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Evidence for urban food limitation in a widespread invasive lizard

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Abstract

Declining diversity, abundance, and body size of arthropods are characteristic features of urbanization. Recent work indicates that arthropod declines can cascade through urban food webs and limit consumer populations. However, the magnitude and extent of urban food limitation remains unknown. To expand our understanding of the consequences of urban arthropod declines, we examined signatures of food limitation in a widespread, urban-tolerant lizard, the brown anole (*Anolis sagrei*). Our results show that male brown anoles exhibit significant decline in body condition, but not body size, across a gradient of increasing urbanization in south Florida, USA. Further, we observed a positive relationship between arthropod biomass and lizard body condition, as well as declining arthropod biomass with increasing urbanization. Our results contribute to a growing realization that urbanization-driven arthropod declines are likely to adversely impact a variety of predators—even the most urban-tolerant ones.

Keywords *Anolis sagrei* · Arthropods · Body condition · Food web · Reptile

Introduction

In urbanized areas, pollution, heat stress, trampling, and loss of native vegetation can devastate arthropod abundance and diversity (McIntyre 2000; Piano et al. 2020; Fenoglio et al. 2020). These declines narrow the ecological roles of arthropods in urban ecosystems as decomposers, pollinators, predators, and prey (Kotze et al. 2022; Chatelain et al. 2023) and can cascade through food webs and contribute to consumer declines in urban environments (Tallamy and Shriver 2021; Grames et al. 2023). The decline of arthropods, and the species that depend on them, may be a general consequence of urbanization and an emerging global concern (Wagner 2020; Bowler et al. 2025; Edwards et al. 2025).

Urbanization-mediated arthropod decline can impact arthropod-dependent species in many ways. For example, arthropod specialist birds often exhibit lower body condition (Lazić et al. 2017), lower fecundity (Dahirel et al. 2019), smaller body size (Miyashita et al. 1998), and reduced reproductive success in urban areas (Baldan and Ouyang 2020). Even generalist birds exhibit signs of nutritional stress and reduced fitness in urban habitats if high-value arthropod foods are necessary at key life stages (Liker et al. 2008; Narango et al. 2018; Seress et al. 2020; Sinkovics et al. 2021). Together, emerging evidence for urban food limitation indicates adverse effects of arthropod decline should be expected—even for urban-tolerant species.

Here, we explore the effects of urbanization-mediated arthropod decline on the brown anole lizard (*Anolis sagrei*). The ability of brown anoles to tolerate a wide range of habitats, including the urban core, is well established (Battles and Kolbe 2019; Chejanovski et al. 2022; Stroud et al. 2024). Such broad tolerance gives the impression that urbanization presents little ecological resistance to the brown anole (French et al. 2018). However, given the well-documented loss of arthropod prey from urban areas (e.g., Fenoglio et al. 2020), and the detrimental effect of food limitation on brown anole body condition (Warner et al. 2015) and somatic growth (Wright et al. 2013; Warner et al. 2015; Hall et al. 2018), we hypothesized that urban anole populations

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might be food limited. To evaluate our hypothesis, we tested three general predictions consistent with food-limitation: 1) arthropods decline in abundance (biomass and number) with increasing urbanization, 2) brown anole body condition and body size are positively correlated with arthropod abundance, and 3) brown anole body condition and body size decline with increasing urbanization. We evaluated our predictions by examining how body condition, body size, and arthropod abundance vary across an urbanization gradient in Florida, USA.

Material and methods

Study system

The setting for our study is Broward County—a metropolitan county in Florida with nearly two million inhabitants. Broward County urbanization is characterized by impervious surfaces, high human densities, reduced vegetation cover, and high temperatures (Chejanovski and Kolbe 2019; Battles and Kolbe 2019). We conducted our study at six sites chosen because they spanned a large portion of the urbanization gradient that characterizes south Florida (Supporting Information, Section S1; Fig. 1a). More specifically, we selected study sites based on estimated vegetated cover, the presence of brown anoles, and the absence of a widespread terrestrial predator, the northern curly-tailed lizard (*Leiocephalus carinatus*). Our six sites ranged from remnant natural forest (Fig. 1b) to urban core habitats characterized by impervious surface replacing vegetation cover (Fig. 1c, d).

