
Credit or debit? Resource input changes population dynamics of city-slicker birds

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The underlying evolutionary mechanisms of urban bird populations have hardly been studied. High food density and low predation risk serve to explain the global pattern of extremely high urban bird population densities. Both these bottom-up and top-down effects are paradoxical since the per capita amount of food is small due to competition, and domestic predator density is high in cities. The bottom-up paradox can be resolved by taking into account the high food resource-predictability in cities. Concerning the top-down effect, recent studies suggest that at least when it comes to nest predation the effect of cats is minor. I suggest that the combination of high food predictability and low predation risk in cities alter bird foraging behaviour, which in turn affects population dynamics. In terms of density, the result is that bird populations exceed the carrying capacity of the urban environment, costing heavily on body condition and/or life span. Under such conditions the population should consist of a few winners and many losers. Only the winners have sufficient access to food resources and the opportunity to reproduce. The highly predictable continuous input of food in the urban environment allows them to "live on their credit". They may trade off between offspring body condition and clutch size. In the lack of predation, the losers among the fledglings may survive for a relatively long period, getting just enough energy to survive. Though they may never become healthy enough to reproduce, they will have a major contribution to the observed population density. Results of several case studies seem to support the credit card hypothesis and suggest that it can serve as a general rule for the evolution of animal populations and communities in highly predictable human managed environments.

With the rapidly growing body of evidence on patterns in urban bird populations and communities it is surprising how little we know about their underlying evolutionary mechanisms. Compared with adjacent wildlands, cities are characterized by higher bird population densities and lower species diversity (Marzluff 2001). Two major factors have been suggested to explain the increase in densities: a bottom-up effect (the increase in food abundance) and a top-down effect (a decrease in predation). Interestingly, both factors are paradoxical. While food may be more abundant at the population level (Marzluff 2001), it may be scarce at the individual level due to high competition (Sol et al. 1998). While domestic predators may be highly abundant in cities

(Sorace 2002), their effects on prey behaviour or nest mortality may be negligible (Bowers and Breland 1996, Gering and Blair 1999).

Though the principles may be similar in other taxa, most studies on urban animals were done on bird communities (Marzluff et al. 2001a). Therefore, in this paper I focus on birds. I also use "desert" as an example for an extreme contrast to urban, being an unpredictable and resource-impoverished environment. Desert and urban can therefore serve as the two edges of the productivity gradient. I first attempt to resolve the paradox of food and predation, and then suggest a possible way in which the two work together, creating a unique process of urban bird population dynamics. I draw special attention to food predictability and its continuous input into the urban environment. Albeit largely ignored so far, this factor plays an important role in cities. I suggest that the high predictability of food availability changes foraging behaviour and consequently decision making on trade-offs between clutch size and nestling body condition. This, in turn, results in an increase in bird densities and may change not only population dynamics, but also community structure and species diversity.

Population bottom-up regulations: the first paradox

The response of population density to changes in food density can be defined in terms of the resource-matching rule (RMR) in which foragers distribute themselves according to the distribution of resources in the environment (Parker 1978, Pulliam and Caraco 1984). This equilibrium predicts higher densities of birds in an urban environment compared with wildlands (Fig. 1). It also predicts that fitness or payoff should be equal across habitats (the ideal free distribution, IFD, Fretwell and Lucas 1969). However, foragers in many cases fail to

match resource density (Kennedy and Gray 1993). Several mechanisms have been suggested for deviations from the RMR: unequal competitive abilities, aggression, imperfect knowledge of resource distribution, and travel cost (reviewed by Kennedy and Gray 1993). All these models predict under-matching (over exploitation of the poor habitat). This has a cost, and individuals in the poor habitats may experience a lower energetic gain than those in the rich habitat (Shochat et al. 2002).

