

Linking Optimal Foraging Behavior to Bird Community Structure in an Urban-Desert Landscape: Field Experiments with Artificial Food Patches

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ABSTRACT: Urban bird communities exhibit high population densities and low species diversity, yet mechanisms behind these patterns remain largely untested. We present results from experimental studies of behavioral mechanisms underlying these patterns and provide a test of foraging theory applied to urban bird communities. We measured foraging decisions at artificial food patches to assess how urban habitats differ from wildlands in predation risk, missed-opportunity cost, competition, and metabolic cost. By manipulating seed trays, we compared leftover seed (giving-up density) in urban and desert habitats in Arizona. Deserts exhibited higher predation risk than urban habitats. Only desert birds quit patches earlier when increasing the missed-opportunity cost. House finches and house sparrows coexist by trading off travel cost against foraging efficiency. In exclusion experiments, urban doves were more efficient foragers than passerines. Providing water decreased digestive costs only in the desert. At the population level, reduced predation and higher resource abundance drive the increased densities in cities. At the community level, the decline in diversity may involve exclusion of native species by highly efficient urban specialists. Competitive interactions play significant roles in structuring urban bird communities. Our results indicate the importance and potential of mechanistic approaches for future urban bird community studies.

With the worldwide rapid urbanization, there is a growing interest in urban animal populations and communities (McIntyre 2000; Marzluff 2001). Most studies in urban ecosystems involve birds (reviewed by Marzluff et al. 2001*b*), probably because of higher public interest in this taxon and the relative ease of monitoring birds. Studies from different continents reveal similar patterns: compared with the wildlands it is replacing, in the urban habitat species diversity tends to decrease (Marzluff 2001); community composition shifts as native species are replaced by human commensals, some of them exotic (Emlen 1974); evenness sometimes decreases (dominance increases), with urban specialists constituting a high proportion of the community (Marzluff 2001); and density increases, with total urban bird populations becoming much larger than in wildlands (Marzluff 2001).

Mechanisms underlying these patterns remain unclear. Though many studies on urban bird communities suggest mechanisms for the increase in density (reviewed by Marzluff 2001), few address the decrease in diversity. Moreover, these studies focused particularly on landscape or habitat structure (e.g., housing density, vegetation density; Marzluff 2001), with less attention paid to other important factors such as resource availability and species interactions (e.g., Emlen 1974; Bolger 2001). Yet, the only hypothesis that has been tested experimentally is that the increase in bird abundance in urban environments is due to a decrease in predation pressure (reviewed by Marzluff 2001). Experiments to date have addressed only nest predation (Major et al. 1996; Gering and Blair 1999; Matthews et al. 1999; Jokimaki and Huhta 2000; Haskell et al. 2001; Marzluff et al. 2001*a*), but it remains unclear how changes in predator abundance affect survival or behavior of adult birds.

Another cause for the higher urban bird densities may

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simply be higher resource abundance in cities (Bolger 2001; Marzluff et al. 2001a; Mennechez and Clergeau 2001). Urbanization is hypothesized to enhance the overall carrying capacity of the environment (Emlen 1974). In addition to natural food, urban birds obtain food from feeders (Brittingham and Temple 1992), exotic vegetation (Reichard et al. 2001), and human refuse (Marzluff et al. 2001a). In arid environments, water may also be a crucial factor (Emlen 1974) in that available water may facilitate dry seed intake by granivorous birds (Kotler et al. 1998).

The decline in species diversity may be attributable to more complex processes involving both changes in habitat structure and interspecific interactions. Species that adapt well to humans may competitively exclude native species. For example, the European starling (*Sturnus vulgaris*) and the house sparrow (*Passer domesticus*), two of the most common birds in urban North America, are known to outcompete other species for nesting sites and food (Bennett 1990; Copley et al. 1999; Tryjanowski and Kuczynski 1999). Species that are less efficient foragers than the house sparrow may fail to persist in cities. In contrast, factors such as predation, climatic conditions, or low water availability may shape community structure in wildlands.

Marzluff et al. (2001b, p. 14) stated that “the lack of experimental studies in urbanizing areas is puzzling.” Most studies on urban bird communities have been correlative. Only in recent years have ecologists started to use experimental approaches to reveal mechanisms. In particular, the question of whether urban bird densities respond to the increase in food resources remains unclear because of the difficulty in quantifying resource abundance. However, resource-consumer relationships can be assessed, without a direct measure of resources, on the basis of equilibrium models such as the “ideal free distribution” (Fretwell and Lucas 1969) or the “resource-matching rule” (Parker 1978).

Optimal foraging theory (Charnov 1976; Brown 1988) can also serve as a useful tool to assess differences in resource-consumer relationships between different habitats. According to Brown (1988), foragers should quit food patches when their benefit equals the cost of foraging:

$$H = C + P + \text{MOC}, \quad (1)$$

where H is harvest, C is metabolic cost, P is predation cost, and MOC is the missed-opportunity cost. If harvest rate is a function of resource density and patch type, the leftover amount of food in a patch (the giving-up density [GUD]) can serve as a surrogate to the quitting-harvest rate (QHR). The QHR is difficult to measure because it requires information on resource encounter rate (Brown 1988). As the summed energetic cost increases, foraging efficiency ($H/[C + P + \text{MOC}]$) decreases and GUD in-

creases. Thus, the density of food remaining in a patch after quitting foraging is an indicator of the forager’s perception of foraging costs and predation risk (Brown 1988).