Our focal species, the brown anole, is a small, semi-arboreal, diurnal lizard common in urbanized and natural habitats across its extensive range (Fig. 1e). Brown anoles perch in a characteristic head-down posture and make brief trips to the ground to capture prey—typically arthropods (Giery et al. 2013; Chejanovski et al. 2022; Kolbe et al. 2023; Lapiedra et al. 2024). In south Florida, brown anoles exhibit a distinct annual cycle of lipid storage (Lee et al. 1989). By late summer, the lipid reserves of brown anoles are near their lowest point, presumably due to several months prioritizing energetic investment in reproduction and somatic growth. Thus, late summer variation in body condition presumably reflects a net gain, or loss, of lipid stores across a period of peak brown anole activity.

Urbanization

Urbanization is a multivariate phenomenon often summarized by variation in vegetation and impervious cover. Here, we represent the urbanization continuum with the Enhanced Vegetation Index (EVI), a remotely sensed measure of 'greenness'. EVI and related indices are frequently employed as continuous representations of urbanization (e.g., Zhao et al. 2016). To characterize the urbanization gradient, we generated a single layer from averaging MODIS-derived EVI data from 2000 to 2022. We then sampled this layer with a 3 × 3 pixel kernel (~ 56 hectares) centered on our six

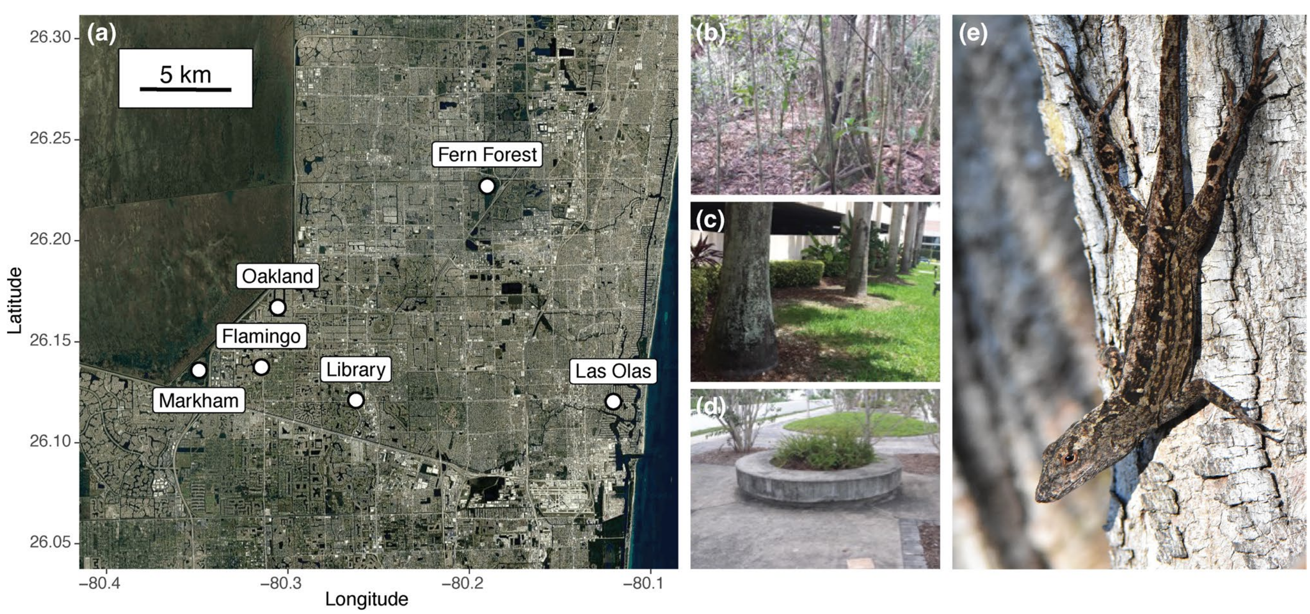

Fig. 1 Our study was designed to evaluate evidence for food limitation in a generalist predator among six sites in Broward County, Florida that spanned an urbanization gradient in South Florida, USA (**a**). The urbanization gradient was characterized by a decrease in canopy cover and an increase in impervious surface (**b**-**d**). Our focal consumer was the brown anole (*Anolis sagrei*), a common generalist predator found throughout the study area (**e**). Photo credit: Braulio Assis (**e**)

study sites and calculated the mean. Because EVI is negatively correlated with urbanization, we used the inverse EVI values (Table 1). The resulting variable was centered and standardized and is positively correlated with urbanization. Additional details are available in the Supporting Information (Section S2).

Arthropod sampling

We sampled brown anole prey availability with pitfall traps. At each study site, in August 2015, we positioned four pitfall traps in vegetated areas used by brown anoles. Traps were arranged haphazardly along a 100-m-long transect with a minimum distance of 10 m between traps. Traps were set into soil flush with the ground, then filled with water and a trace amount of soap to prevent arthropods from escaping. After 24 h, trap contents were collected