

A multivariate approach to understanding shifts in escape strategies of urban lizards

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Abstract

Escape strategies of animals are economic decisions, expected to vary as a function of both intrinsic (e.g., performance ability) and extrinsic factors (e.g., level of threat and microhabitat). Anthropogenic disturbance, especially urbanization, changes a range of environmental factors including habitat characteristics and predation risk. As a consequence of differences in microhabitat structure and repeated exposure to anthropogenic disturbance, we hypothesize that animals in urban environments will be less risk averse than those in rural environments. Here, we examined the importance of extrinsic and intrinsic factors to understand the escape strategies of *Psammophilus dorsalis* across an urban-rural gradient. First, urban lizards used lower perches and chose refuges that were closer to their perches compared to rural lizards. Flight initiation distance (FID) of urban lizards in the field was shorter than that of rural lizards, but only for males. In response to a second attack, only rural males decreased their FIDs, whereas urban males showed low and invariable FIDs. Laboratory

measures of sprint performance showed expected differences between the sexes, but no significant difference between urban and rural populations. Unlike the strong differences between males across habitats, escape strategies of females were similar in urban and rural areas, most likely because females generally rely on crypsis to minimize predation risk and are resistant to flee when approached. In sum, urban lizards have access to a more complex structural environment, with greater perch and refuge options, and have habituated to non-lethal anthropogenic disturbance. These extrinsic and intrinsic factors combine to result in lower risk aversion and may explain the ability to tolerate urban environments.

Significance statement

Rapid urbanization is at its peak globally, and many animals are forced to adjust to the associated environmental changes or face local extinction. Some species, however, seem to persist in urban areas, and we hypothesize that they behaviorally respond by being less risk averse. We used a multivariate approach to understand the escape strategies of the peninsula rock agama across an urban-rural gradient. Lizards in urban areas use a more complex structural environment, with greater perch and refuge options, compared to rural lizards. Urban lizards also allow closer approaches. Because of the differences in body coloration and size, escape strategies of females were less affected by urbanization as they use crypsis to minimize predation risk. All these extrinsic and intrinsic factors combine to result in lower risk aversion by urban lizards and may explain their tolerance of human altered environments.

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Introduction

All organisms experience environmental fluctuations and shifts over ecological and evolutionary timescales. The speed and unpredictability of environmental changes caused by urbanization, however, are unprecedented (McKinney 2008; Schlaepfer et al. 2002). Urbanization rapidly alters natural habitats of animals, from reducing and fragmenting the landscape with anthropogenic structures, to altering the availability and type of food sources as well as the predator community (McKinney 2008; DeStefano and DeGraaf 2003; Ditchkoff et al. 2006). Due to the rapid and dramatic change in these environmental factors, many species are not able to tolerate urbanization, which often leads to a loss of biodiversity (Marzluff et al. 2008). Some species, however, have greater plasticity and can tolerate such environmental changes by altering their behaviors. As a first-response mechanism, behavioral modifications to novel human-induced challenges can prevent individuals from suffering high fitness losses and aid in population survival.

Predation is one of the most ubiquitous threats to the survival of organisms, and thus, a diverse range of antipredatory strategies has evolved to minimize the risk of mortality (Lima and Dill 1990; Cooper and Blumstein 2015). In response to an approaching predator, the most typical response in animals is to flee. Flight initiation distance (FID), defined as the distance between a potential threat and the prey at the onset of escape, has therefore been a widely used measure of antipredator responsiveness (Ydenberg and Dill 1986; Cooper and Blumstein 2015). Since FID is an economic decision, FID will typically increase as predation risk (cost of remaining) increases and will decrease as the cost of escape increases (Ydenberg and Dill 1986). The decision of when to escape an approaching predator is influenced by numerous intrinsic and extrinsic factors. Extrinsic factors such as the level of threat associated with the predator, ease of escape, and distance from refuge (Engelhardt and Weladji 2011; Bateman and Fleming 2014b), along with intrinsic factors such as physiological or performance ability (Herrel et al. 2011; Qi et al. 2014) and level of habituation to risk (Brown and Chivers 2005; Engelhardt and Weladji 2011), can all affect escape strategies of animals.

