

Dining in the City: Dietary Shifts in Indian Rock Agamas across an Urban–Rural Landscape

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ABSTRACT.—Rapid urbanization is a growing threat to biodiversity, causing wide-scale extirpation of species from their natural habitats. Some species such as rock agamas, *Psammophilus dorsalis*, seem to be sufficiently tolerant and continue to persist in urban environments. Given that urbanization alters species composition at multiple trophic levels, we expect a shift in the diet composition and hunting modes of populations across rural and urban areas. Based on identified contents from stomach flushes, we found that *P. dorsalis* are generally myrmecophagous, and their diet is mainly composed of ants (Hymenoptera: Formicidae). Diet of males and females in each area overlapped highly (80–91%), even though males were significantly larger than females. Dietary overlap between urban and rural populations also was high (80.3%). Surprisingly, rural lizards had lower body mass indices than did urban lizards, despite the greater diversity of prey types and the larger volume of food consumed. This species uses a sit-and-wait hunting strategy, but we found that the rate of movement of males was higher in rural areas compared to urban areas, which likely results in higher energy expenditure. Individuals of *P. dorsalis* do not seem to be negatively affected by urbanization but instead manage to hunt in and around the small patches of vegetation that remain, enabling them to maintain a higher body condition than that of lizards in undisturbed rural habitats.

Habitat degradation, as a consequence of urbanization, has impacted herpetofaunal diversity in a devastating way worldwide (Gibbons et al., 2000; Cushman, 2006), especially when urban development occurs in areas that support high native species richness (Lugo, 2002). Urbanization of such areas results in a matrix of unsuitable habitats within the biogeographical range of a species. The effects of such fragmentation on native organisms can be a function of many simultaneous environmental alterations, such as changes in the type of vegetation (Vallan, 2002), the sizes and shapes of fragments (Scott et al., 2006), and the type of anthropogenic activity (Greenberg et al., 1994; Ryan et al., 2002). One of the first consequences of habitat fragmentation attributable to urbanization is the reduction in population size of native species and the subsequent demographic and genetic structure changes that increase the probability of local extirpation (Gilpin and Soule, 1986, but see Luniak, 2004; Møller, 2009).

Studies along natural environmental gradients consistently record changes in lizard species composition (e.g., Whiting et al., 2005; Pelegrin et al., 2009; D’Cruze and Kumar, 2011), typically attributable to the differences in the availability of suitable habitats for activity (e.g., nesting and basking) or of suitable prey to consume. Urbanization, however, is a very common but extreme environmental condition, and lizard species assemblages are known to decline with anthropogenic disturbance (Germaine and Wakeling, 2001). The effects of urbanization, however, remain understudied, because we still lack a comprehensive understanding of the strategies that enable survival, especially for lizards that seemingly persist in urban environments (but for birds and mammals, see Luniak, 2004; for birds, Møller, 2009). Because rapid adaptations to changes in available and limiting resources are important to the survival of an organism (Carroll et al., 2007), we expect lizards living in urban environments at least to show flexibility and shifts in their diet, as commonly reported in birds and mammals (Daniel et al., 2013).

In lizards, diet composition can be influenced by multiple factors, including the mode of hunting (Pianka, 1966). Lizards with a sit-and-wait hunting strategy target prey that are actively moving through the environment, whereas widely foraging lizards consume prey that are relatively sedentary, unpredictably distributed, and clumped (Huey and Pianka, 1981). Regardless of their hunting mode, most lizards are thought to be opportunistic feeders (Parker and Pianka, 1975). For example, populations of the Desert Horned Lizard (*Phrynosoma platyrhinos*) and the Regal Horned Lizard (*Phrynosoma solare*) persist in urban reserves of central Arizona mainly because of the presence of seed-harvester ants (*Pogonomyrmex rugosus*) but are apparently absent in some surveyed reserves because of the direct impact of anthropogenic disturbance on their habitat (Sullivan et al., 2014). For these species, survival in urban areas is possible because of the flexibility in diet and a tolerance for some level of anthropogenic disturbance. Therefore, an effective and flexible foraging strategy can allow the persistence of species in disturbed environments.