and stored in ethanol. For each trap, we counted all arthropods (number) and identified them to order before measuring the combined dry mass to the nearest milligram (biomass). One trap (Library trap #4) contained a large millipede (= 0.07 g). Millipedes are infrequently consumed by brown anoles and were subtracted from analyses. One replicate pitfall trap was lost during sampling (Markham trap #4); all other sites have four (Table 1).

Body condition and size

Various indices of ecological performance can serve as proxies of fitness. The most commonly used proxy is body condition—a morphology-based indicator of how heavy an individual is for their length (Peig and Green 2009, 2010). While the relationship with fitness is sometimes unclear (Cox et al. 2015), variation in body condition seems to capture related elements of ecological performance integrated over time (Peig and Green 2010). To evaluate our hypothesis that urban lizards are food limited, we collected 20 adult male brown anoles from each site in August 2015, when effects of food limitation should be pronounced. For each individual, we measured body size with snout-to-vent body length (SVL)—the distance between the tip of the snout and the cloaca, as well as body mass to the nearest tenth of a gram. From these measures, we estimated body condition with the scaled mass index (M_i) following other studies of brown anoles (e.g., Cox et al. 2015; Warner et al. 2016). Briefly, the scaled mass index (*M*i) was calculated following Peig and Green (2009) with the bSMA coefficient estimated with standardized major axis regression of log(mass) ~ log(SVL) in the package smatr (Warton et al. 2012). Pairwise correlations between body condition (*M*i), SVL, and mass showed the expected strong positive relationship between mass and length ($r = 0.90$) and weak correlations between body condition and body size (SVL: $r = -0.20$; mass: $r = 0.22$). Scaled mass index (*M*i) values generated in our study ranged from 2.97 to 5.81 with a mean of 4.44 and are within the range observed in other brown anole studies (Cox et al. 2015; Warner et al. 2016).

Data analysis

We evaluated our predictions with a series of linear regressions. Given that our predictions were developed a priori, we assessed support with one-tailed tests (Table 2). We evaluated our predictions with population-level summaries (means and medians) so that each site functioned as an independent replicate (i.e., $n_{sites} = 6$). Because arthropod abundances (biomass and number) were noticeably right skewed, we used the median to describe pooled trap samples. We used population means for all other analyses. All analyses were run in R version 4.4.0 (R Core Team 2024).