The GUD method has been used widely in evolutionary ecology and has become a powerful tool in assessing habitat and microhabitat selection (Abramsky et al. 1990; Hughes et al. 1994), patch assessment (Valone and Brown 1989), competition and coexistence (Brown 1989; Mitchell et al. 1990; Brown et al. 1994), and predator-prey interactions (Kotler et al. 1991, 1993; Bouskila 1995). Furthermore, the immediate energetic gain from foraging can be linked to long-term population dynamics (Yunger et al. 2002) and community structure (Rosenzweig and Abramsky 1997). Therefore, understanding how urbanization affects foraging behavior can provide insights into processes at the population and community level. We used the simple yet robust GUD method as a framework to address some of these processes. In the context of our study, the three cost components of equation (1) relate to three major drivers of the structure of urban bird communities. The metabolic cost, C , relates to physiological constraints, which may decrease with water availability. The cost of predation, P , relates to changes in densities of predators in urban environments. Finally, the missed-opportunity cost, MOC, relates to the increase in food availability in cities. Consequently, measuring bird response after manipulating each component while holding the two others constant, we can address the relative importance of each factor to foraging behavior and in turn to population density and community structure.

Using optimal foraging theory as a framework, we combined observations and field experiments to assess several mechanisms underlying urban bird community structure. We designed our experiments to test independently the effect of competition, predation, metabolic cost, and missed-opportunity cost on bird foraging behavior and food intake. These in turn may explain patterns and processes at the population and community levels. Given the contradictory results from the few mechanistic studies on urban wildlife communities, we followed the rationale of Bowers and Breland (1996) in treating the ideal free distribution as our null hypothesis and predicting equal GUDs between habitats. Specific assumptions concerning treatments and microhabitats are specified in the methods.

Methods

Study Area

We selected 20 sites within the greater Phoenix area, central Arizona. Ten of the sites were in three large desert parks: four in Usery Mountain Park, to the east; four in South Mountain Park, to the south; and two in McDowell Park,

to the north of the city. The other 10 sites were residential backyards; six mesic yards (with lawns and flood irrigation) and four xeric/disturbed yards (with a high proportion of Sonoran desert vegetation and gravel).

Seed Trays

We mixed 20 g of millet seed with 3 kg of sifted sand in green plastic trays (36-cm diameter) to simulate resource patches. Trays were placed in the field for 24 h, during which minimum and maximum ambient temperatures were measured to serve as covariates; temperature is known to influence metabolism and, therefore, food consumption (Dawson and O'Connor 1996). In desert sites, we placed the trays on Cholla (*Opuntia* sp.) cactus to prevent rodent access (see under "Coexistence"), whereas urban trays were placed on 1-m-high stools. All cases where ants were recorded on the trays were omitted from the data. We used both direct observations and video monitoring to assess which species forage on the trays. We watched all trays for the first and last 2 h of each experiment. This enabled us to identify most species visiting the trays and determine which species was the last forager on the trays. We found that in >90% of the sessions lasting 4 d, species composition remained the same for each tray. Therefore, our observations gave a good indication of species composition on each tray. Video monitoring of 20 trays also suggests that all species visiting the trays were detected during the 4 h of tray observations. After collecting the trays, we sifted the sand in the lab, cleaned all organic matter other than millet, and measured the GUD to the nearest 0.01 g.

General Patterns

To determine whether urban and desert foragers differ in their efficiency to exploit food patches, we compared GUDs between habitats, controlling for temperature. We used ANCOVA with GUD as the effect, habitat as the factor, and temperature as a covariate. We compared data from both multispecies trays and trays where only one species (house finch) foraged in each habitat.

Assessing the Cost of Predation

For this experiment, we assumed that trees and bushes serve as shelters from predators. Therefore, between microhabitats (bush and open) we expected higher GUDs in the open, where predation risk is higher. An experiment included two seed trays in each habitat (urban or desert) placed on stools, one close to a tree or bush and one at a distance of 3 m (56 trays: 2 habitats \times 2 microhabitats \times 14 replicates). We recorded species

composition and compared GUDs between treatments (bush vs. open) after removing the effect of temperature. We used repeated measures (rm) ANOVA with habitat as the between-subject factor and microhabitat as the within-subject factor.

Manipulating MOC

In rich environments, foragers are expected to quit patches earlier than in poor environments, due to a higher MOC. In both urban and desert habitats, we tested whether food enrichment increases the MOC and consequently the GUDs. We conducted this experiment over two consecutive days. After measuring GUDs following 24 h of foraging, we created a rich environment by placing a feeder tray next to the seed tray (28 trays: 2 habitats \times 2 days \times 7 replicates; two urban trays that dropped to the ground were deleted from the analysis). The feeder contained 100 g of millet seed with no sand, increasing the forager's missed opportunity cost. We used rmANOVA with habitat as the between-subject factor and enrichment (before and after) as the within-subject factor. We used ANOVA to compare the leftover amount of seed on the feeder between desert and urban habitats.

Coexistence

Brown (1989) demonstrates how differences in GUDs can explain coexistence between sympatric species due to different trade-offs (e.g., between food vs. safety and foraging efficiency vs. travel cost). Therefore, to assess possible mechanisms of coexistence, we compared species GUDs in three different ways.

House sparrow (*Passer domesticus*) *versus* *house finch* (*Carpodacus mexicanus*). We compared the GUDs of two sympatric, small, granivorous species, house finch and house sparrow. Since these species are similar in body size, they could not be separated by cages. Therefore, we placed seed trays in different microhabitats within the urban environment. While we could not exclude the house finch and study the GUD of the house sparrow alone, we managed to find several sites where the house finch was the only forager. GUDs were compared between trays where the house finch was the sole forager (ANOVA, $N = 16$) to those from trays where both species were foraging ($N = 9$). In all the latter cases, the house sparrow was the last species on the tray, indicating that the GUDs we measured were house sparrow GUDs.

