, 2004). The model shows that the energy state of individuals increases slightly as predation increases (because higher predation reduces competition for resources). For the range of death rates due to predation in Fig. 2(A) the equilibrium energy level of the strong competitor varies between 1.2 and 1.6 while that of the weak competitor varies between 0.35 and 0.45 (note: strong competitor's energy state is roughly 4 times higher than the weak competitor's regardless of predation pressure). However, depending on external conditions, this individual dominance may result in different outcomes at the *population level*.

As predicted by predator–prey theories (McNamara and Houston, 1987, 1990b), the death rate of weak competitors is higher because their lower energy level makes them more susceptible predation (e.g. individuals in poor or worsening condition take more risks to obtain critical resources, Dierschke (2003); Murray (2002) or are targeted as a specific hunting strategy of predators, Wirsing et al. (2002)). As a result, the total population skews in favor of strong competitors at equilibrium. Under lower predation, the death rates of the two types is similar; more of the type 2 individuals survive despite their energy state being lower than that of type 1 individuals. Meanwhile, more type 2 individuals are being produced, given the overall birth rate bias in favor of weak competitors. As a result, the total population skews in favor of weak competitors at equilibrium.

These results, however, depend on the choice of other key parameters. The equilibrium populations shown in Fig. 2(A) were computed with $\alpha_{11} = \alpha_{12} = 0.1$, $\alpha_{21} = \alpha_{22} = 0.9$, $\bar{b} = 0.003$ (choosing the time unit of \bar{c}_j as days, $\bar{b} = 0.003$ corresponds to a maximum *per capita* birth rate of roughly 100% per year), and $\bar{e} = 10$ (no practical constraint on the ability of birds to store food). The bias favoring production of weak competitors is based on several considerations. First, in many species, parents are known to invest differentially among their offspring, either through differences in egg mass (intra- and inter-clutch) or nestling provisioning (reviewed in Clutton-Brock, 1991). Second, parental (female) body condition influences investment, with egg size often declining with laying order within a clutch and laying date between clutches (Clutton-Brock, 1991). We assume that, on average, this leads to fewer strong offspring and more weak offspring. The empirical evidence on this point is yet unclear because although numerous studies report differential resource-allocation among eggs (e.g. Rutkowska and Cichon, 2005; Rutstein et al., 2004) and subsequent (intra-clutch) variation in offspring quality or success (e.g. Clotfelter et al., 2000; Pettifor et al., 2001), none report the actual distribution of offspring quality within clutch. Therefore, we believe our assumption is reasonable but also recognize that it needs further empirical support.

Note that regardless of predation pressure, at equilibrium n_1 is a source population and n_2 is a sink (see Appendix A). Because n_2 is a sink, the choice of α_{12} (and thus α_{22}) has very little effect on model results. On the other hand, because n_2 is a source, the choice of α_{11} is important. For any α_{11} sufficiently small (i.e. a bias against strong competitors) the model results are qualitatively the same—i.e. increasing predation will produce a shift in dominance of winners and losers. For the parameter set used in the analysis, when $\alpha_{11} < \sim 0.3$, this shift in dominance obtains. However, smaller values of α_{11} produce more dramatic shifts in dominance.

This analysis indicates that reducing predation pressure can cause a shift in dominance from strong to weak competitors. However, can this shift in dominance and the

resulting source sink dynamic allow more individuals to survive than if the population were homogeneous? This question can be addressed by fixing the death rate due to predation and varying \tilde{c}_2 . If $\tilde{c}_1 = \tilde{c}_2$, the population is homogeneous, and the credit card hypothesis would predict that the total population would be less than if $\tilde{c}_1 < \tilde{c}_2$. With \tilde{c}_1 set at its default value of 1 and $\bar{d}_p = 0.001$, as \tilde{c}_2 is increased from 1 (homogeneous) to 3 (heterogeneous), the total population increases from 8 to 9.6, or by 20%. The model thus confirms that this mechanism can produce sustained resource overmatching when measured by numbers of individuals.