The higher population density in the urban environment may increase competition for food and yield a paradox in which, at the population level, the urban environment is richer in food than wildlands, whereas at the individual level, less food is available. Cities represent a perfect case of a continuous input environment, with refuse sources and bird food on feeders being reloaded on a daily basis. Anyone who has ever fed pigeons is familiar with the following situation: the foragers sit and wait for the food. As soon as the food appears, the birds rapidly deplete the supply. There is never enough food to feed all the pigeons. Add more grains and more and more birds will gather. This situation is well described in Sol et al. (1998). Furthermore, food quality may be as important as its quantity. It has been shown that

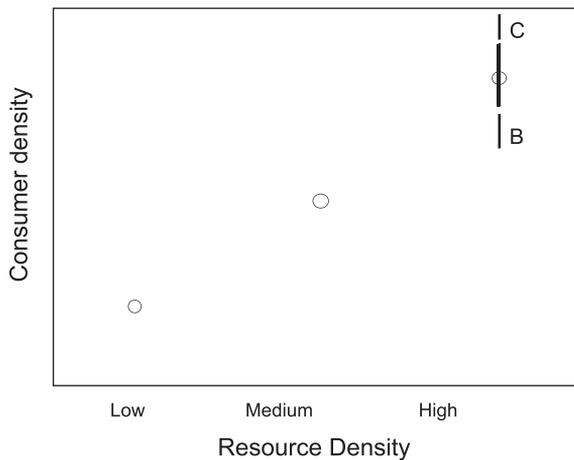


Fig. 1. The resource matching rule - forager density as a linear function of resource density. Of the three habitats, the low resource and high resource environments represent desert and urban respectively. In a long-term urbanisation process we may turn 1 into 3 by increasing resource density, and consequently forager density. For each resource density I assume an average consumer density, with a standard deviation (bold lines). Deviations from the average may be the result of individuals moving between patches, assuming that not all foragers are ideal or free to select where to live or forage. As long as these fluctuations of forager densities in a given patch do not exceed the standard deviation we can assume that the system is at equilibrium. If changes in population density exceed the standard deviation the line B represents an over-exploitation of the poor habitat, where foragers in the urban environment may benefit, and C represents an overexploitation of the rich habitat, where foragers in the urban environment have costs.

although more food is available in cities, in some cases it consists of mainly 'junk food' which may be adequate for adult birds but inappropriate for their nestlings (Pierotti and Annett 2001, Schoech and Bowman 2001). Altogether, the balance between food input and intake in the urban habitat may have a major effect on foraging behaviour. Therefore, when studying bottom-up effects on urban birds we should be careful not to overestimate the amount of food available to individuals.

Population top-down regulations: the second paradox

Densities of urban birds, together with their general tame behavior, may appear surprising given the extremely high densities of both domestic/feral predator and corvids in cities. Woods et al. (2003) suggested that cats might kill around 27 million birds in the UK in one year. Most feral cats are found in urban habitats where bird populations are extremely high. This may suggest that urban bird population control is not top-down regulated. Indeed, despite the high abundance of domestic and feral predators, the general assumption is that predation pressure declines in cities. Do case studies support this hypothesis? To address this question we need to consider the following issues:

- 1) Nest predation and adult predation are different issues. Most of the experimental studies on urban birds addressed predation of artificial nests. Some concluded that nest predation increased in cities (Jokimaki and Huhta 2000, Thorington and Bowman 2003), while others found no differences (Matthews et al. 1999) or even a decrease in nest predation (Gering and Blair 1999). Cats may not be responsible for the majority of nest predation (Haskell et al. 2001), but may rather represent a high risk to adult birds. Studies on nest predation by corvids are again, ambiguous. Some argue that corvids are major nest predators in cities (Groom 1993, Major et al. 1996, Matthews et al. 1999), though more recent studies indicate that it is not necessarily the case (Marzluff et al. 2001b).
- 2) Generally, it is hard to assess whether urban predator abundance is lower or higher than in wildlands. Cities are characterized by decreasing numbers of native predators, increasing numbers domestic or feral predators (dogs, cats and rats) and increasing numbers of corvids. Concerning adult predation, an important issue is both predator and prey identity. It is not clear whether all potential predators indeed act as predators in reality. Many of the urban predators may not hunt but rather, rely on human refuse. Therefore, only focusing on predator abundance (Sorace 2002) may miss the crux of the issue, because predator

abundance is not necessarily an indication for predation pressure. Possibly, species composition in urban areas reflects the “ghost of predation past”. The remaining urban species may be those that cope with domestic and feral predators. For example, cats may not affect the breeding bird population as much as the more naïve migratory birds passing through urban environments.