Large versus small granivores. This experiment was designed to exclude larger species. We placed two seed trays on stools—one control tray that allowed free access for all species and one caged tray (4-cm mesh size). The caged tray allowed curve-billed thrasher (*Toxostoma curvirostre*),

house sparrow, and house finch to enter while excluding all dove species. Since species composition differed between backyard types, we analyzed data from xeric and mesic yards separately (28 trays: 2 yard types \times 2 treatments \times 7 replicates). We used rmANOVA, with habitat (desert vs. city) or yard (mesic vs. xeric) as the between-subject factor and exclusion treatment (caged vs. control tray) as the within-subject factor. Two mesic-yard trays that dropped to the ground were deleted from the analysis). In xeric yards, the foragers were house finches versus white-winged doves (*Zenaida asiatica*) and mourning doves (*Zenaida macroura*). In mesic yards, the foragers were house sparrows versus Inca doves (*Columbina inca*). In several cases, curve-billed thrashers also foraged on both caged and control trays. However, video monitoring confirmed that thrashers quit seed trays much earlier than most urban foragers do (except for house finches). Therefore, to assess house finch GUDs, we excluded all cases where both curve-billed thrashers and house finches foraged on caged trays in xeric yards.

Desert birds versus ground squirrels. We placed desert trays on Cholla, assuming that rodents are unable to climb this very thorny cactus. This assumption was wrong because observations, video monitoring, and feces found on trays revealed that round-tailed ground squirrels (*Spermophilus tereticaudus*) started to visit the tray at one site in Utery Mountain Park beginning early April 2002 (1.5 yr after we began the field experiment). This site included a wash, where squirrel abundance was particularly high. Consequently, we stopped studying bird GUDs in the wash. However, following the results from this accidental experiment, we continued measuring squirrel GUDs from this site and two adjacent sites to compare with desert bird GUDs (ANOVA, 20 trays: 2 forager types \times 10 replicates). The bird trays were placed in new locations within the same sites, away from washes, and were not visited by squirrels as confirmed by video monitoring.

Water Effect (Manipulation of C)

According to equation (1), the GUD should increase with the metabolic cost (C). Water availability influences the cost of digesting dry food, a component of the overall metabolic cost. We manipulated water availability in both urban and desert habitats. During the summer, we carried out the experiments in the desert at least 3 d after monsoon events. Each session lasted 4 d. Seed trays were placed without water on the first and third days. On the second and fourth days, we added water bowls to the trays. The amount of water was sufficient for the 24-h trial period (92 trays: 2 treatments \times 2 habitats, with 37 replicates in desert and 9 in urban). We used a multivariate rmANOVA with habitat as the between-subject factor, water as the

within-subject factor, and maximum ambient temperature as a covariate.

Results

General

Fifteen bird species visited the seed trays. Ten species were recorded on urban trays and nine on desert trays (fig. 1). Four species—house finch, curve-billed thrasher, Abert's towhee (*Pipilo aberti*), and brown-headed cowbird (*Molothrus ater*)—were recorded on trays in both habitats. The species shown in figure 1 are mostly granivorous, although curve-billed thrasher and cactus wren (*Campylorhynchus brunneicapillus*) are omnivores that occasionally feed on seeds. The curve-billed thrasher was a frequent visitor to both desert and urban trays.

We compared the GUDs of urban and desert foragers using maximum ambient temperature (MAT) as a covariate at both the community (all trays) and the population (house finch only) levels. At the community level, both habitat ($F = 35.52$, $P < .001$) and MAT ($F = 4.250$, $P = .041$) affected GUDs (ANCOVA, $F = 8.64$, $df = 1, 215$, $P = .004$). Urban foragers had lower GUDs than desert foragers, especially at high temperatures. Urban foragers were not affected by temperature, while GUDs of desert foragers increased with temperature (fig. 2). In general, urban birds appear to be more efficient foragers than desert birds. Results were similar when GUDs were correlated with minimum temperatures.

To test for differences in GUDs between habitats, we selected the house finch because it is widespread in both desert and urban habitats and because we had a sufficient sample of trays where this species foraged solely. House finch GUDs were positively correlated with ambient temperature in both habitats (fig. 2B). Interestingly, in the desert, house finch GUDs were lower than in the urban habitat (ANCOVA, $F = 0.005$, $df = 1, 29$, $P = .94$), the reverse of the pattern at the community level (fig. 2A).

Assessing the Cost of Predation

The GUDs of desert and urban foragers in bush and open microhabitats are shown in figure 3. Again, desert GUDs were higher than urban GUDs (rmANOVA, $F[\text{habitat}] = 5.81$, $df = 1, 26$, $P = .023$). GUDs in the open were significantly higher than in the bush (rmANOVA, $F[\text{microhabitat}] = 8.33$, $df = 1, 26$, $P = .008$). The interaction between habitat (desert vs. urban) and microhabitat (bush vs. open) was also significant (rmANOVA $F[\text{habitat} \times \text{microhabitat}] = 10.87$, $df = 1, 26$, $P = .003$). The open versus bush disparity was greater in the desert than in the urban habitat.