4.2. Storage capacity

Our results summarized in Fig. 2(A) are based on a value of $\bar{e} = 10$. Clearly, the ability to store resources influences the benefits associated with being a strong competitor and will, in turn, affect the population structure at equilibrium. We thus conducted a comprehensive analysis of model behavior as a function of \bar{e} and \bar{d}_p . Fig. 3(A) shows the equilibrium population densities as \bar{e} varies between 0 and 6 with \bar{d}_p and \bar{b} both held constant at 0.003 and illustrates how the population structure and dynamics under high predation change when the strong competitors are constrained—i.e. their competitive abilities are lessened because they cannot store any surplus resources taken up. We saw in Fig. 2(A) that when individuals are unconstrained, and the death rate due to predation is 0.003, strong competitors dominate. However, Fig. 3(A) shows that this is only true if \bar{e} is greater than roughly 2.6. When $\bar{e} < 2.6$, poor competitors dominate despite the higher predation level. Finally, if \bar{e} gets too low, birds cannot store enough energy to survive, and both populations go to zero.

Clearly there is an important interaction between the ability to store resources and predation in structuring populations. In order to explore this interaction, extensive numerical experiments were used to map out the possible model behaviors as a function of the values of \bar{d}_p and \bar{e} (Fig. 3(B)). In region A, the model exhibits a stable equilibrium with strong competitors dominant. In region B, the model exhibits a stable equilibrium with weak competitors dominant. Finally, in region C, the model exhibits a stable equilibrium with $n_1 = n_2 = 0$ and $s = I/D$, i.e. neither individual can store sufficient energy to survive and both populations die out.

4.3. Fluctuating resources

If resource availability varies, it makes sense to maintain higher reserves and stay in better body condition to cope with periods of resource scarcity. Thus, a second mechanism that might favor weak competitors in the city is simply that there is a constant resource input rate (Shochat, 2004). We wished to assess the relative importance of this effect *vis à vis* predation. To accomplish this, we replace the

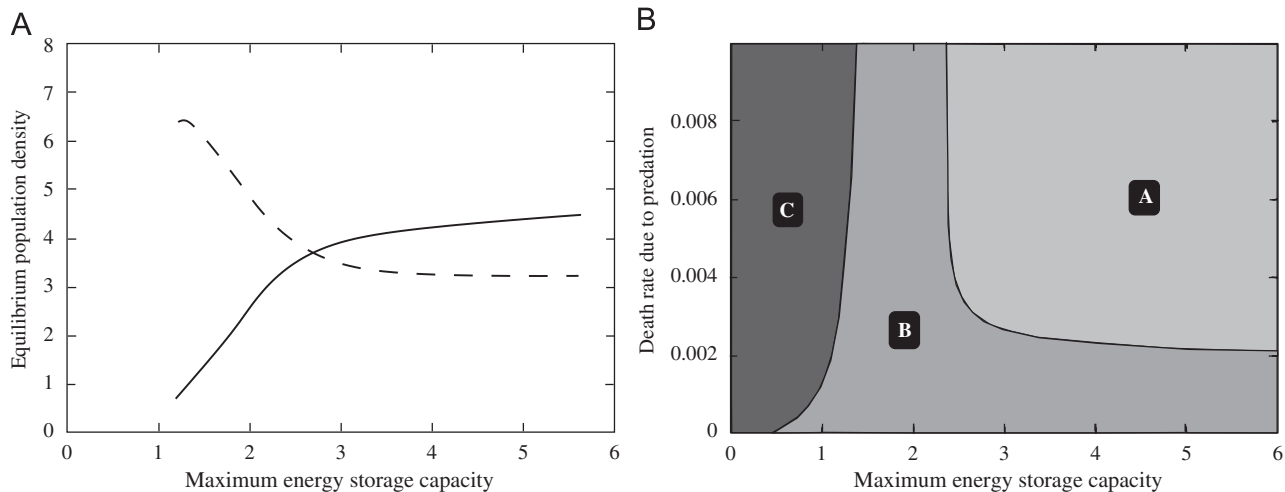


Fig. 3. (A) Shows the equilibrium population size of type 1 (solid curve) and type 2 (dashed curve) individuals as a function of energy storage capacity, \bar{e} , under a predation rate of $\bar{d}_p = 0.003$. The solid circles (black and gray correspond to weak and strong competitors, respectively) show the maximum and minimum population levels as the system moves through a stable limit cycle. The open circles correspond to unstable limit cycles; (B) shows the behavior of the model for any combination of \bar{e} and \bar{d}_p . See the text for descriptions of the model behavior in regions A–C.