Because of the complexity in addressing the bottom-up effects on urban bird population densities, we need to ask whether the perceived predation risk is higher in cities. Predation affects not only prey evolution and abundance, but also behavior (Sih et al. 1985, Lima 1998, 2002). Short-term behavioral responses to predation risk are useful in studying top-down effects, because whether predator abundance increase or decrease, the most important issue is how the birds view the urban environment. Results from central Arizona suggest that compared with desert, predation risk is indeed reduced in cities. Bird foraging behavior near bushes differed from their behavior out in the open microhabitat in the desert, but not in the urban habitat (Shochat et al. in press).

The increase in food and the reduction in predation may be sufficient to explain the increase in urban bird population densities. The question remains: what controls population density, and will it eventually reach a new equilibrium that is expected under the RMR?

Credit or debit? Population response to food predictability

In the desert-urban landscape an over-matching situation (over-exploitation of the urban habitat) may arise due to differences in food input rates into the system. Therefore, urban bird densities may actually be higher than expected under the RMR. While extremely unpredictable environments like deserts will select for the best competitors for food (most efficient foragers), such a natural selection will become mollified in the urban environment with its daily continuous input of food. Furthermore, with the low predation pressure, inferior competitors that are permanently being removed from the desert may persist for fairly long periods in cities. These birds may gain just enough energy to survive on a day-to-day basis. Their contribution to the next generation will be negligible, unlike their contribution to the total population density.

This situation can also be viewed as a special case of source-sink populations, in which both populations share the same environment, and individual turnover is higher in the sink population. Alternatively, Marzluff et al. (2001b) suggested that in cases where breeding territories are limited but food is abundant, immigration may be responsible for the high urban densities. Urban

centers might act as ‘sponges’ by attracting many pre-breeders from suburban areas where populations grow rapidly. The sponge hypothesis has therefore a similar outcome to the case described here, though the source of the floater individuals is different. The floaters I describe here are produced in the urban habitat, while in sponge populations they are immigrants from close suburban areas.

The high predictability of food input into the urban ecosystem may also affect decision-making in the long term. Where competition for food is very high there must be winners and losers. Winners will respond faster to food renewal than losers (Sol et al. 1998), and consume a sufficient amount of food for more than just surviving. In the long term, their decision-making rules may be as follows: have a permanent income? Live on your credit. An ‘overdraft’ in your energy balance account is affordable, since tomorrow’s income should cover for it. In contrast, in the desert save what you have before you can gain more energy, since you never know when the next resource input event will occur. Under such rules, a snapshot of each population at any given time predicts a relatively small population in the desert with individuals with a superior body condition, versus a much larger population with, on average, individuals with an inferior body condition.

In the urban environment, the dominant individuals may increase their investment in reproduction to a level even higher than expected, due to the increased chance of nestling survival. For example, adults will choose to trade clutch size for fledgling body mass. That is, they will fledge more but leaner chicks, each one with potentially a good chance of finding a sufficient amount of food to survive and “wait for better days”. A minority of the many fledglings may indeed experience better days, but the majority may wait forever. They may survive for a relatively long period of time and remain as floaters in the population. In addition to being in an inferior condition, they may also experience a shorter life span compared with the winners. But in the absence of predators to remove them they will live long enough, contribute to the population size, and make the big difference compared with a wild population where their alike do not survive.

The described scenario goes beyond a simple RMR situation in explaining the high urban bird densities. It describes an over exploitation of the rich habitat where the apparent ‘beyond-k density’ does not decline to the expected k (in terms of density) due to a continuous input of a highly predictable resource, and at a cost in the average body condition that is lower than in a wild land. The distribution around the average body condition in the urban environment is skewed to the right, since losers outnumber the winners (Fig. 2).