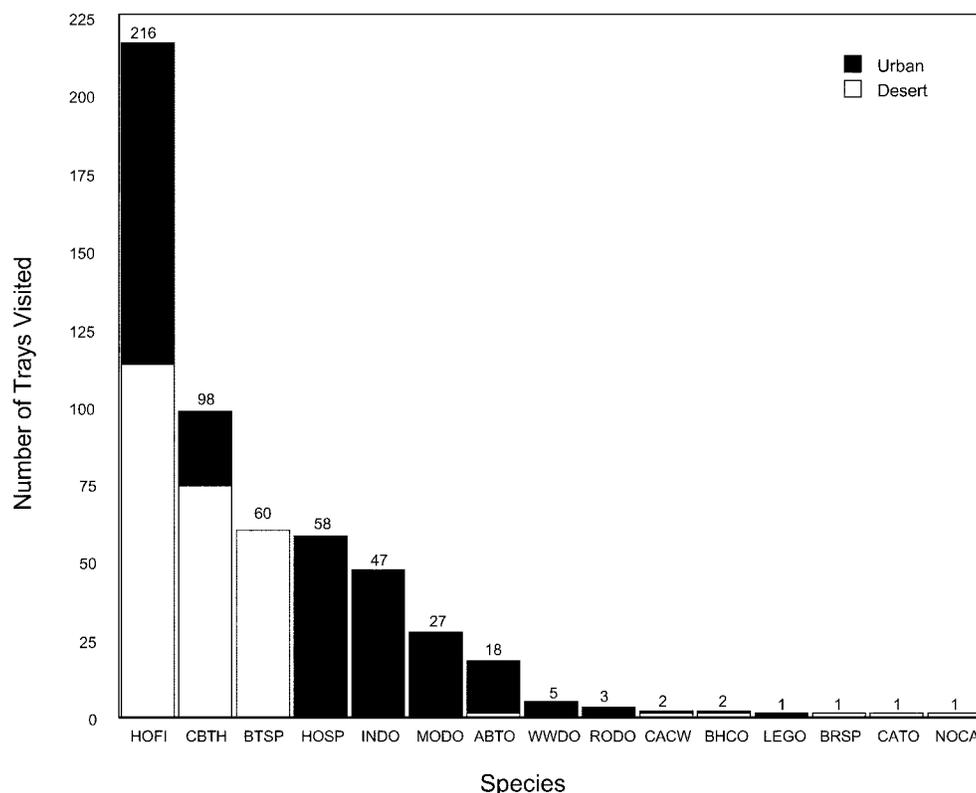


Figure 1: Fifteen species of birds recorded on seed trays in desert and urban habitats in central Arizona. Numbers above bars indicate number of seed trays visited. *HOFI* = house finch, *CBTH* = curve-billed thrasher, *BTSP* = black-throated sparrow, *HOSP* = house sparrow, *INDO* = Inca dove, *MODO* = mourning dove, *ABTO* = Abert's towhee, *WWDO* = white-winged dove, *RODO* = rock dove, *CACW* = cactus wren, *BHCO* = brown-headed cowbird, *LEGO* = lesser goldfinch, *BRSP* = Brewer's sparrow, *CATO* = canyon towhee, *NOCA* = northern cardinal.

Manipulation of MOC

To investigate MOC, we compared the GUD measured from a tray without a food-rich feeder with the GUD from a tray near a feeder (fig. 4A). GUDs were low in the urban habitat and high in the desert habitat (rmANOVA, $F[\text{habitat}] = 69.2$, $df = 1, 11$, $P < .0001$); GUDs after enrichment were significantly higher than before enrichment (rmANOVA, one-tailed, $F[\text{enrichment}] = 3.83$, $df = 1, 11$, $P = .038$). The interaction between habitat (desert vs. urban) and enrichment (before vs. after) was also significant (rmANOVA, one-tailed, $F[\text{habitat} \times \text{enrichment}] = 3.99$, $df = 1, 11$, $P = .035$), indicating that enrichment had a stronger effect on GUD in the desert than in the city. The leftover amount of seeds on the feeder trays was significantly higher in the desert, where birds consumed an average of 8.58 g of seed, while urban birds consumed 98.16 g (ANOVA, $F = 1,493.49$, $df = 1, 11$, $P < .0001$; fig. 4B).

Coexistence

House finch versus house sparrow. To address the coexistence of these two species, we compared GUDs of house finch-only trays with GUDs of house finch + house sparrow trays. GUDs where both species foraged together were significantly lower than GUDs of only house finches (fig. 5A; ANOVA, $F = 29.33$, $df = 1, 24$, $P < .0001$). Since all trays were visited by house finches but differed in the presence of house sparrows, the lower GUDs where house sparrows were present can be attributed to this species. Video monitoring strongly supports this claim, with house finches quitting seed trays much earlier than house sparrows (E. Shochat, unpublished data).

Exclusion experiments. Exclusion of doves allowed us to measure the GUD of smaller species, especially house sparrow and house finch. The difference between habitats remained consistent with higher GUDs in the desert than in the urban habitat (fig. 5B; rmANOVA, $F[\text{habitat}] = 20.93$, $df = 1, 26$, $P < .0001$). GUDs on caged trays were