constant resource input rate I with the time-varying rate $I(t)$ given by

$$I(t) = \Theta \exp(\beta(u(t) - 1)), \quad (8)$$

where $u(t)$ varies sinusoidally with period ω . The function $u(t)$ is generated using a simple system of two differential equations given by

$$du/dt = u(1 - u^2 - v^2) - 2\pi v/\omega, \quad (9a)$$

$$dv/dt = v(1 - u^2 - v^2) + 2\pi u/\omega \quad (9b)$$

so that our model remains autonomous (does not explicitly depend on time). Eq. (8) produces pulses of resource inputs. The sharpness of the pulses are controlled by β while their size is controlled by Θ . We chose these parameters (see Table 1) so that the average resource input is 1 to allow direct comparison with the constant resource input case. An example of the resource dynamics generated by (8) when $\omega = 7$ (i.e. there is a weekly resource pulse) is shown in Fig. 4(B) (bottom), in comparison with the dynamics under constant input.

There are three key factors that influence the effect of fluctuating resources on population structure: the frequency of pulses, the bias toward producing fewer type 1 individuals, and the relative time scales for demographic and metabolic processes. Here, we maintain $\bar{\tau}_i = 1$, $\bar{b} = 0.003$, and $\bar{d}_p = 0.001$ and vary the pulse frequency. The result of this analysis is that fluctuating resources can indeed generate a shift in population structure as hypothesized by Shochat (2004) (Fig. 4(A) (top)). When the period between resource pulses is small, weak competitors dominate by “living on credit”. However, as the period becomes longer, living on credit becomes more difficult. When the period between pulses becomes larger than 20, strong competitors begin to dominate. During these longer periods with no resource input, resources become very

scarce and the ability of type 1 individuals to out-compete type 2 individuals for resource enables them to dominate.

At intermediate periods (e.g. 10–15 days), however, weak competitors actually benefit from fluctuating resources. Fig. 4(B) (top) compares energy states of weak (dotted) and strong (solid) competitors for two cases: constant and pulsed (weekly intervals) resource input. Note that the energy state of the weak competitors is on average higher than with constant resource input while the energy state of the strong competitors is relatively lower. This result follows directly from the shape of the resource uptake curves (Fig. 2). When resources are abundant, the disadvantage of weak competitors is less, e.g. when $s(t)$ is 3.5, the resource uptake of type 2 individuals is 82% that of type 1 individuals compared to 50% that of type 1 when $s(t)$ is 0.2. Further, both types have higher birth rates when resources are abundant, thus relatively more type 2 individuals are being produced. The costs of fluctuating resources to type 2 individuals occur between pulses when resources are rare. If the duration of the period between pulses is relatively short, then these costs are outweighed by the benefits of relaxed competition during periods of resource abundance. The difference between these benefits and costs is greatest when the resource pulses come at roughly 12 day intervals. At longer periods, the costs of intense competition start to increase and being a strong competitor begins to pay dividends.

There are three additional important points to take away from this analysis. First the shift in dominance from type 2 to type 1 as pulse period increases depends on the parameter α_{11} . If $\alpha_{11} = 0.1$, this shift still has not occurred up to a pulse frequency of 4 weeks (Fig. 4(A) (bottom)). The trend suggests that if pulse period continues to increase, a shift in dominance would eventually occur. However, near a pulse period of 34 days, the equilibrium population cycles become unstable—both types die out.