Escape decisions are crucial to an individual's fitness (Cooper and Frederick 2007), and these decisions may depend upon the intrinsic capacity to escape predation, such as the degree of crypticity, the propensity and rate of learning, and performance capabilities. Performance abilities such as sprint speed can aid in escape responses, and this often differs depending on the sex, morph, and habitat of animals (Qi et al. 2014). In *Anolis sagrei*, longer-limbed individuals sprint faster on broader surfaces and thus preferentially use broader surfaces as perches (Calsbeek and Irschick 2007). Therefore, habitat structure can be tightly associated with the escape

capabilities of animals. Ability and rate of learning are also expected to differ between species and even between individuals of a species because environmental factors such as predation pressure, microhabitat characteristics, and exposure to anthropogenic disturbances interact to influence habituation or learning (Runyan and Blumstein 2004; Ellenberg et al. 2009). Several studies have found that frequent exposure to low-risk novel threats, such as human activity, results in habituation of escape responses through learning (Frid and Dill 2002; Engelhardt and Weladji 2011).

Among the many extrinsic conditions that influence escape responses, anthropogenic environmental disturbances should strongly affect risk perception and escape strategies of animals (Shochat et al. 2006). Animals living in urban habitats experience novel physical and microhabitat structures that are generally more varied in type, such as cement walls, metal sheets, and ornamental plants that are not found in natural undisturbed habitats. Natural habitats are often more homogeneous, with less variation in the type of physical structures (typically rocks and boulders for perch and refuge) and a higher proportion of native vegetation (Young and Jarvis 2001; Balakrishna et al. 2016). For many terrestrial animals, the availability and type of refuge are strong extrinsic factors that affect escape strategies (e.g. Martin and López 1995; Schooley et al. 1996; Cooper and Whiting 2007). Escape theory predicts that FID will increase with distance to refuge (Ydenberg and Dill 1986); a result that has been supported by empirical data from many terrestrial vertebrates, including lizards (Samia et al. 2016), birds (Guay et al. 2013), and mammals (Stankowich and Blumstein 2005; Engelhardt and Weladji 2011).

Many studies so far, especially in lizards, have examined the importance of either extrinsic factors or intrinsic factors on escape responses. Using the Indian rock agama *Psammodromus dorsalis*, we investigated the effect of urbanization on escape strategies taking into account both intrinsic and extrinsic factors that might affect escape decisions. As a consequence of differences in habitat structure and repeated exposure to human activity (resulting in habituation), we hypothesize that lizards in urban environments will be less risk averse than lizards in rural environments. Specifically, we expect urban lizards to perch at lower heights and when approached, have shorter FIDs and choose closer refuges than rural lizards. For a subset of individuals from both rural and urban areas, we also simulated repeated predator attacks to test the rate of habituation, with the prediction that urban lizards will more rapidly habituate to a low-risk human threat. Since intrinsic performance ability can directly influence escape decisions, we measured the sprint speed of wild-caught lizards from both urban and rural environments to determine if running speed was a factor in the escape strategies of urban lizards. Finally, we expected sex differences in antipredator responses and sprint speed, regardless of habitat, as sexes are

dimorphic and dichromatic, with starkly different levels of crypticity.

Methods

Study species and sites

Psammophilus dorsalis is a common rock agama found across most of the semi-arid regions of peninsular India, especially in areas with rocky outcrops and boulders (Radder et al. 2006). This species is sexually dimorphic, with males larger and more colorful than females (Balakrishna et al. 2016; Radder et al. 2006; see also Online Resource 1). During the breeding season, typically from April to August, males of *P. dorsalis* develop conspicuous dynamic coloration which becomes dull by winter (December/January), whereas females maintain cryptic coloration year-round (AB and MT unpublished data). We conducted this study across three different urban areas located in Bangalore city (centroid 13.0422° N and 77.5940° E) and two rural areas located near Antharagange forest range of Kolar district (centroid 13.1243° N and 78.0346° E), approximately 60 km from the urban study sites (Online Resource 1). Replicate sites within urban and rural areas were at least 5 km apart (Online Resource 1). The urban area comprised human settlements interspersed with little scrub vegetation, whereas the rural habitat comprised rocky boulders and scrub vegetation (Balakrishna et al. 2016; see also Online Resource 1).