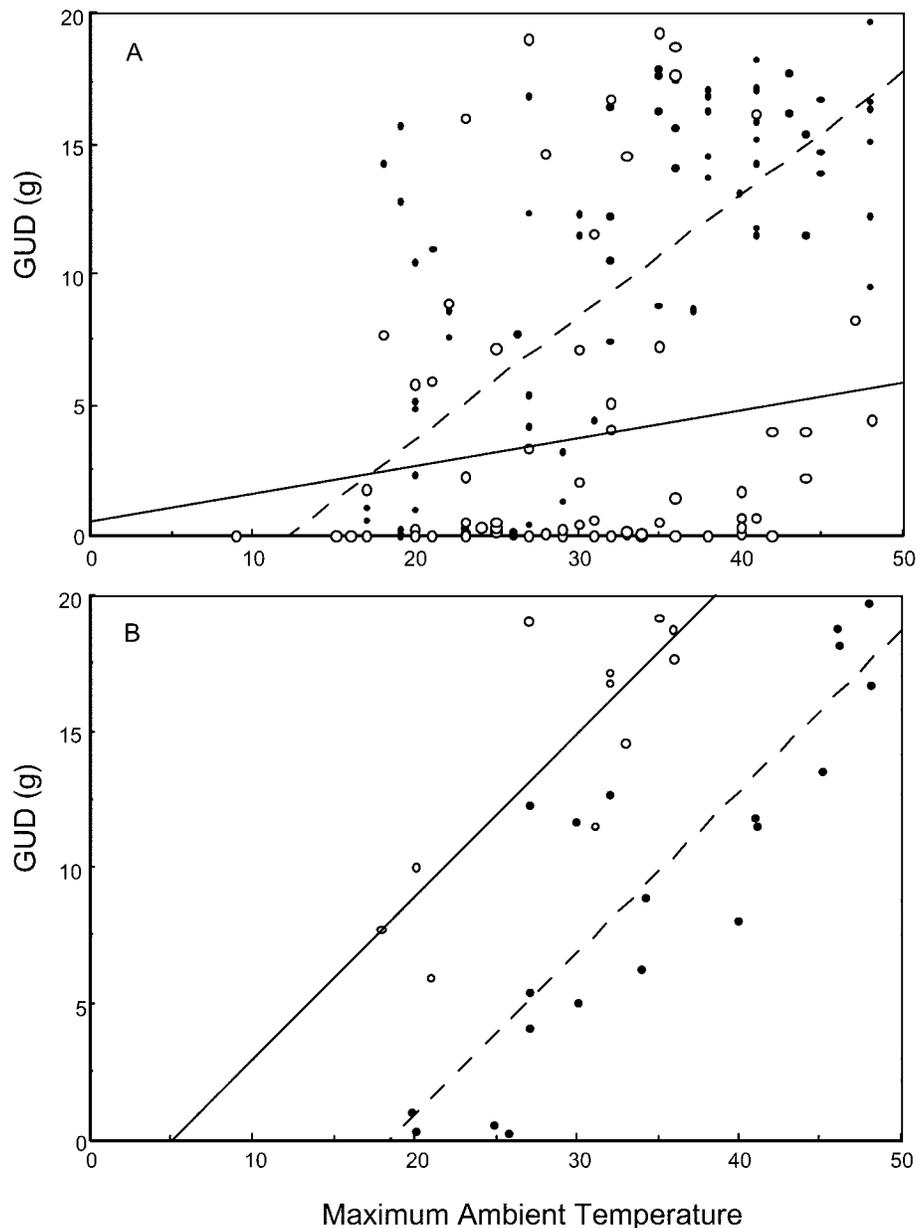


Figure 2: A, Relationship between ambient maximum temperature (Celsius) on bird giving-up densities (GUDs; to normalize variance of the residuals, we employed a Box-Cox transformation, $\lambda = 0.82$) in urban and desert habitats. In the desert (*filled circles, dashed line*), $GUD = -5.75 + 0.47 \times MAT$, $r^2 = 0.447$, $P < .001$. In the urban habitat (*open circles*), $GUD = 0.61 + 0.11 \times MAT$, $r^2 = 0.025$, $P = .186$. B, ANCOVA of the influence of habitat and ambient maximum temperature on the GUD of the house finch. GUDs increased with temperature in both urban ($y = -3.06 + 0.60x$, $r^2 = 0.681$, $P = .003$) and desert ($y = -10.88 + 0.59x$, $r^2 = 0.750$, $P < .001$) habitats, with GUDs being higher in the urban habitat for any given temperature.

higher than GUDs on control trays (fig. 5B; rmANOVA, $F[\text{cage}] = 37.39$, $df = 1, 26$, $P < .0001$), indicating that doves are more efficient foragers than small passerines. The interaction between habitat (desert vs. urban) and treatment (cage vs. control) was also significant (rm-

ANOVA, $F[\text{habitat} \times \text{cage}] = 5.92$, $df = 1, 26$, $P = .02$), indicating that caging had a stronger effect on GUDs in the desert than on GUDs in the city.

Within the urban habitat, GUDs in xeric yards were significantly higher than in mesic yards (fig. 5B; rm-

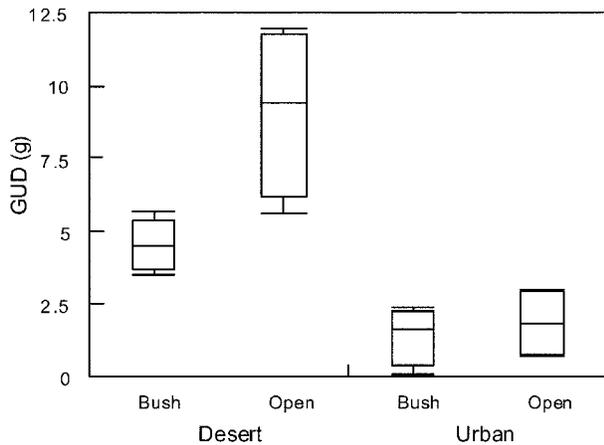


Figure 3: Box and whisker plots showing the effect of microhabitat (bush or open) on giving-up density (GUD; normalized values, Box-Cox transformation, $\lambda = 0.82$). In the desert, GUDs were higher in the open than in the bush. In the urban habitat, there was no microhabitat effect on GUDs.

ANOVA, $F[\text{yard}] = 10.79$, $df = 1, 11$, $P = .007$), indicating that caging had stronger effect on GUDs in xeric yards than on GUDs in mesic yards. Again, GUDs on caged trays were higher than on control trays (rmANOVA, $F[\text{cage}] = 45.90$, $df = 1, 11$, $P < .0001$), and the interaction between yard (mesic vs. xeric) and treatment (cage vs. control) was also significant (rmANOVA, $F[\text{yard} \times \text{cage}] = 10.88$, $df = 1, 11$, $P = .007$). On the basis of observations and video monitoring, these results indicate that in mesic yards, the GUDs on control trays are probably due to Inca dove, whereas the GUDs in caged trays can be attributed to house sparrow. In xeric yards, the GUDs on control trays were due to white-winged dove and mourning dove, whereas GUDs on caged trays can be attributed to house finch. In both cases, dove GUDs are extremely low (fig. 5B). House sparrow GUDs are also relatively low, especially when compared with house finch GUDs.

The differences between desert and urban GUDs could be driven by the higher incidence of doves on the urban trays (fig. 1). To assess this, we compared desert GUDs to xeric yard GUDs where both white-winged and mourning dove occur. Xeric yard GUDs were lower than in the desert (rmANOVA, $F[\text{habitat}] = 7.14$, $df = 1, 20$, $P = .015$), with a significant interaction between habitat and cage (rmANOVA, $F[\text{habitat} \times \text{cage}] = 17.54$, $df = 1, 20$, $P = .0005$), lending support to this hypothesis.

Bird-ground squirrel coexistence. In the desert, ground squirrels had a much lower GUD than birds (fig. 5C; ANOVA, $F = 46.54$, $df = 1, 19$, $P < .0001$). Squirrel GUDs averaged 0.9 g, whereas birds (mostly curve-billed

thrasher, black-throated sparrow, and house finch) GUDs were never < 11.0 g and averaged 15.0 g (fig. 5C).