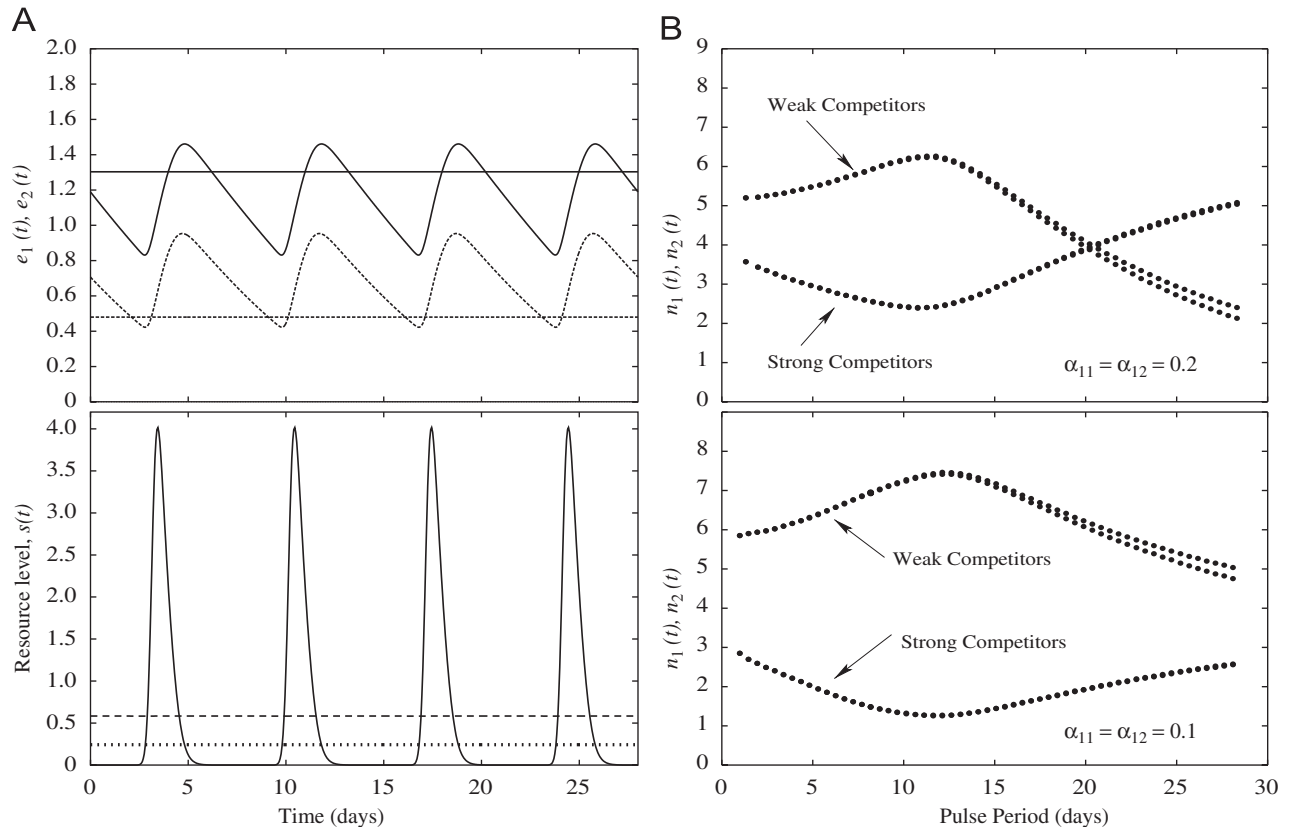


Fig. 4. Population and resource dynamics with fluctuating resources: (A) shows the long run population levels as a function of pulse period (days between pulses) for two different cases $\alpha_{11} = \alpha_{12} = 0.1$ (bottom) and $\alpha_{11} = \alpha_{12} = 0.2$ (top). The solid circles represent maxima and minima achieved during one period just as in Fig. 3(A), but in this case the amplitude is so small that it is not visible until the period is larger than approximately 18. Even then, fluctuations at the population level are only visible in the poor competitors; (B) compares resource (bottom graph) and energy state (top graph) dynamics with pulsed and constant resource inputs. Bottom graph: the solid curve shows the long run resource density when resource pulses enter the system every 7 days. The dotted line shows the corresponding long-run resource density for constant resource input. The dashed line shows the average resource density corresponding to the solid curve. Top graph: the solid and dashed curves show the energy levels of the strong and weak competitors, respectively, with pulsed resource inputs. The solid and dashed lines show the corresponding energy levels for the constant resource inputs.