Like many developing countries in the world, urbanization in India is increasing at a rapid pace, and much of the native biodiversity is increasingly being lost. Several species, however, seem to be sufficiently tolerant and continue to persist in completely altered urban environments. One such species is the Indian Rock Agama, *Psammophilus dorsalis*, which have a widespread distribution throughout the Indian peninsula and is seen up to 1,800 m above mean sea level (Daniel, 2002). To understand the persistence of *P. dorsalis* despite anthropogenic disturbance, we examined the diet composition, hunting behavior and body condition of this species from both urban and rural populations. Given the dramatic differences in the local environment (see description below) and the prevailing assumption that urban habitats are less suitable than natural habitats, we expect to find shifts in these traits such that lizards in urban areas will have lower activity and movement, a narrower diet, and lower body condition than those living in rural areas.

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DOI: 10.1670/14-073



FIG. 1. Example of sampling sites in (A) urban and (B) rural habitats in and around Bangalore, India.

MATERIALS AND METHODS

Study Species and Areas.—*Psammophilus dorsalis* are common agamas found in semiarid habitats across India. This species shows distinct sexual dimorphism, where males are larger and more brightly colored than females (Daniel, 2002). We conducted this study in the greater Bangalore city region (India). The urban study site was situated within the city of Bangalore in a suburban area (13°1'26"N 77°39'59"E; datum WGS84) containing mostly houses separated by empty plots that were overgrown with the invasive plant *Lantana camara* (Fig. 1A). The lizards in this site were restricted to fragmented areas with vegetation and were typically found basking on ledges and walls of concrete buildings. The rural study site was located near Antharagange forest range in Kolar district (13°08'25"N 78°05'48"E; datum WGS84), 62 km east of the urban study area. This site has low hills with large boulders, surrounded by *Opuntia* sp. and other small native bushes and trees. The invasive shrub *L. camara* was also found at the rural site (Fig. 1B) and lizards in that area were typically found perching on boulders.

Dietary Analyses.—Forty-nine lizards (urban: $N = 13$ males and 8 females; rural: $N = 15$ males and 13 females) were captured between 1000–1600 h from August to November 2012, during the end of the breeding season. Only adult lizards with snout to vent length (SVL) > 70 mm were included in the study (SVL range: rural: males = 94–138 mm and females = 75–96 mm; urban: males = 121–146 mm and females = 74–108 mm). Within 15 min of capture by noosing, all lizards were stomach flushed using the protocol for stomach flushing lizards and anurans (Legler and Sullivan, 1979; Solé et al., 2005). We used stomach flushing over fecal pellet examination to determine diet of free-ranging lizards, because fecal pellets are small and difficult to find amid vegetation. The stomach contents were stored in vials containing 70% ethanol and transported to the laboratory where they were identified to the level of order. Each prey item was considered an operative taxonomic unit (OTU). These sample sizes were determined sufficient, based on the Chao 2 nonparametric estimator (Chao, 1987; Chao et al., 2009) and accumulation curves of prey taxa found in the stomachs.

Frequency of occurrence (FO) of each prey type for males and females at each site was calculated as:

$$FO = \frac{S(100)}{N}$$

where S is the number of samples containing each prey type and N is the total number of samples. Percent of relative occurrence (RO) was calculated as:

$$RO = \frac{p(100)}{T}$$

where p is the number of occurrences of each prey type and T is the occurrence of all prey types in all samples, therefore representing the relative importance of a given food type in the diet (Loveridge and Macdonald, 2003). For each sex and for lizards at each site, we determined the most dominant prey item using an index of relative importance (Pianka, 1973):

$$IRIt = (POt)(PIt + PVt)$$

where POt = percentage of occurrence (number of stomachs that contained "t" item / total number of stomachs $\times 100$), PIt = percentage of individuals (total number of individuals of "t" in all stomachs / total number of individuals of all taxa in all stomachs $\times 100$), and PVt = percentage of volume (total volume of individuals of "t" in all stomachs / total volume of all taxa in all stomachs). For the $IRIt$ calculation, the volume of each prey item was calculated assuming an ellipsoid body (Griffiths and Mylotte, 1987), such that:

$$V = \frac{4\pi L}{3} \left[\frac{W}{2} \right]^2$$

where L = the length of the prey and W = width of the prey. We used a two-way ANCOVA to compare the volume of food consumed between sexes and across sites using the number of fragments as the covariate. Finally, we calculated dietary overlap (Pianka, 1973) between sexes and sites using the formula

$$O_{xy} = \frac{\sum X_i Y_i}{\sqrt{(\sum X_i^2 \sum Y_i^2)}}$$

where, X_i is the relative frequency of occurrence of food item "i" in one population and Y_i is the relative frequency of occurrence of food item "i" in another population.