Manipulation of C

A multivariate analysis revealed that water, MAT, and habitat all had significant effects on bird GUDs (table 1). Within habitat, water and temperature affected GUD only in the desert (table 2), while in the urban habitat GUDs were generally low, regardless of temperature and water manipulation (table 3). Therefore, a further analysis of the effect of water and MAT on different species was done for the desert only. The results of this analysis indicated that although harsh desert conditions (lack of water, heat load) affect GUDs, their effects are species dependent (table 4). Of the three most common species on desert trays, curve-billed thrasher was not affected by either factor, house

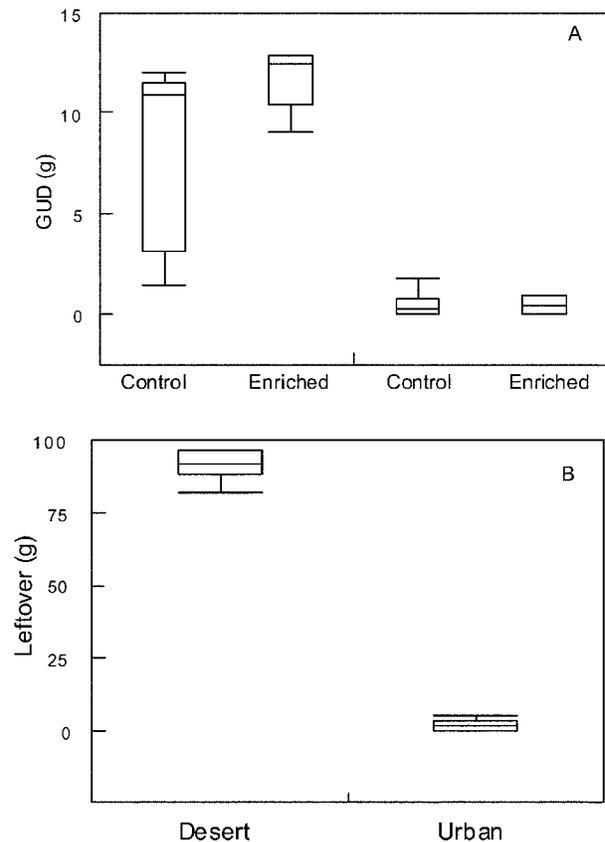


Figure 4: Box and whisker plots showing the effect of food enrichment on giving-up density (GUD; normalized values, Box-Cox transformation, $\lambda = 0.82$). GUDs were measured on control trays, and a repeated measure was done on a tray placed by a feeder (100 g millet) A, Food enrichment increased GUD only in the desert. B, In the desert, the leftover amount of seed on the feeder was much higher than in the urban habitat.

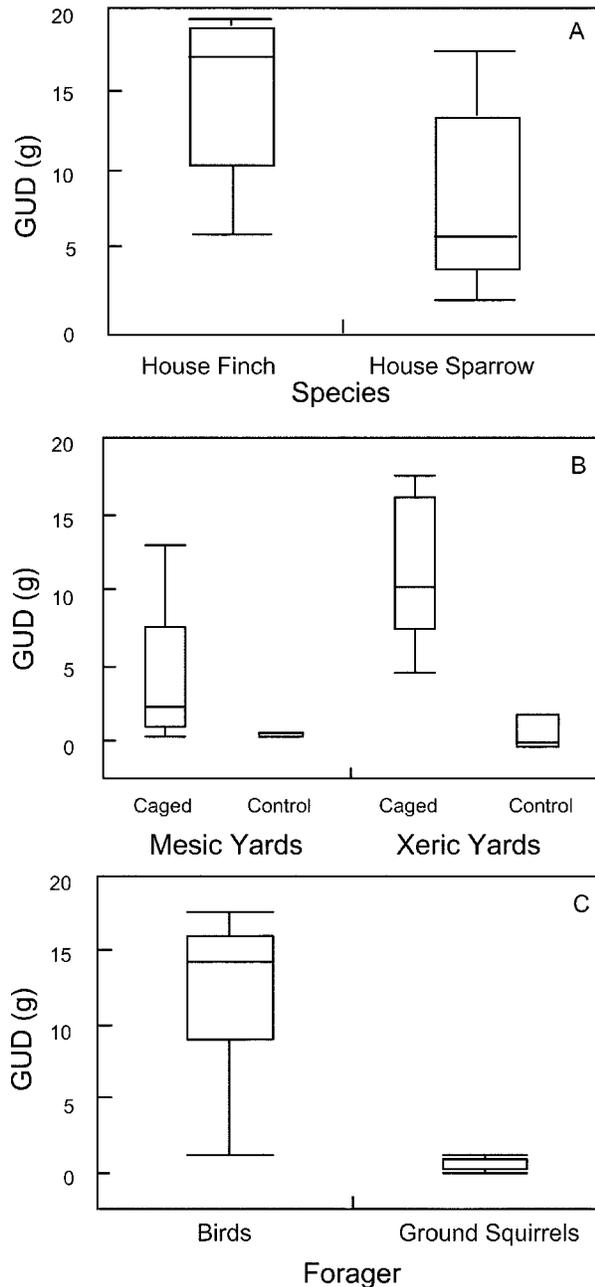


Figure 5: A, Differences in giving-up density (GUD; normalized values, Box-Cox transformation, $\lambda = 0.82$) between house finch and house sparrow in the urban habitat. B, Results of the exclusion experiments in the urban habitat. Control trays allowed all species access, whereas caged trays excluded all dove species. GUDs in control trays can therefore be attributed to doves. In both mesic and xeric yards, doves had lower GUDs than small passerines. In mesic yards, doves were mostly Inca doves, and passerines were mostly house sparrows, whereas in xeric yards, dove species were mourning and white-winged doves, and passerines were house finches. C, Differences in GUD between ground squirrels and birds in the summer in Sonoran desert habitat.

finch GUD was positively correlated with MAT with no response to water, and black-throated sparrow GUDs increased with MAT and decreased with water availability.