Type 1 individuals must produce sufficient copies of themselves to keep the population viable during periods of scarce resources.

The second point is that with pulsed inputs, the average resource level (dashed line in Fig. 4(B) (bottom)) is higher than in the constant environment (dotted line in Fig. 4(A) (bottom)). We can interpret this average available resource level as the amount not consumed by the birds. This is analogous to GUD, which is an empirical measure of when animals give up on or depart from a food patch (Brown, 1988). Under this interpretation, the GUD is higher in the pulsed than in the constant environment. This parallels what was observed in foraging studies comparing urban and desert environments in the Phoenix metro area: desert GUDs were significantly higher than urban GUDs (Shochat et al., 2004a; Bowers and Breland, 1996).

The third and final point concerns the relative time scales between metabolic and demographic process. The above results rely on the fact that demographic processes are two orders of magnitude slower than metabolic processes (reasonable for birds). In our analysis of the model when these processes occur roughly on the same time scale,

fluctuating resources do not produce a shift in dominance—weak competitors always do relatively better. This is because population dynamics are fast enough to track fluctuations in resource dynamics. We would thus not expect to see a shift in dominance induced by fluctuating resources in smaller organisms.

5. Discussion and conclusions

The main insights from our model can be summarized as follows: given intraspecific phenotypic diversity, fluctuations in the resource environment favor weaker competitors when periods between pulses is short (high frequency resource input as may occur in urban areas) and stronger competitors when periods between pulses are long (lower frequency inputs as may occur in wildlands). High predation also favors stronger competitors. Thus, either one or a combination of these two factors can generate a shift in population structure as predation and resource dynamics change. This shift in population structure can, in turn, lead to higher population sizes than would be predicted by the resource-matching rule. This is consistent

with empirical observations and the “credit card hypothesis” suggested by Shochat (2004). Which factor is more important in a specific context will depend on the change in predation pressure and pulse frequency across habitats, the relative time scales on which metabolic and demographic processes operate for the organism in question, and the relative proportion of offspring of each type.

Concerning differences between resource dynamics in urban and desert areas, the change in resource pulse period (months or longer in the desert, days or shorter in urban areas) is sufficient to generate a shift in population structure. In this case, constant resource input can generate the resource overmatching that has been suggested to be the equilibrium condition in cities (Shochat et al., 2004a), with a large sink population of poor competitors in relatively poor body condition being maintained by a smaller source population of strong competitors in good body condition. If *per capita* predation pressure is lower in urban areas despite the higher abundance of predators (Shochat, 2004; Kays and DeWan, 2004; Blair, 2004), this may also be a contributing factor to observed higher proportion of losers in urban bird populations. The model suggests that in the case of an urban–wildland gradient for which changes in resource dynamics may be less pronounced, change in predation may be a more significant factor in altering population patterns.

Obviously whether or not these rules apply depends on the spatial scale at which the analysis is conducted. By exploring the dynamics of the model under different environmental conditions, we tacitly assumed that the spatial scale is sufficiently large such that system attributes of one habitat do not affect the other—e.g. attributes of urban areas don’t spill into wildlands. Our model was developed to compare a large urban area (hundreds of square miles or larger) with a similar sized wildland. At this scale it is reasonable to assume that, on average, urban and wildland birds are affected only by attributes of their respective landscapes. At smaller scales, this may not be the case. For wildland remnants embedded in urban areas, there may be spillover effects and the different outcomes predicted by the model may not be realized. The critical scale at which the predictions would breakdown occurs when the home range of an organism is sufficiently large to overlap different habitat types. A bird population living in a wildland remnant that can reach resources in the surrounding urban area will likely more resemble an urban population than a wildland one. The model could be easily extended to explore this issue by using multiple copies of the existing model to represent different habitat patches that are then linked through migration. By exploring the dynamics of the resulting metapopulation model for different assumptions about animal movement patterns, the scale at which the predictions breakdown could be determined; a result that would be, in principle, empirically testable.