Results

Characterization of the urbanization gradient with remotely sensed reflectance data generated a continuous axis corresponding to previous classifications of these study sites (Chejanovski and Kolbe 2019; Chejanovski et al. 2022). The most urbanized areas had the highest inverse Enhanced Vegetation Index (-EVI) values due to low green reflectance

Table 1 Prey availability varied substantially among study sites. Summaries of arthropod abundance were calculated from three or four replicate pitfall traps within each sample location. Site-level summaries are arranged here in order of increasing urbanization (-EVI is positively correlated with urbanization)

	Fern forest	Flamingo	Markham†	Library	Oakland	Las olas
urbanization (-EVI)	− 0.354	− 0.294	− 0.285	− 0.263	− 0.241	− 0.228
total number (n)	87	705	305	175	808	31
total biomass (mg)	60.3	63.2	15.2	57.1	43.5	8.3
biomass/trap (mg)	15.6	16	5	6.7	8.4	1.2
number/trap (n)	22.5	201	65	45.5	179.5	6

† One of four replicate pitfall traps was lost during sampling

Table 2 Model results from regression analyses evaluating our three primary predictions for urban food limitation. Significant ($p < 0.05$) terms are in bold

Predictions	Model	Results		
		β	$F_{1,4}$	p (1-tailed)
1: Arthropod abundance decreases with urbanization	biomass/trap (mg) ~ -(EVI)	− 0.77	5.95	**0.0356**
	number/trap (n) ~ -(EVI)	0.11	0.05	0.4209
2a: Body condition increases with arthropod abundance	condition (M_i) ~ biomass (mg)	0.78	6.10	**0.0345**
	condition (M_i) ~ number (n)	− 0.15	0.09	0.3872
2b: Body size increases with arthropod abundance	size (SVL) ~ biomass (mg)	− 0.10	0.04	0.4233
	size (SVL) ~ number (n)	0.02	0.01	0.4638
3a: Body condition decreases with urbanization	condition (M_i) ~ -(EVI)	− 0.96	48.8	**0.0011**
3b: Body size decreases with urbanization	size (SVL) ~ -(EVI)	0.45	0.99	0.1875

of non-vegetated surfaces such as roads, rooftops, and parking lots. The lowest -EVI value reflected continuous, mature broadleaf forest cover. As predicted, we observed significant variation in arthropod abundance and lizard body condition across this urbanization gradient and correlation between arthropod abundance and the body condition of lizards.

Arthropods recovered from our pitfall traps included nine arthropod orders (Supporting Information, Section S3). Across all sites, Diptera (flies) and Hymenoptera (predominantly ants), were numerically dominant in our pitfall traps. Except for Diplopoda (millipedes), orders represented in pitfall traps are typical of the broad dietary niche of the brown anole (Supporting Information, Section S3). The abundance of arthropods varied considerably among sites, decreasing with urbanization (Table 1).

We found support for each of our predictions (Table 2). First, though only detected for biomass, arthropod abundance decreased with urbanization (biomass: $p = 0.0356$; number: $p = 0.4209$; Fig. 2a; Table 2). Second, anole body condition (Mi) and arthropod abundance were positively associated. Again, the relationship was restricted to arthropod biomass ($p = 0.0345$; Fig. 2b) with no significant relationship with arthropod number ($p = 0.3872$; Table 2). Body size was not associated with prey biomass ($p = 0.4233$) or numerical prey abundance ($p = 0.4638$; Table 2. Third, while anole body condition (Mi) declined with increasing urbanization ($p = 0.0011$; Fig. 2c), variation in body size was not explained by urbanization ($p = 0.1875$; Table 2).

Discussion

We used a survey of brown anole body condition and the arthropods they consume across an urbanization gradient to evaluate the hypothesis that urban consumers are food limited. Our results contribute new support for the urban food-limitation hypothesis. First, our data indicate that arthropod biomass declines with increasing urbanization (Fig. 2a). Second, we provide evidence for a positive correlation between arthropod biomass and lizard body condition (Fig. 2b). Finally, we show that lizard body condition declines with increasing urbanization (Fig. 2c). These results are consistent with the food-limitation hypothesis and support a growing realization that diminished nutritional quality of urban habitats negatively affects individual body condition and limits consumer populations from the bottom up.