To what extent urban bird population dynamics follow the described scenario is yet to be addressed, but the

results of several empirical studies appear highly supportive of it. Concerning the shift in foraging behaviour, a study on urban squirrels (Bowers and Breland 1996) demonstrated that leftover amount (the giving up density or GUD) of seed on artificial food patches decreases along a wildland–rural–urban gradient. GUD measuring is a reliable tool to assess how optimal foragers perceive the environments (Brown 1988). Lower costs of foraging lead to lower GUDs and vice versa. Consequently GUDs have been largely used to assess foraging behaviour and forager decision-making under different situations of predation risk, competition and resource abundance (Mitchell et al. 1990, Kotler et al. 1991, 1993, Bouskila 1995). In the case of the urban squirrels, GUDs indicated that the forest squirrels quit the food patches much earlier than urban squirrels. Forest squirrels experienced high exposure to predators and little competition compared with the more efficient urban squirrels. Shochat et al. (in press) observed similar patterns in a study where urban and desert bird GUDs were compared.

Yet, another study on an “urban” population of gulls in Alcatraz Island, California, revealed how extreme the differences between winners and losers can be. Though Alcatraz is not an urban habitat, the island is highly developed and is located only two km from the large urban core of San Francisco (Pierotti and Annett 2001). Moreover, some of the gulls that breed on the island fly to feed in the urban area. In a long-term study on Alcatraz, Annett and Pierotti (1999) assessed the reproductive success of

winner and loser western gulls. Though the gulls were not initially defined as winners or losers, the results indicate that they fall into these categories. The initial discrimination was due to their diet. Some gulls foraged on refuse-chicken leftovers, while others fed on fish caught out in the sea. The gulls that provided fish to their nestlings fledged up to 27 chicks in 12 years, while those providing chicken, were unable to fledge one chick due to the lack of calcium in the chicken diet. A similar problem of ‘junk food provisioning’ in the Florida scrub jay (Schoech and Bowman 2001) may suggest that even in cases when birds find enough food to reproduce, they access the wrong kind of food, lowering their fitness dramatically (Annett and Pierotti 1999).

Finally, a study on pigeons in Spain (Sol et al. 1998) supports different aspects of the credit card hypothesis. Urban pigeon predators were scarce, and competition for food was intense, especially when pigeons were fed by humans. The study focused on differences in competitive abilities between adult and young pigeons. It showed that juvenile pigeons had less competitive skills than adults. Juveniles were less likely to attain a positive energy balance during the day and were more vulnerable to starvation and disease. Indeed, more juvenile corpses than expected were found during the study. Differential mortality of juvenile and adult pigeons could in part arise from differences in competitive abilities over food. Although this study distinguished between winners and losers based on age criteria, separation can be based on other criteria since winners in this case were the successful individuals among the past losers.

The credit card hypothesis captures the dominant processes in urban bird ecology, and may extend to other habitats with high food abundance and predictability. Cities may only represent the most extreme case of habitats with such conditions, where the game rules change and dramatically affect foraging behavior, decision-making and population density. Such changes may further reflect on community structure and species diversity.

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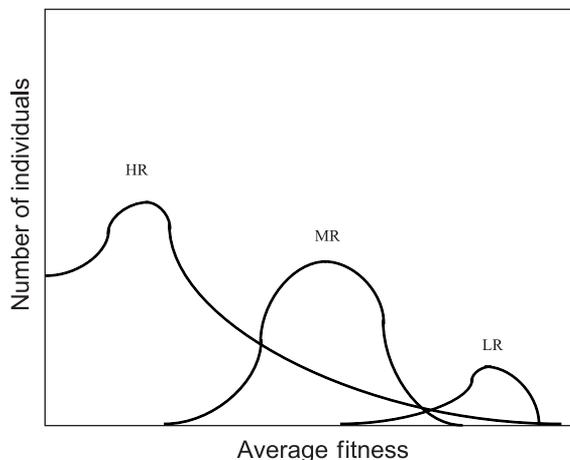


Fig. 2. The number of individuals and the distribution of their fitness in the three habitats shown in Fig. 1. HR (high resource density) and LR (low resource density) represent urban and desert population densities respectively. Population density is higher but fitness is on average lower in the urban habitat. In the urban habitat the distribution around the average is skewed to the right, as there are less winners than losers. MR = Medium resource density.

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