Data on Hunting Behavior and Body Size.—We conducted focal observations of 80 lizards (urban: $N = 20$ males and 20 females; rural: $N = 20$ males and 20 females) from 1000–1300 h and from 1600–1700 h when lizards are most active. Observations were

TABLE 1. Absolute prey numbers for males and females of *Psammophilus dorsalis* from urban and rural habitats.

Order	Rural		Urban	
	Male	Female	Male	Female
Hymenoptera:Formicidae	35	45	105	72
Other Hymenoptera	6	10	7	8
Lepidoptera	7	9	2	2
Diptera	14	3	7	4
Coleoptera	12	5	2	8
Heteroptera	4	7	10	5
Neuroptera	2	4	0	0
Isoptera	3	4	0	0
Orthoptera	6	7	0	2

conducted from June to September 2014, toward the end of the breeding season when females were not likely to be gravid. During the focal observations, two observers would stand at approximately 20 m from a focal lizard on opposite sides and continually record the lizard's movements using Sony® HDR-CX330 and Canon® EOS 500D digital cameras. Undisturbed recording for durations of 10 min were taken for each lizard. To maximize the probability of capturing hunting activity, data were not collected from lizards that were in a thigmothermic body posture (showing a possible sign of basking), exhibiting tail raises or head bobs, or were actively involved in social interactions. Of the 80 observations, four observations from the rural site ($N = 3$ males and 1 female) and three observations from the urban site ($N = 1$ male and 2 females) lasted only for approximately 5 min because these lizards moved out of view during the recording. We did not obtain stomach contents from these lizards because we wanted to minimize stress caused by gut flushing and because we had already obtained a sufficient sample size for dietary information (see above).

Typical of other agamas, *P. dorsalis* uses a sit-and-wait hunting mode (Miles et al., 2007). From the videos, we quantified the differences in hunting activity between urban and rural populations using two robust measures: movements per minute (MPM) and percent of total time spent moving (PTM) (similar to Cooper et al., 2013). Proportion of prey attacks initiated while moving or when immobile were infrequent events and were not the target of focal observations, because recording these behaviors are known to prolong observations and hinder multiple comparisons (Cooper and Whiting, 2000). Given the heteroscedasticity of the hunting activity variables, we used non-parametric Kruskal–Wallis one-way analysis of variance to

determine behavioral differences between sexes and across populations.

Finally, to compare the body condition of lizards across urban and rural habitats, we recorded body mass (g) and SVL (mm) from a total of 185 lizards (urban: $N = 70$ males and $N = 36$ females; rural $N = 37$ males and $N = 42$ females). As a measure of body condition, we calculated the Body Mass Index (BMI) which is the ratio of body mass (g) to the square of SVL (mm^2). We used a two-way ANOVA with Tukey's post-hoc tests to compare BMI between sexes and across sites. All statistical analyses were conducted in SPSS 20.0 (IBM).

RESULTS

Of the 49 lizards captured and gut flushed, five lizards (urban: $N = 2$ males and $N = 1$ female; rural: $N = 2$ females) had an empty stomach, and one lizard yielded just one prey item ($N = 1$ rural male). Based on the gut contents of the rest, we found the diet of *P. dorsalis* to consist mainly of arthropods, of which Hymenoptera: Formicidae was the predominant prey taxon consumed (Table 1).