A common and widespread urban-tolerant lizard, brown anoles have withstood extensive urbanization and continue to rapidly invade intensively urbanized regions throughout the world (Tan and Lim 2012; Batista et al. 2019; Fisher et al. 2020; Alvarez 2024). Such broad success in urban habitats suggests they are well adapted to the ecological challenges of urbanization. Indeed, they may be, but without food, body condition in anoles declines rapidly due to progressive depletion of lipids (Gist 1972; Fokidis and Brock 2020; Himmelstein et al. 2021). Given that restoring lipids takes a week or longer of resumed feeding, low-condition animals risk tipping into a state of starvation and rapid physical decline in food-limited environments (Gist 1972). Thus, the decline of arthropod biomass and the corresponding diminishment of anole body condition across our urbanization gradient suggests that food limitation plays a role in determining the limits of urbanization tolerance.

Although our study only included male lizards, well-evidenced connections between food abundance, body condition, somatic growth, and reproduction in anoles suggests that urban anoles should be morphologically and demographically distinct from ones inhabiting more natural contexts (Licht 1974; Stamps 1977; Stamps and Tanaka 1981; Rose 1982; Guyer 1988a, b). Effects of food abundance are particularly well established in brown anoles with field and laboratory experiments demonstrating increased somatic growth from nutritional supplementation (Wright et al. 2013) and detrimental effects of food limitation on body condition, individual growth rate, survival, and fecundity (Warner et al. 2015; Hall and Warner 2017; Hall et al. 2018).