Discussion

Results from multispecies trays indicate that urban foragers are more efficient than desert foragers, especially at high temperatures (fig. 2A). This general pattern concurs with a study on squirrel GUDs along an urban-rural forest gradient by Bowers and Breland (1996) despite two major differences. First, the nonurban habitat in our case was much less productive. Second, while Bowers and Breland (1996) concentrated on one species, we compared GUDs between two habitats with fairly different species assemblages. Nevertheless, the similar trends toward lower GUDs in urban habitats may be the result of the same processes. Urban animals may be less influenced by climatic factors, predators, or resource availability than animals in the wild. In contrast, they experience a much higher competition for resources. Accepting lower GUDs in urban environments as a general pattern requires a different explanation for the house finch, which shows an opposite trend (fig. 2B). We discuss possible mechanisms for this pattern under “Coexistence.”

Predation

The different responses of birds to microhabitats between urban and desert habitats (fig. 3) support the idea that predation risk is higher in the desert and that vegetation serves as a shelter from predators. In high temperatures,

Table 1: The effect of water on giving-up density (GUD): general differences between desert and urban habitats

	<i>F</i>	<i>P</i>
Between subject:		
Overall	13.78 (2, 44)	<.0001
Intercept	2.53 (1, 44)	.1183
Habitat	9.20 (1, 44)	.0040
MAT	21.24 (1, 44)	<.0001
Within subject:		
Overall	10.76 (2, 44)	.0002
Water	17.87 (1, 44)	.0001
Water × habitat	.48 (1, 44)	.4886
Water × MAT	21.51 (1, 44)	<.0001

Note: Repeated measures ANOVA on normalized GUD values (Box-Cox transformation, $\lambda = 0.82$), for the effect of water, with maximum ambient temperature (MAT) and habitat as covariates. Numbers in parentheses = degrees of freedom (numerator, denominator).

Table 2: The effect of water on giving-up density (GUD): within–desert habitat test

	<i>F</i>	<i>P</i>
Between subject:		
Overall	30.40 (1, 35)	<.0001
Intercept	1.23 (1, 35)	.2742
MAT	30.40 (1, 35)	<.0001
Within subject:		
Overall	20.24 (1, 35)	<.0001
Water	16.71 (1, 35)	.0002
Water × MAT	20.24 (1, 35)	<.0001

Note: Repeated measures ANOVA on normalized GUD values (Box-Cox transformation, $\lambda = 0.82$), for the effect of water, with maximum ambient temperature (MAT) and habitat as covariates. Numbers in parentheses = degrees of freedom (numerator, denominator).

it is also possible that the differences in GUDs may be the result of high metabolic cost. Urban areas may offer more shade and water to ameliorate the negative physiological cost of high desert temperatures. In contrast, when ambient temperature is low, desert GUDs decrease to a level comparable to the urban GUDs (fig. 1). Food intake may increase during colder periods. As suggested by Brown (1988), the marginal rate of substitution of energy for predation risk depends on the body condition of the forager. If individuals require more energy in cold periods, their perceived cost of predation should decrease. In other words, birds may take a greater risk of predation since their chances of starvation are also higher.

In contrast to the desert, proximity to trees and bushes does not affect foraging efficiency in the urban habitat (fig. 3). Since GUDs are always low in the city, it appears that the perceived risk of predation by urban birds is very low. This result is interesting given that while the abundance of natural predators may decrease in urban areas, the abundance of domestic and feral predators increases. Experimental studies on nest predation have yielded contradictory results, leaving the question of predation risk in urban environments open (Gering and Blair 1999; Matthews et al. 1999; Jokimaki and Huhta 2000). Although our results indicate a lower perceived predation risk by adult birds in urban environments, it does not necessarily mean that predator abundance is low. Further, predators may affect nesting success, though the high densities of birds in urban habitats may suggest that, altogether, nest predators do not affect their population dynamics.

Missed Opportunities

Our attempts to create a rich patch in the urban habitat failed (fig. 4). However, the negative results of this ex-

periment support the idea that bird communities in urban and desert habitats respond to different factors. Desert birds offered a rich food patch and no diminishing returns consumed on average only 10 g millet/d. This result concurs with Bowers and Breland (1996), indicating that while food may be scarce in the wild, it is not the limiting factor on foraging. High risk of predation and probably, in our study, lack of water may influence food intake and patch depletion more strongly in the desert. In contrast, 100 g of millet, which seemed overabundant in the desert, was not sufficient to enrich the patch in the urban habitat. Bird densities were so high that patches were depleted within 5 h in some cases (E. Shochat, video monitoring, unpublished data). This indicates that although food density may be much higher in cities, food may still be a limiting factor on foraging and population growth in urban environments. Given the high food demands, it may be impossible to create a rich patch. Add more food, and more foragers will join and deplete the patch in a relatively short time. How this desperation for food affects bird physiology and health is an interesting question that is yet to be addressed.

Competition and Coexistence

The competition between house sparrow and house finch had previously been studied only across very large scales (e.g., Bennett 1990). Our observations suggest that house sparrow specializes in heavily urbanized mesic areas, avoiding rural areas with more natural structures. In our study, it was missing from several xeric neighborhoods. Because our comparison was based on the presence or absence of house sparrows at different sites, the observed differences in GUDs between house sparrow and house

Table 3: The effect of water on giving-up density (GUD): within–urban habitat test

	<i>F</i>	<i>P</i>
Between subject:		
Overall	.07 (1, 8)	.7975
Intercept	.40 (1, 8)	.5430
MAT	.07 (1, 8)	.7975
Within subject:		
Overall	.67 (1, 8)	.4378
Water	.78 (1, 8)	.4015
Water × MAT	.67 (1, 8)	.4378

Note: Repeated measures ANOVA on normalized GUD values (Box-Cox transformation, $\lambda = 0.82$), for the effect of water, with maximum ambient temperature (MAT) and habitat as covariates. Numbers in parentheses = degrees of freedom (numerator, denominator).