In the urban habitat, lizards fed mainly on Hymenoptera: Formicidae with ants being the most common prey item, occurring in 100% (FO) of the samples for both sexes (Table 2). Considering all prey items, ants constituted 37.1% (RO) of the diet of males and 26.6% (RO) of females in the urban habitat (Table 2). Apart from ants, urban females ate mainly Hymenoptera (75% FO) and Coleoptera (62.5% FO), whereas urban males ate Heteroptera (53.8% FO) and Diptera (46.1% FO). All other prey items contributed to less than 39% of the samples collected from urban lizards (Table 1). Prey from three orders, namely Neuroptera, Isoptera, and Orthoptera, were absent in the diet of urban male lizards, but Orthoptera was found in small quantities in the diet of urban female lizards.

In the rural habitat, Formicidae also dominated the diet of lizards, occurring in 60% of samples (FO) in males and 76.9% (FO) in females. As a consequence, 15.3% (RO) of the diet of rural males and 21.2% of the diet of rural females consisted of ants (Table 2). For rural males, prey items from the orders Diptera (20.5% RO) and Orthoptera (15.3% RO) were common, whereas for rural females, prey items from Hymenoptera (19.1% RO) and Lepidoptera (17.0% RO) were common. Other prey items contributed to less than 15% of the diet of rural lizards (Table 2).

Information on diet composition can be used to understand the degree of niche overlap within (Rocha and Anjos, 2007) and across species (Ortega-Rubio et al., 1995; Vieira and Port, 2007).

TABLE 2. Frequency of occurrence (FO), relative occurrence (RO), and the index of relative importance for males and females of *Psammophilus dorsalis* from urban and rural habitats.

Order	Frequency of occurrence				Relative occurrence				Index of relative importance			
	Rural		Urban		Rural		Urban		Rural		Urban	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
Formicidae	60.0	76.9	100.0	100.0	15.3	21.2	37.1	26.6	3,817.2	6100.5	15,214.3	12,891.1
Hymenoptera	30.0	69.2	38.4	75.0	7.6	19.1	14.2	20.0	3,84.6	1442.6	476.4	12,95.2
Lepidoptera	50.0	61.5	15.3	25.0	12.8	17.0	5.7	6.6	1,284.0	2007.7	101.7	196.2
Diptera	80.0	15.3	46.1	37.5	20.5	4.2	17.1	10.0	2,374.8	95.3	566.3	320.9
Coleoptera	50.0	23.0	15.3	62.5	12.8	6.3	5.7	16.6	1,583.1	298.6	69.9	1,368.4
Heteroptera	30.0	30.7	53.8	50.0	7.6	8.5	20.0	13.3	1,88.7	326.5	648.0	377.1
Neuroptera	10.0	30.7	0	0	2.5	8.5	0	0	24.6	144.3	0	0
Isoptera	20.0	15.3	0	0	5.1	4.2	0	0	1,08.6	108.0	0	0
Orthoptera	60.0	38.4	0	25.0	15.3	10.6	0	6.6	1,340.2	990.6	0	199.3

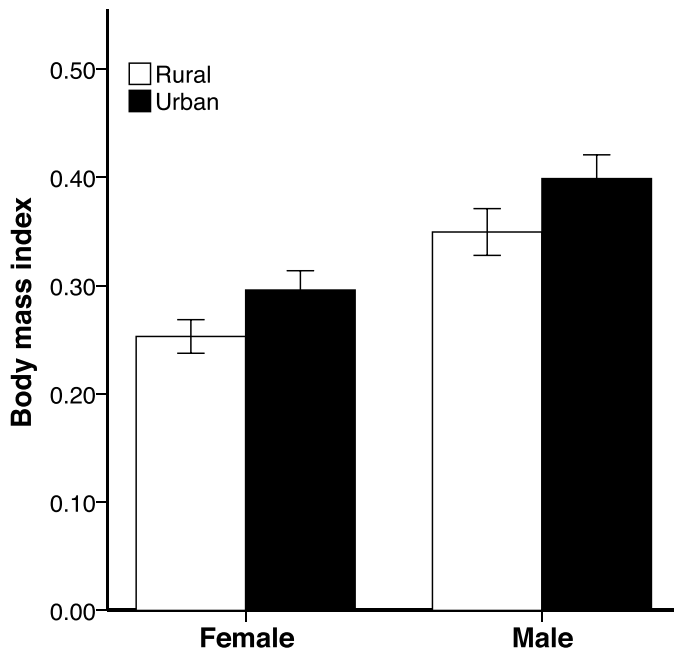


FIG. 2. Body mass index (g/mm²) of males and females of *Psammophilus dorsalis* from rural and urban sites. Bars represent mean \pm 1 SE.

