

Introduction

Urbanization results in higher bird population densities, even as species diversity declines. This may be due to higher resources (amount and input rate), and lower predation risk in cities.

Optimal foraging models predict that birds exploit habitat patches in proportion to resource input rates in those patches, and net fitness should be equal across patches. Our studies of birds foraging in urban and desert habitats did not support this prediction. We found over-exploitation in urban habitat, which should raise fitness costs: poorer body condition / shorter life-span. Yet, urban densities remain consistently high.

Observed foraging behavior

We measured giving up densities, GUD, in artificial food patches. Urban GUDs were significantly lower than desert GUDs.



Hypothesis & modeling approach

We propose the hypothesis that lower predation and more predictable (and higher) resource inputs in cities allow poorer quality individuals to persist, thereby inflating densities. Here, we present a mathematical model that provides some insights into this seemingly paradoxical phenomenon.



The model tracks the populations of two types of individuals defined by their ability to forage. We define the better foragers as type 1 and the poorer foragers as type 2. The number of each type of individual is denoted by n_1 and n_2 respectively. The two populations are not distinct species, can interbreed, and produce offspring of either type. Type j individuals produce type i individuals at the rate α_{ii} where *i* and *j* can take on values of 1 or 2.

An important aspect of the model is the rate at which individuals can add to their energy store through foraging. Thus, in addition to the number of individual of each type, we track the (average) energy state of each type. The energy state of an individual of type i is denoted by e_i . We assume that an individual's energy state affects its ability to forage, reproduce, avoid predators, and maintain metabolic processes. Thus, births and deaths are both functions of the energy state. E.g., the birth rate of type 1 individuals at time t is given by $b(e_1(t))$ where b(x) has the shape shown in the birth and death rate diagrams. An analogous relationship holds for deaths.

Energy uptake e3 metabolism

The foraging ability of each of the foragers is a simple Michalis-Menton functional form as shown in the competitive ability diagram. The energy uptake depends on the available resources, and type 1 individuals always outcompete type 2 individuals. Mathematically, this means that $c_1(s)$ > $c_2(s)$, $\forall s$ as is apparent from the diagram. We model basal metabolic rate, $b_{mr}(e_i)$, in the same way. Above a certain threshold, the bmr is constant. When an individual's energy falls below the threshold, activity and *bmr* necessarily decrease, as seen in the diagram. The last element if the model is that the populations compete for a single resource with a constant input rate, I.



A two-population model



The nature of birth & death



1.2

Mathematical representation of model

$\frac{ds}{dt} = I - n_1 c_1(s) - n_2 c_2(s)$	(1)
$\frac{dn_1}{dt} = (\alpha_{11}b(e_1) - d(e_1))n_1 + \alpha_{12}b(e_2)n_2$	(2)
$\frac{dn_2}{dt} = \alpha_{21}b(e_1)n_1 + (\alpha_{22}b(e_2) - d(e_2))n_2$	(3)

- $\frac{de_1}{dt} = c_1(s) b_{mr}(e_1)$ (4)
- $\frac{de_2}{dt} = c_2(s) b_{mr}(e_2)$ (5)

A role for predation

A simple change in the death rate function, such as might occur due to a change in predation risk, had a significant effect on the relative abundance of the two types of individuals.

Under low predation (city-like conditions), type 2 individuals in poorer energy states dominate the population.

Under high predation (desert-like conditions), type 1 individuals in better energy states dominate the population.

Simple models can explain complex population phenomena

We are further developing these models by addressing the other major factor: resource input rate, and expect the population patterns observed here to be strengthened under cyclic or stochastically varying resource conditions.

While the results we present here are preliminary, they illustrate how relatively simple changes that affect bird behavior, might aggregate to the very different community level patterns seen in cities.