Escape behavior

We measured the escape behavior of adult males ($N = 20$ per area, i.e., $N = 40$ total) and females ($N = 20$ per area, i.e., $N = 40$ total) during peak activity periods from 0900 to 1100 and 1500–1700 h in the post breeding season from August to October 2014. By August, most females had laid their last clutch of the year. To avoid the potential effects of gravidity on antipredatory behavior and sprint speed, we verified the non-gravid status of females by careful observation based on abdomen shape. Before the start of each field trial, the observers (AB and SB) scanned the study areas and located lizards that were sitting on a perch and not actively engaged in foraging or social activities. Only lizards that were perched at approximately 1–1.5 m above ground level and were initially 10–12 m away from the observer were selected for simulated predator attacks. All “predator attacks” were simulated by the same observer (AB) wearing the same colored clothes (dull olive green) on sunny days only and involved approaching each lizard at an approximate speed of 1.5 m/s directly in a straight line where there was no obstruction of visual field between the lizard and the attacker. Using binoculars from at least 20 m from the lizard, the second observer (SB) recorded the location of the initial perch and the path

taken to the refuge. After the attack, the following parameters were measured: (1) flight initiation distance (FID) as the distance between the attacker and the initial perch when the lizard started escape, (2) hiding duration, (3) perch height and type, (4) refuge site, and (5) perch-to-refuge distance. If the focal lizard returned to the same perch or to a perch within a 2-m radius of the first attack by 10 min, a second and third predator attack was simulated in the same way. We restricted our statistical analysis of repeated attacks to only lizards that were attacked twice, because only 50% of rural lizards (of 40) and 20% of urban lizards (of 40) returned to their perch in time for three attacks. Repeated attacks of focal lizards were completed within 30 min, and all focal lizards attacked during the same day were at least 200 m apart to prevent disturbance and repeated sampling of individuals.

Sprint speed

To measure sprint speed, a different set of lizards from the same urban and rural habitat were captured by noosing and transported to the laboratory in cloth bags ($N = 26$ males and 25 females from urban; 26 males and 24 females from rural). We first measured mass (g) and snout-to-vent length (SVL) (mm) of all individuals and then housed them in glass tanks ($60 \times 30 \times 25$ cm) lined with a sandy substratum, in a room with natural lighting and ambient temperature (28–30 °C). Additional heat for basking was provided using 60-W incandescent bulbs that were suspended above each tank and turned on for 2–3 h a day. Water was provided ad libitum, and crickets and grasshoppers were provided daily. Lizards were habituated to laboratory conditions for 2 days before sprint speed was measured. Before the trials, all lizards were first allowed to attain their preferred body temperatures (cloacal temperature was 30–34 °C measured using a thermometer) by basking in a thermal gradient for 30 min. Each lizard was then placed individually on a racetrack (4.2-m length \times 0.1-m width \times 0.4-m height) that was fitted with an overhead camera and lined with a fine-grained sandpaper. Lizards were stimulated to run at their maximal speed by gently tapping the base of the tail with a soft brush. All lizards were induced to run three times with a 15-min recovery period between each run. To obtain a measure of burst sprints similar to antipredator escape responses, without subsequent exhaustion, we used a short racetrack (~60 SVL of an average female; 30 SVL of an average male). We also determined that 15 min was a sufficient recovery period between successive runs, as over 65% of lizards performed their fastest sprints during the second or third run. Any trials in which the lizard did not run beyond 1 m after ten tail taps were excluded. Video recordings of all runs from each lizard were used to calculate sprint speed, measured as the time taken to travel across a 0.75-m length along the middle of the track. We used the single fastest sprint speed from all three runs by each individual in subsequent

statistical analyses. To minimize observer bias, blinded methods were used for measurements of sprint speed, but it was not possible to record data blind for escape responses and habitat characteristics as these involved measurements in the field.

Statistical analyses

We performed repeated measures ANOVAs to determine the effect of attack number (1, 2), habitat (urban, rural), and sex (male, female) on FID and hiding duration separately. For hiding duration data, we performed an aligned rank transformation before analysis, as the data were non-normal (using ARTool package 2016). For both hiding duration and FID, we included a two-way interaction term between habitat and sex. We used data from the first attack only to determine the effects of habitat and sex on FID, hiding duration, perch-to-refuge distance, and perch height (separate two-way ANOVAs with an interaction term). Hiding duration and perch-to-refuge distance from the first attack were transformed using aligned rank-based transformation before analysis as data were non-normal (ARTool package 2016). We also compared body size of lizards as a function of habitat and sex using a two-way ANOVA with an interaction term. We first examined the relationship between SVL and sprint speed by computing an overall Pearson's correlation analysis. We then controlled for body size using an analysis of covariance (ANCOVA) when examining the effect of habitat and sex on sprint speed (with interaction). Tukey's post hoc analyses were performed wherever relevant. All data analyses were performed in R studio version 3.2.1 (R Core Team 2015).