Table 4: Response of three species to water and MAT effect in the desert

Species	MAT		Water		Water × MAT	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Curve-billed thrasher	2.60 (1, 4)	.1820	.06 (1, 4)	.8111	.12 (1, 4)	.7463
House finch	12.98 (1, 8)	.0070	2.50 (1, 8)	.1522	2.18 (1, 8)	.1779
Black-throated sparrow	17.43 (1, 10)	.0019	12.10 (1, 10)	.0059	15.37 (1, 10)	.0029

Note: Repeated measures ANOVA on normalized GUD values (Box-Cox transformation, $\lambda = 0.82$), for the effect of water, with maximum ambient temperature (MAT) and habitat as covariates. Numbers in parentheses = degrees of freedom (numerator, denominator).

finch may be confounded by subtle habitat differences. Yet, video monitoring indicated that the house finch quits the trays much earlier than the house sparrow (E. Shochat, unpublished data). Therefore, it appears to be a cream skimmer in terms of foraging behavior (*sensu* Brown et al. 1997). The facts that house finch had lower GUDs in the desert than in the urban habitat (fig. 2B) and that house sparrow had much lower GUDs than house finch (fig. 5A) strongly suggest that coexistence between these two species is facilitated by spatial variation in resource abundance. On this axis, coexistence is possible if there is a trade-off between foraging efficiency and travel cost (Brown 1989). House finches have much larger home ranges than house sparrows, and they fly long distances between foraging patches (Bennett 1990). House sparrows are more localized foragers and spend more time in a given food patch. Therefore, they are more efficient in exploiting a particular patch.

Our exclusion experiments demonstrate that, except for the house finch, other urban granivores are very efficient foragers (fig. 5B). All three dove species are more efficient than house sparrow, possibly since the latter's diet is more varied. The Inca dove is extremely efficient in patch depletion (fig. 5B). Since doves, unlike the passerines, do not peel the seeds, their food handling time may be shorter and food intake rate higher. The fact that doves were abundant on urban trays but were never seen on desert trays may explain the differences between desert and xeric yard trays and indicates very different foraging strategies in different habitats. In the Sonoran desert, white-winged dove forages mainly on saguaro flowers (Wolf and del Rio 2000), whereas in the urban habitats, it feeds mostly on grains.

Our results may explain why species diversity declines in cities. Although the similar number of species foraging on urban and desert trays may not concur with this general trend, it is more likely to be the result of a bias in sample size because urban trays attracted many more individual birds than desert trays. In general, if native species must forage on leftovers of dominant urban species, then for many native species such a mechanism of coexistence is impossible in urban environments because most urban-dwelling species are very efficient foragers. Cream skim-

ming, as in the house finch case, would be a more realistic mechanism of coexistence in cities. How different dove species coexist in urban environments remains unclear.

A similar mechanism of coexistence is evident in the desert, where house finch is a skimmer but with a probable higher travel cost between patches that decreases its GUDs compared with the urban habitat (fig. 2B). Here, the local black-throated sparrow represents the more efficient competitor. Yet, all bird species had much higher GUDs than ground squirrels (fig. 5C). This result is similar to what Brown et al. (1997) described for crested larks (*Galerida cristata*) and gerbils (*Gerbillus* sp.) in the Negev desert. Compared with rodents, most birds are highly mobile and can be defined as cream skimmers in a local scale.

Metabolic Costs

Hot and dry environments may favor rodents over birds. Since many rodents do not require water, their digestive cost is lower than the digestive cost for birds. Results from the water enrichment experiment partially support this hypothesis. Water did not affect curve-billed thrasher and house finch GUDs but decreased black-throated sparrow GUDs. The difference may be related to home range in the case of the house finch and diet in the case of the curve-billed thrasher. The thrasher is an omnivorous species and may obtain its water from insects and fruits, while the black-throated sparrow is an obligate granivore. Our results demonstrate that the very hot and dry conditions in the Sonoran desert constrain black-throated sparrow dry seed consumption capability. In the only published study addressing the effect of water on GUDs when foraging on dry food, Kotler et al. (1998) reported a decrease in Australian raven (*Corvus coronoides*) GUD and also mentioned a similar effect on crested lark GUDs in the Negev Desert, Israel.

The idea that cities mollify temporal variability (Shochat et al. 2004) is also supported by our results (fig. 2A). Many of the constraints that exist in wild habitats seem to be removed in urban environments. Urban birds may suffer less from predation and climatic stress. They have water available all year round, and food is abundant. These con-

ditions increase the carrying capacity of the environment, and bird populations can become extremely high. Previous studies focused largely on habitat effects on urban bird diversity. While habitat is clearly important, we suggest that competition for food, an outcome of the population growth, is also a major factor that limits further population growth. Furthermore, some of the decrease in species diversity in cities is very likely the result of competitive exclusion, given the very low GUDs of most urban specialists (e.g., Inca dove, mourning dove, and house sparrow).

Our results emphasize the importance of and the need for a stronger evolutionary approach in the study of urban bird communities. Most of the published literature on urban birds not only has been correlative but also has failed to go beyond simple effects of habitat structure (e.g., housing density, vegetation volume; Marzluff 2001) on birds. Addressing the more complex evolutionary interactions among species will not only improve our understanding of how bird communities evolve in an urban landscape but also provide the tools for better management of urban biodiversity. For example, future effort in urban landscape planning for species-rich communities may be more efficiently directed toward the rural end of the urban-rural gradient where dominant species like house sparrow, European starling, and rock pigeon are less abundant than in city centers. Increasing habitat heterogeneity may also allow a greater coexistence between urban specialists and native species. Given the rapid rate of urban development and habitat conversion worldwide, we urgently need more studies employing evolutionary approaches to address mechanisms of urban adaptation and extinction.

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