Our analysis suggests that the model results are robust to quite a wide range of choices for all but two parameters, \bar{e} ,

α_{11} , and the relative time scales of demographic and metabolic processes. The importance of these factors is not surprising. The ability to store resources goes hand in hand with the ability to take them up. Increased competitive ability has little value if additional resources cannot be stored. Thus, decreased ability to store resources prevents strong competitors from dominating the population by erasing their advantage (region B, Fig. 3(B)). While unimportant for our results regarding predation, the issue of relative time scales of demographic and metabolic processes can affect our results regarding fluctuating resources. Metabolic processes must occur relatively fast compared to demographic processes for pulsed resource inputs of sufficiently low period to generate a shift in population structure. Otherwise, the population tracks the resource fluctuations too closely, again erasing the competitive advantage of type 1 individuals. Finally, in both cases there must be a skew in the proportion of offspring in favor of type 2 individuals ($\alpha_{11} < 0.5$). Otherwise, strong competitors will always dominate the population. This skew may be reasonable for reasons discussed in Section 4.1, but needs to be empirically established in future studies. Interestingly, as long as α_{11} is sufficiently small, the results concerning predation are insensitive to the actual value of α_{11} , but those concerning fluctuating resources are not— α_{11} cannot be too small for reasons discussed above.

The development and analysis of the model has allowed us to assess whether two proposed mechanisms underlying urban bird population structure are theoretically possible. In the process, the model helped clarify under what conditions these mechanisms may be at work. Our model, under a range of conditions, produces a switch in the population structure when one goes from a more natural environment (variable and presumably more risky) where stronger competitors dominate to an urban environment (constant and presumably safer) where weaker competitors dominate. Urbanization may therefore be viewed as leading to a shift from key selection pressures in wildlands (e.g. relatively low competition for food, high risk of predation) to others, such as noise, foraging efficiency and food quality (Shochat et al., 2006). Thus, under “natural” conditions, weak competitors are normally selected out of the population by predation or starvation. If these selection pressures are relaxed, we find that the dynamics change in interesting ways, which suggest some directions for future theoretical and empirical work. For example: in our model we assumed that winners are in a better body condition. It has been shown that this function has an optimum, and that in some cases being “too fat” can be a disadvantage, because it can make it harder to escape predators (Gosler et al., 1995). If predation pressure is low on adult birds (Shochat, 2004) or squirrels (Bowers and Breland, 1996) in cities, the cost for very high body mass may be much lower in cities than in wildlands.

A key theoretical issue is the existence of an intermediate time scale between metabolic and demographic processes.

Body condition is not simply a matter of whether a bird has eaten in the past 24 h. It is the integral of several effects over some longer time period that determines overall condition, which, in turn, influences reproductive success. The next step in the development of the model will be to add this intermediate time scale and introduce seasonality into the demographic process. Several recent studies have suggested that human modification of habitats may be altering the phenology of climate and resource dynamics in ways that can cause a mismatch between processes occurring at different time scales, with negative fitness consequences for some species, e.g., nesting too early to ensure sufficient food for fledglings (Stenseth and Mysterud, 2002; Schoech and Bowman, 2001, 2003). Second, the “losers” continue to consume resources and create greater interference competition as their numbers increase. This has some effect on the conspecific “winners”, but may have a greater effect on other species with different competitive abilities. One way to extend our model to address these interspecific effects would be to add a second species that differs in its resource uptake function. Alternatively, one may add species with different birth or death functions. Our model thus provides a way to link intraspecific competition with interspecific interactions to generate insights into community level phenomena.

A third interesting theoretical extension of the model would be to include the potential effects of novel stressors such as noise or pollutants stemming from urbanization. If such stressors impact all individuals equally, they would not change our basic results. If, however, they affect losers more than they may affect winners, such stressors may reduce the skew in population structure. Pollutants that disrupt endocrine processes can also alter the timing of reproductive and other life-history events (Clotfelter et al., 2004; McCarty and Secord, 1999), potentially amplifying phenological mismatches for some species (Stenseth and Mysterud, 2002; Schoech and Bowman, 2001, 2003). An extended model that includes seasonality and intermediate time scales would allow us to explore these effects.