Based on the index of relative importance, ants dominated the diet of the lizards in both the urban and rural habitats; however, this domination was less in rural compared to urban lizards (Table 2). Other prey types contributed minimally to the dietary composition of urban lizards, whereas more prey types were found in rural lizards (Table 2). Overall, the dietary overlap of males and females was high in both the urban habitat (91.1%) and the rural habitat (80.6%). When comparing across urban and rural sites, the overlap in diet of males was 74.3%, whereas that of females was 87.7%. Regardless of sex, rural and urban lizards overlapped in their diets by 80.3%. Despite this, the volume of food consumed was lower in urban populations compared to rural, and this difference was greater for males than for females ($F_{1,37}$ for interaction = 4.80, $P = 0.035$).

As expected, males had greater BMI ($F_{1,181} = 83.62$, $P < 0.001$) than did females in both urban and rural habitats. Interestingly, however, lizards from the urban population had significantly greater BMI ($F_{1,181} = 37.56$, $P < 0.001$, Fig. 2) than those from rural populations. There was no significant interaction effect of site and sex for BMI.

From the focal observations of lizards, we found that rural males had higher MPM ($\chi^2 = 4.11$, $df = 1$, $P = 0.039$) and PTM ($\chi^2 = 4.11$, $df = 1$, $P = 0.039$) compared to urban males (Fig. 3). There was no statistical difference in the activity measures of females between urban and rural populations. There also was no significant difference in activity between the sexes at each site.

DISCUSSION

An environmental gradient from undisturbed to urbanized represents a dramatic environmental axis with which many organisms currently face (McDonnell and Pickett, 1990). The geographical distribution of *P. dorsalis* is widespread, and this species does not seem to be negatively affected by urbanization, because individuals in urban habitats are larger and have a better body condition than do those in rural habitats. The ability

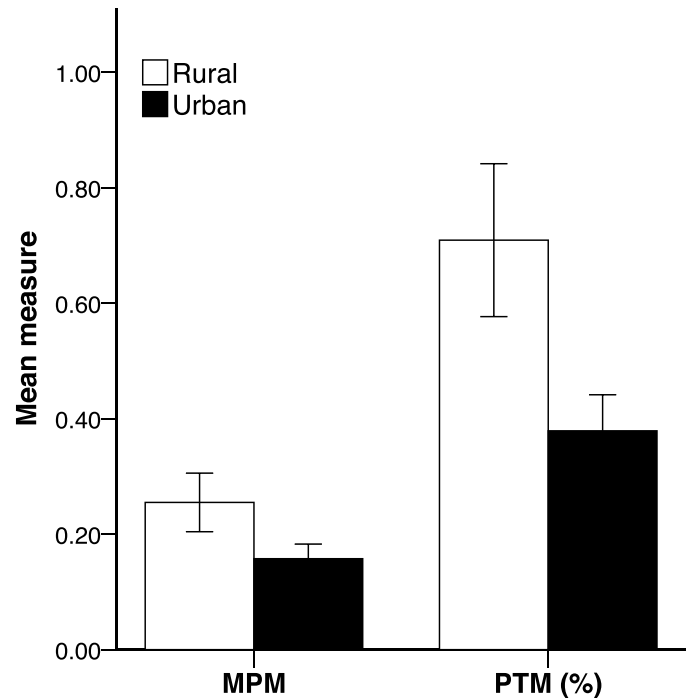


FIG. 3. Foraging behaviors of rural and urban males: movements per minute (MPM) and percent of total time spent moving (PTM). Bars represent mean \pm 1 SE.

to survive in anthropogenic areas, therefore, requires changes in behavior. Based on our observations of the hunting behavior and diet of *P. dorsalis*, we find that these lizards consume mainly ants. This myrmecophagous behavior of *P. dorsalis* is magnified in the urban habitat, which is not surprising given that Hymenoptera is the most abundant insect order found in urban Bangalore (Jaganmohan et al., 2013). By comparison, lizards in the rural habitat had a wider range of prey items in their total dietary composition.