Results

Escape responses

In response to the first attack, FID was significantly affected by an interaction between habitat and sex (ANOVA: $F_{1,76} = 14.22$, $P < 0.001$). Rural males had significantly longer FIDs than urban males (mean \pm 1 SE: rural 3.86 ± 0.22 m; urban 2.42 ± 0.16 m; post hoc $P < 0.001$, Fig. 1) and all females (mean \pm 1 SE: rural 2.11 ± 0.22 m; urban 2.13 ± 0.14 m; post hoc $P < 0.001$, Fig. 1). Thus, males from urban areas initiated escape later than rural males, allowing closer approaches of the predator before running. Hiding duration after the first attack for those lizards that were relocated was similar across individuals (mean \pm 1 SE: rural male 165.55 ± 26.52 s; rural female 123.8 ± 28.38 s; urban male 236.4 ± 20.82 s; urban female 166.92 ± 30.74 s), with no significant difference between habitats (ANOVA: $F_{1,47} = 2.56$, $P = 0.115$) or sexes (ANOVA: $F_{1,47} = 2.54$, $P = 0.117$).

For those lizards that were attacked twice ($N = 48$ total), FID was influenced by an interaction between habitat, sex,

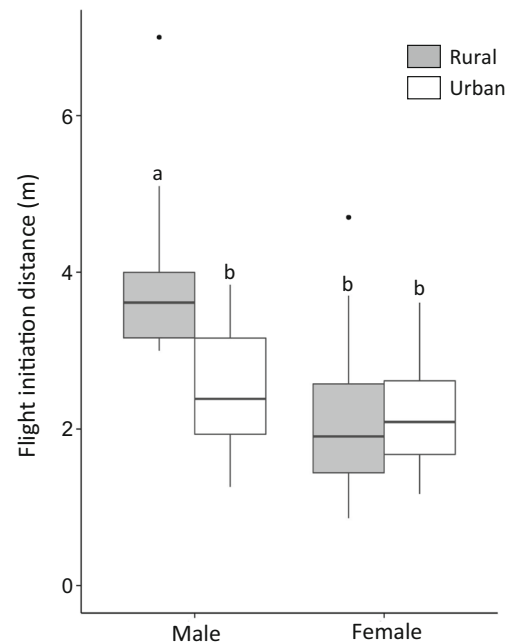


Fig. 1 Flight initiation distance of *Psammophilus dorsalis* after one attack was highest in males from rural areas, compared to males from urban areas and all females. Shown are boxplots, with medians, quartiles, 5th and 95th percentiles, and extreme values. Different letters indicate significant post hoc differences at $P < 0.01$

and attack number (ANOVA: three-way interaction: $F_{1,43} = 7.47$, $P = 0.009$, Fig. 2). To further examine the individual effects of each factor, we classified the responses separately for males and females and found that FID was influenced by an interaction between habitat and attack number for

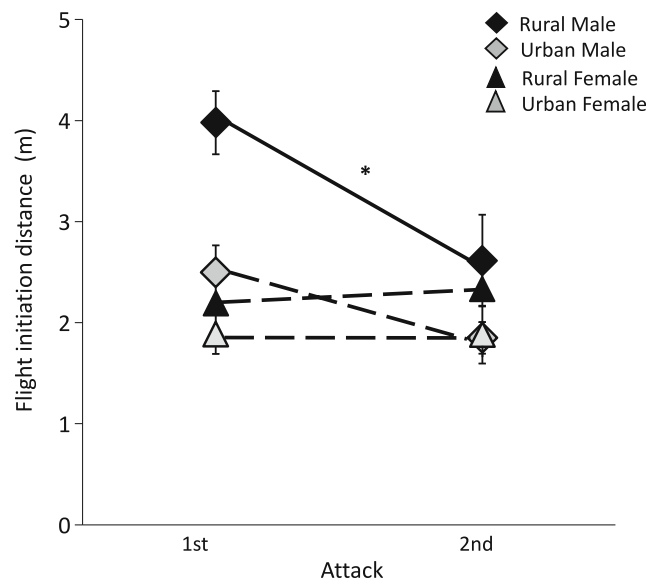


Fig. 2 In response to a repeated attack, only rural males of *Psammophilus dorsalis* decreased their flight initiation distance (FID; mean \pm 1 SE). Asterisk denotes post hoc significant difference at $P < 0.001$