In addition to these theoretical issues, the model suggests two areas for future empirical investigation. First, since the total amount of resources increase substantially in cities, the total population size scales up (see Appendix A). This is consistent with empirical observations (Marzluff, 2001). In our model, this increase is, in part, driven by the strong competitors who, due to their higher individual resource use and reproductive capacity, produce a larger number of offspring. This effect may be magnified in opportunistic breeders, i.e. species that can expand their breeding season and produce multiple clutches per year, rather like some Darwin’s Finches in el niño years (Grant et al., 2000). Second, although most of the offspring produced are weak competitors, they can survive for longer periods and become numerically dominant. This sets up an intraspecific source–sink dynamic within the urban populations, with a few “winners” producing a lot of “losers”, as has been

observed in some cases. For example, urban populations of western gulls (Pierotti and Annett, 2001) exhibit just such a skew in reproductive success, while Florida scrub jays exhibit a spatial source–sink pattern in a suburban-wildland matrix (Schoech and Bowman, 2001; Mumme et al., 2000).

Finally, urbanization may also have important implications for species that are predisposed (due to intrinsic resource uptake, or birth and death functions) to succeed under such conditions. We have shown that overall body condition (energy levels) is poorer under urban-like conditions, and weaker competitors dominate. This may lead to even successful urban species becoming more vulnerable to sudden changes in the environment as seems to be happening with the house sparrow in Europe (Hole et al., 2002). Further development of the model may link the resource uptake and birth/death functions more explicitly to empirically measured life-history parameters, in turn providing a theoretical basis for predicting which species may do better or worse under continued urbanization.

Acknowledgments

We are grateful to Paige Warren, Tom Hahn, and Sue Bertram for intellectual stimulation and comments on the manuscript. We are especially grateful to James Grover for detailed, extremely helpful comments on an earlier version of this manuscript. M. Katti and E. Shochat were supported by the Central Arizona Phoenix Long-Term Ecological Research project under the grant NSF LTER DEB #9714833.

Appendix A

Here, we establish the existence of a non-trivial fixed point, $(s^*, n_1^*, n_2^*, e_1^*, e_2^*)$ for the five dimensional-ode given by (2a)–(2e) in the case when $I(t) = I$ is a constant. To do this, we must establish the existence of a solution to the system of nonlinear equations

$$0 = I - c_1(s^*, e_1^*)n_1^* - c_2(s^*, e_2^*)n_2^* - Ds^*, \quad (\text{A.1a})$$

$$0 = \alpha_{11}b(e_1^*)n_1^* + \alpha_{12}b(e_2^*)n_2^* - d(e_1^*)n_1^*, \quad (\text{A.1b})$$

$$0 = \alpha_{21}b(e_1^*)n_1^* + \alpha_{22}b(e_2^*)n_2^* - d(e_2^*)n_2^*, \quad (\text{A.1c})$$

$$0 = c_1(s^*, e_1^*) - m_r(e_1^*), \quad (\text{A.1d})$$

$$0 = c_2(s^*, e_2^*) - m_r(e_2^*), \quad (\text{A.1e})$$

where we use superscript star to denote the steady state values of the state variables. From Eqs. (A.1d) and (A.1e) we can solve for e_i^* in terms of s^* . Recall that the functions c_1 and m_r (and in fact all the functions in the model) are generated by an instance of $f(x; a, b, c)$ defined by (3) for a particular choice of the parameters a , b , and c . For notational convenience, we refer to these parameter choices using a subscript referring to the function they generate, i.e. $c_1(s^*, e_1^*) = f_{c_1}(s^*)(1 - e_1^*/\bar{e})$, and $m_r(e_i^*) = f_{m_r}(e_i^*)$. Using