Observations of hunting activity in *P. dorsalis* revealed some key differences between urban and rural populations. Rural males showed greater activity than did urban males, as measured by their movements per minute and the percent of total time spent moving. Changes in foraging strategies in urban environments have been seen in other taxa as well (Luniak, 2004; Møller, 2009; Daniel et al., 2013). For example, individuals of the Tonkean macaque, *Macaca tonkeana* in heavily altered human habitats spend more time foraging but less time moving compared to those from minimally altered human habitats (Riley, 2007). Similar to *M. tonkeana*, dietary diversity in *P. dorsalis* was lower in the heavily human-altered habitats. The greater movement and greater amount of food consumed by rural males of *P. dorsalis*, however, does not seem to increase body condition. The higher energy expenditures of the rural males as expected by the greater movement and the need to patrol larger territories (unpubl. data) may, instead, explain their smaller body size and lower body condition compared to urban males (Huey and Pianka, 1981). Although no social displays were seen during the observation period, movement patterns recorded for these urban and rural males may be related to both general hunting strategies as well as territory defense. Female lizards from urban habitats were also heavier, despite the higher overlap in diet between females across sites and the lack of a difference in foraging. Increase in body size in

urbanized environments could convey an increase in reproductive capacity (Lowe et al., 2014).

Given the striking sexual dimorphism in *P. dorsalis*, we were not surprised that differences in diet composition between the sexes were more apparent than differences across habitats. Besides the most dominant prey (Formicidae), Diptera and Heteroptera were the second most frequently occurring and the second dominant prey item found in males from both rural and urban sites. Prey members of Diptera and a few members of Heteroptera are capable of flight, which is consistent with the observation that males perch higher than females throughout the year and especially during the breeding season (Radder et al., 2006), enabling better access to aerial prey. Lepidoptera (mainly caterpillars) and Hymenoptera (mainly wasps/bees) were the second most dominant and frequently occurring prey items in rural females and urban females, respectively. Given that females perch at lower heights on rock substratum than do males, females are more likely to encounter such prey items at either habitat if they forage widely.

Although we found only invertebrate prey in the stomachs of *P. dorsalis*, others have observed the consumption of vertebrate prey. Sreekar et al. (2010) recorded the occurrence of an adult male *P. dorsalis* feeding on *Hemidactylus treutleri* in a rural habitat, and Balakrishna (2014) reported an adult female *P. dorsalis* feeding on a juvenile *Rattus rattus* in the urban habitat. These observations suggest that the diet of the individuals of *P. dorsalis* can be very diverse and is not greatly constrained by anatomy or morphology. Prey availability in our study areas is unknown, but given the diversity of prey in the diet and their hunting strategy, *P. dorsalis* are likely to be opportunistic foragers.

In sum, *P. dorsalis* are generalist foragers, with a predominantly myrmecophagous diet. We found a high degree of dietary overlap between the sexes and across urban and rural areas. The range of secondary prey constituents, which includes smaller vertebrates, indicate that this species can exploit a diverse array of prey items. Although multiple other factors also are known to affect the foraging behavior of lizards (Cooper et al., 2006; Werner et al., 2006), a generalist and sit-and-wait hunting strategy that includes myrmecophagy (similar to Sullivan et al., 2014) seems to allow the survival of *P. dorsalis* in a range of habitats. Because ant abundance, especially of those species that are tolerant of disturbance, can be high in urbanized areas (Buczowski and Richmond, 2012), a hunting strategy to include this common prey can be effective. Contrary to expectation, individuals of *P. dorsalis* do not seem to be negatively affected by urbanization but instead manage to successfully hunt in and around the small patches of vegetation that remain. This, in turn, could enable them to maintain a better body condition than lizards in undisturbed rural habitats.

Acknowledgments.—We thank A. T. Vanak, K. S. Seshadri, and two anonymous reviewers for comments on an earlier version of this manuscript. This species is not covered under the Schedules of the Indian Wildlife (Protection) Act; therefore, collection permits are not required. All capture and handling methods were approved by the Institutional Animal Ethics Committee at the Indian Institute of Science (CAF/Ethics/394/2014).

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Accepted: 26 January 2016.