males (ANOVA: $F_{1,19} = 11.39$, $P = 0.003$, Fig. 2) but not females (ANOVA: $F_{1,24} = 0.26$, $P = 0.615$, Fig. 2). With the second attack, FID significantly decreased in rural males (ANOVA: $F_{1,12} = 41.78$, $P < 0.001$, Fig. 2) but not urban males (ANOVA: $F_{1,7} = 5.39$, $P = 0.053$, Fig. 2). The FID of females was not significantly affected by habitat (ANOVA: habitat: $F_{1,24} = 0.87$, $P = 0.360$) or attack number (ANOVA: $F_{1,24} = 0.36$, $P = 0.552$, Fig. 2).

Similarly, hiding durations across multiple attacks for those lizards that were relocated were not significantly affected by either sex (ANOVA: $F_{1,32} = 0.01$, $P = 0.970$), habitat (ANOVA: $F_{1,32} = 1.45$, $P = 0.232$) or attack number (ANOVA: $F_{1,32} = 0.32$, $P = 0.569$). Thus, all lizards maintained similar hiding durations, regardless of habitat, sex, or repeated attacks.

Habitat characteristics

Given that escape behaviors can be influenced by key local habitat characteristics, we compared perch characteristics (type and height) and refuge characteristics (type and perch-to-refuge distances) of lizards in both habitats. Urban areas have higher variation in the type of perches and refuges compared to rural areas. Lizards in rural areas ($N = 40$) perched on rocks and small boulders (100%) and took refuge in rock crevices (75%) or scrub vegetation (25%) when attacked. By contrast, lizards in urban areas ($N = 40$) were found perched on wall ledges (75%), rocks (10%), brick piles (7.5%), drain trenches (2.5%), and house roofs (5%). Refuges for lizards in urban habitats included all the various structures listed earlier (87.5%) as well as scrub and ornamental vegetation (12.5%).

Regardless of perch type, perch height of lizards was influenced by an interaction between habitat and sex (ANOVA: $F_{1,76} = 4.69$, $P = 0.033$, Fig. 3a). In rural areas, males were found on significantly higher perches compared to females (mean \pm 1 SE: rural male 7.62 ± 0.79 m; rural female 4.2 ± 0.64 m; post hoc $P < 0.001$, Fig. 3a). Perch heights were also higher for rural males compared to urban males (post hoc $P = 0.004$, Fig. 3a), but not for females (mean \pm 1 SE: urban male 4.90 ± 0.21 m; urban female 3.85 ± 0.32 m). As expected, the relative location of refuges from perches influenced escape decisions. In response to the first attack, perch-to-refuge distance of a fleeing lizard was significantly shorter in urban habitats compared to rural habitats (ANOVA: $F_{1,76} = 45.41$, $P < 0.001$, Fig. 4b), with no significant differences between the sexes (ANOVA: $F_{1,76} = 0.36$, $P = 0.550$, mean \pm 1 SE: rural male 0.86 ± 0.06 m; rural female 0.92 ± 0.10 m; urban male 0.37 ± 0.10 m; urban female 0.53 ± 0.13 m).

Body size and sprint speed

We found a significant interaction between habitat and sex for SVL ($F_{1,97} = 17.72$, $P < 0.001$). As expected, males were