this notation, we have

$$e_i^*(s^*) = \frac{\bar{e}}{2} \left[-B_i(s^*) \pm \sqrt{B_i^2(s^*) + \frac{\tilde{m}_r}{\bar{e}}} \right], \quad (\text{A.2})$$

where $B_i(s^*) = 1 - (\tilde{m}_r/\bar{e}) - \bar{m}_r/f_{c_i(s^*)}$. Eq. (A.2) implies that for any given s^* , there are two values of e_i^* , one positive and one negative. The latter is not biologically meaningful and we disregard it. We can now replace e_i^* in (A.1a)–(A.1c) with $e_i^*(s^*)$ and express the right-hand sides of these equations in terms of s^* only. To simplify notation, we denote these new functions of s^* with hats, i.e. $\hat{c}_1(s^*) = c_1(s^*, e_1^*(s^*))$, etc. Rewriting (A.1a)–(A.1c) yields

$$0 = I - \hat{c}_1(s^*)n_1^* - \hat{c}_2(s^*)n_2^* - Ds^*, \quad (\text{A.3a})$$

$$0 = \alpha_{11}\hat{b}(s^*)n_1^* + \alpha_{12}\hat{b}(s^*)n_2^* - \hat{d}(s^*)n_1^*, \quad (\text{A.3b})$$

$$0 = \alpha_{21}\hat{b}(s^*)n_1^* + \alpha_{22}\hat{b}(s^*)n_2^* - \hat{d}(s^*)n_2^* \quad (\text{A.3c})$$

which constitute a system of three equations and three unknowns. Adding (A.3b) and (A.3c) yields the relationship $n_1^* = A(s^*)n_2^*$ where

$$A(s^*) = -\frac{(\alpha_{12} + \alpha_{22})\hat{b}(s^*) - \hat{d}(s^*)}{(\alpha_{11} + \alpha_{21})\hat{b}(s^*) - \hat{d}(s^*)} \quad (\text{A.4})$$

which, combined with (A.3a) allows us to compute $n_1^*(s^*)$, and $n_2^*(s^*)$:

$$n_1^*(s^*) = \frac{I - Ds^*}{\hat{c}_1(s^*) \left(1 + \frac{\hat{c}_2(s^*)}{A(s^*)\hat{c}_1(s^*)} \right)},$$

$$n_2^*(s^*) = \frac{I - Ds^*}{\hat{c}_1(s^*)A(s^*) + \hat{c}_2(s^*)}. \quad (\text{A.5})$$

Note that for a biologically meaningful equilibrium, both $n_1^*(s^*)$ and $n_2^*(s^*)$ must be positive which implies that $A(s^*) > 0$. The biological interpretation for this condition is that at equilibrium, there must be a source and a sink population. The numerator of (A.4) represents the net production of the poor competitors. At equilibrium, the poor competitors are a sink, and thus have a net loss, that is $(\alpha_{12} + \alpha_{22})\hat{b}(s^*) - \hat{d}(s^*) < 0$ while the strong competitors are a source population and $(\alpha_{11} + \alpha_{21})\hat{b}(s^*) - \hat{d}(s^*) > 0$. This guarantees that $A(s^*) > 0$, yielding a biologically meaningful equilibrium. Also notice from (A.5) that the term $I - Ds^*$ appears in both expressions for equilibrium population sizes. This expression merely scales both the equilibrium population sizes, and does not affect their relative sizes. Thus, $I(t)$ can be normalized to 1 and D can be expressed as a proportion of I .

Finally, the expressions in (A.5) can be substituted back into Eq. (A.3b) to yield an implicit expression for s^* which depends only on parameters. Thus, for a given parameter set, we can compute s^* which we can then use to compute n_1^* and n_2^* via (A.5) and e_1^* and e_2^* via (A.2). A general solution for s^* cannot be written down explicitly, and the general expressions for the equilibrium values of the other variables are too complex to be of much use. We thus use numerical techniques to compute equilibria and explore

their behavior as parameters vary. We use pseudo arclength continuation based on work by Doedel (1981) as implemented in the numerical dynamical systems tool XPPAUT developed by Ermentrout (2002).

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