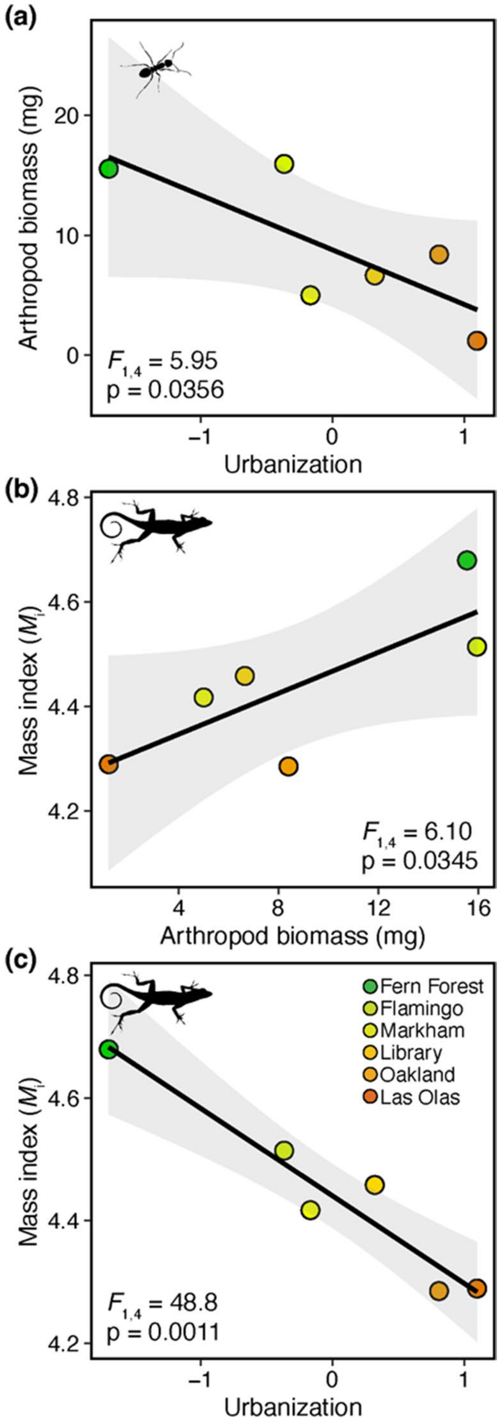

Fig. 2 Results of our linear regression analyses assessing 1) the effect of urbanization (-EVI) on arthropod abundance (biomass/trap) (**a**), 2) the relationship between arthropod abundance (biomass/trap) and anole body condition (M_i; **b**), and 3) the effect of urbanization (-EVI) on brown anole body condition (M_i; **c**). Points represent population-level medians for arthropod biomass and population-level means for all other variables—color variation in these points indicates urbanization (-EVI) with green representing the least urbanized (Fern Forest) and red, the most (Las Olas). Significance was assessed with one-tailed tests. Lines indicate model fits and shaded areas indicate 95% confidence intervals

Despite a plausible link between resource abundance and somatic growth rate, we observed no relationship between arthropod abundance and body size in this case. One explanation is that other factors such as predation (Chejanovski and Kolbe 2019) and competition (Giery and Stroud 2019; Stroud et al. 2024) are influencing the effect of resource supply on somatic growth and body size. Other than selecting sites that lacked influential predators (curly-tailed lizard, *Leiocephalus carinatus*) and competitors (Puerto Rican crested anole, *Anolis cristatellus*), we did not incorporate higher order biotic interactions in this study. Another factor that we do not assess in this study is brown anole population density. If population density is higher in urban areas—as it often seems to be for urban-tolerant species—we might expect that any bottom-up drivers of urban food limitation would be amplified by intensified intraspecific competition for already sparse arthropod prey. It remains possible, perhaps likely, that substantial differences in the strength of predation, competition, and parasitism exist across urbanization gradients and are important to account for. Addressing how interspecific interactions vary across urbanization gradients and influence the ecological performance of urban tolerant species is an important area of research—and one that would benefit from hypotheses that integrate bottom-up and top-down perspectives.

Continued investigation is needed to assess the generality of urban arthropod declines and urban food limitation in this system and others. We suspect that further integration of food limitation and metabolic demands would yield new insights into the challenges of urban living. More specifically, we hypothesize that the individual and population-level consequences of food scarcity will be more severe when energetic demands are high. There is good reason to expect higher energetic demands in urban habitats. The most obvious reason is that urban habitats are stressful (Murray et al. 2019). Extreme heat (Hall and Warner 2018; Battles and Kolbe 2019), elevated predator density (Loyd et al. 2013; Lapiedra et al. 2017), higher parasite burdens (Thawley et al. 2019), exposure to novel competitors (Stroud et al. 2024), altered circadian rhythms (Kolbe et al. 2021), and toxicant exposure (White et al. 2022) can all lead to chronic and intermittent physiological stress responses. While the effects of stressor exposure on condition are variable (Injaian et al. 2020), physiological stress responses are generally energetically costly (Vera et al. 2017). Thus, an individual's ability to sustain or avoid the energetic demands of stressors will influence their vulnerability to food scarcity. In effect, we suspect that urban stressors could amplify food limitation and increase the risk of entering energetic debt, particularly at times of high energetic demand or low lipid reserves.

Our results are consistent with the food limitation hypothesis and contribute to a growing realization that bottom-up processes can be interrupted by the decline of arthropods and the roles they play (Grames et al. 2023). Evidence for urban food limitation continues to develop, primarily through recent research on urban-tolerant birds. These insights have yet to be integrated into long-standing models of urban trophic ecology that tend to emphasize the effects of anthropogenic food inputs on predator–prey interactions and community composition (Faeth et al. 2005; Shochat et al. 2006, 2010; Fischer et al. 2012). Yet, it is increasingly clear that food limitation is also a feature of urban ecosystems—despite massive anthropogenic inputs to ecosystems dominated by urbanization-tolerant generalists.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11252-025-01722-6.

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Data availability Data will be made available upon publication.

Declarations

Competing interests The authors declare no competing interests.

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