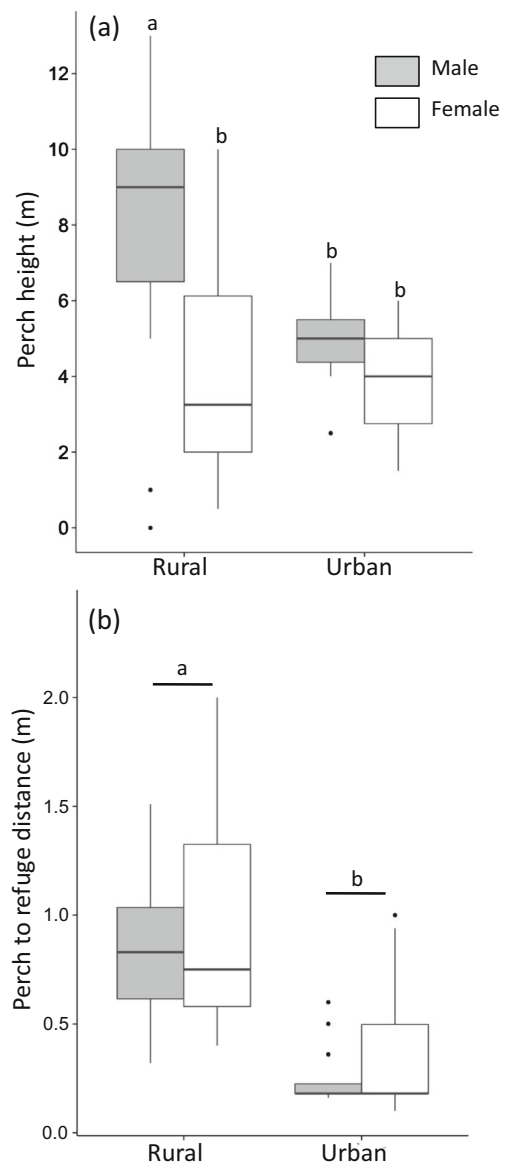


Fig. 3 **a** Perch height and **b** perch-to-refuge distances of *Psammophilus dorsalis* as a function of habitat (urban, rural) and sex (male, female). Shown are boxplots, with medians, quartiles, 5th and 95th percentiles, and extreme values. Different letters indicate significant post hoc differences at $P < 0.005$

significantly larger than females regardless of habitat (both post hoc $P < 0.001$). Between habitats, urban males were significantly larger than rural males (post hoc $P < 0.001$; mean \pm 1 SE: rural males 104.46 ± 2.25 mm; urban males 125.15 ± 1.79 mm), but there was no significant difference in SVL between females across populations (post hoc $P = 0.202$; mean \pm 1 SE: rural females 85.16 ± 1.43 mm; urban females 90.36 ± 1.13 mm).

In general, lizards with larger SVL had faster sprint speed (Correlation coefficient = 0.34, $P < 0.001$). After controlling for this body size effect (covariate term; $F_{1,93} = 0.26$, $P = 0.608$), we find that sprint speed of lizards was only

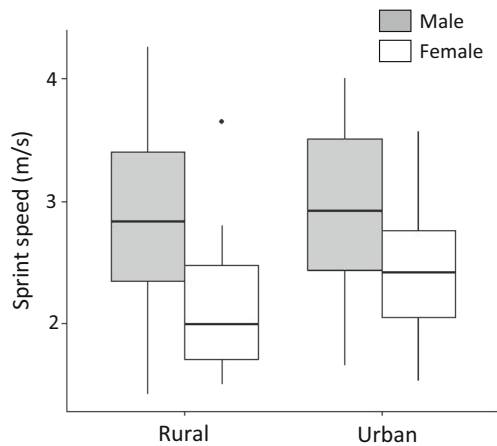


Fig. 4 Sprint speed of *Psammophilus dorsalis* differed only between males and females and not between habitats. Shown are boxplots, with medians, quartiles, 5th and 95th percentiles, and extreme values

affected by sex ($F_{1,93} = 21.17$, $P = 0.001$). Males ran faster than females (mean \pm 1 SE: rural male 2.85 ± 0.16 m/s; rural female 2.14 ± 0.10 m/s; urban male 2.94 ± 0.11 m/s; urban female 2.45 ± 0.11 m/s; Fig. 4). There was no significant effect of habitat (ANCOVA: $F_{1,93} = 2.31$, $P = 0.131$) or an interaction between habitat and sex in predicting sprint speed ($F_{1,93} = 0.49$, $P = 0.484$).

Discussion

We examined the escape strategies of the agamid *P. dorsalis* as a function of multiple extrinsic and intrinsic factors, with the main aim designed to understand the effect of urbanization on antipredator responses. First, urban and rural habitats differed in multiple ways that directly influenced escape decisions. Compared to lizards in undisturbed rural areas, lizards in urban areas used lower perches that varied greatly in type and chose refuges that were more varied and closer to their perches. As expected, the FID of urban lizards was lower than rural lizards, but only for males. Apart from habitat characteristics, intrinsic factors like the propensity to habituate to humans (but not sprint speed) also differed between habitats. When attacked multiple times in the field, rural but not urban males decreased their FIDs significantly across subsequent attacks. For some escape responses, sex differences were more apparent than population differences, such that urbanization affected the escape strategies of males more than females.

Animals living in urban habitats face multiple challenges including a greatly altered abiotic environment with different types of perch and refuge sites. According to optimal escape theory (Ydenberg and Dill 1986), refuge distances greatly influence escape responses. We find that lizards use refuge sites that are significantly closer to their perch in urban areas than in rural areas. Apart from refuge distances, perch and refuge types were also highly variable in urban areas, as

lizards utilized artificial anthropogenic structures in the environment. In fact, the higher perch heights of lizards in rural areas compared to urban areas are unlikely to be a function of perch availability, as building walls and ledges are taller than the boulders in the natural rural habitat (AB and MT personal observation). Instead, higher perches in open rocky natural habitats allow for better vigilance, which would offset the costs of being more conspicuous and having fewer refuge options (Krams 2001). Access to a complex structural landscape, with more perch and refuge options (Prosser et al. 2006), supports the seemingly risky strategy of urban lizards that allow the closer approach of attackers before flight. Although urban lizards had larger body sizes than rural lizards and sprint speed was generally correlated with body size (here, see also Losos 1990; Garland and Losos 1994), we find no significant differences in intrinsic performance ability (sprint speed) between urban and rural lizards.

According to the threat sensitivity hypothesis, prey animals should balance the costs of escape from the risk of attack and adjust their antipredatory response based on the magnitude of predatory threat (Helfman 1989; Chivers et al. 2001). Studies have found lower abundance of native predators in urban areas (McKinney 2008; Shochat et al. 2006), which should reduce overall perceived risk. However, the increase in human disturbance, presence of domesticated animals, and changes in predator species composition can potentially replace the threat from natural predators. Only when human activity is perceived as a low-risk novel threat, frequent exposure should result in habituation through learning (Labra and Leonard 1999; Frid and Dill 2002; Webb and Blumstein 2005; Engelhardt and Weladji 2011; Bateman and Fleming 2014a). Given this, the reduction in FID found in several studies for animals living in human-disturbed habitats, including *P. dorsalis* (this study), is not surprising. All these studies, however, compared the escape strategies of urban and rural populations after a single attack, which is therefore a measure of habituation to lifetime exposure to the low-risk urban threats. Habituation is necessary for survival in novel urban environments as it allows individuals to decrease the cost of fleeing and increase time for other activities, such as foraging and social behavior (Rodríguez-Prieto et al. 2011). Unlike most other studies of escape responses based on lifetime experience, we also measured the ability to learn from repeated attacks over a single day. Male lizards from the rural habitat were the only ones that decreased their FID over subsequent attacks, clearly indicating that *P. dorsalis* is capable of learning about threats in a very short timescale (similar to Marcellini and Jenssen 1991; Thaker et al. 2010; Batabyal et al. 2014). The lack of short-term habituation (i.e., reduction in FID) in urban males further supports the prediction that lifetime exposure to human disturbance in urbanized areas can result in higher threat tolerance, with little required change in behavior in response to repeated directed exposures.

Like most sexually dimorphic species, males and females use different antipredator strategies that correspond to their morphology. In *P. dorsalis*, males are larger and conspicuously colored, whereas females are smaller and cryptically patterned. Performance traits have been found to be sex dependent in dimorphic species, with females typically having slower sprint speed than males (Garland and Losos 1994; Irschick et al. 2008; Van Damme et al. 2008). The cryptic female coloration and smaller body size of *P. dorsalis* support an antipredator strategy that allows for closer approach from predators (i.e., shorter FID), with little change over repeated attacks. Thus, *P. dorsalis* females prefer crypsis over early fleeing (i.e., long FID) to avoid detection from predators (Schwarzkopf and Shine 1992; Stiller and McBrayer 2013). Females also use lower perches than males in general, which not only influences their foraging and diet choices (Balakrishna et al. 2016) but also supports their escape strategies.

In this study, we show that urban habitats support a shift in antipredator strategies, which are mostly driven by habituation to human exposure and modifications in habitat structure. We suggest that urbanization, with the associated suite of ecological changes, may be a strong selective force in shaping the responses of species, as changes in escape strategies enables urban lizards to adjust to the novel environment. What remains to be understood is how urban environments are perceived by animals and the specific ecological factors that drive altered survival strategies.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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Ethical statement This species is not covered under the Schedules of the Indian Wildlife (Protection) Act; therefore, collection permits were not required. All capture, handling, and experiment protocols were approved by the Institutional Animal Ethics Committee at the Indian Institute of Science (CAF/Ethics/394/2014).

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