Urbanization and biological invasion shape animal personalities

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Abstract

Novel selective pressures derived from human activities challenge the persistence of animal populations worldwide. Behavior is expected to be a major factor driving animals' responses to global change because it largely determines how animals interact with the environment. However, the role of individual variation in behavior to facilitate the persistence of animals in changing environments remains poorly understood. Here, we adopted an animal personality approach to investigate whether different behavioral traits allow animals to deal with two major components of global change: urbanization and biological invasions. By studying six populations of *Anolis sagrei* lizards, we found for the first time that anoles vary consistently in their behavior across different times and contexts. Importantly, these animal personalities were consistent in the wild and in captivity. We investigated whether behavioral traits are pulled in different directions by different components of global change. On the one hand, we found that lizards from urban areas differ from nearby forest lizards in that they were more tolerant of humans, less aggressive, bolder after a simulated predator attack, and they spent more time exploring new environments. Several of these risk-taking behaviors constituted a behavioral syndrome that significantly differed between urban and forest populations. On the other hand, the behavior of urban *A. sagrei* coexisting with the invasive predatory lizard *Leiocephalus carinatus* was associated with dramatic changes in their foraging niche. Overall, we provide evidence that differences in animal personalities facilitate the persistence of animals under novel selective regimes by producing adaptive behaviors relevant to their ecology such as predator avoidance. Our results suggest that natural selection can favor certain behaviors over others when animals are confronted with different ecological challenges posed by global change. Therefore, we underscore the need to incorporate behavioral ecology into the study of how animals adaptively respond to human-induced environmental changes.

Introduction

New selective pressures derived from human activities challenge the persistence of animal populations worldwide. Consequently, biological communities around the globe are experiencing biodiversity loss and biotic homogenization. Two of the most important drivers of these processes in the context of human-induced rapid environmental change (*sensu* Sih *et al.*, 2011) are habitat transformation and the introduction of non-native species to new areas (Pimentel *et al.*, 2000; McKinney, 2006; Shochat *et al.*, 2006, 2010; Sol *et al.*, 2014). A major challenge of current studies of biological conservation, ecology, and evolution is to understand why some animals are able to cope with these challenges while others are not.

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Behavior largely determines how animals interact with their environment. Therefore, it has long been expected to be a crucial factor determining how animals deal with new selective pressures (e.g., Baldwin, 1896; Mayr, 1963). A particularly intriguing question is whether individual variation in behavior that is consistent across time and contexts determines the chance of success in rapidly changing environments (Chapple *et al.*, 2012; Sih *et al.*, 2012; Partecke, 2013). These animal personalities – also termed behavioral syndromes, coping styles, or temperaments (Koolhaas *et al.*, 1999; Dall *et al.*, 2004; Sih *et al.*, 2004; Réale *et al.*, 2007) – are widespread across the animal kingdom (Bell *et al.*, 2009). This intraspecific trait variation is relevant because it is a source of ecological variation (Bolnick *et al.*, 2003, 2011; Réale *et al.*, 2007). Individuals with different behaviors can play different ecological roles (e.g., exploit different resources) (Sih *et al.*, 2012). Different behaviors could determine the success of non-native populations in novel environments if some behavioral types are better suited for dealing with

particular environmental challenges than others. Therefore, the study of animal personalities in populations that have experienced recent environmental changes can provide valuable insight to understand how animals cope with human-induced rapid environmental change (Sih *et al.*, 2012).

Risk-taking behavior – the tendency of individuals to be exploratory and take risks in novel contexts (Wilson *et al.*, 1994) – is predicted to be crucial for determining an animal's success under human-induced rapid environmental change. This is because risk-taking, commonly termed boldness, can determine the outcome of the trade-off between the benefits of obtaining novel resources and the costs of avoiding the risks associated with resource acquisition (Lima & Bednekoff, 1999; Verdolin, 2006). Consequently, having an appropriate behavioral type should increase the probability of successfully establishing and persisting in urban environments (Sih *et al.*, 2011; Lowry *et al.*, 2013; Miranda *et al.*, 2013; Sol *et al.*, 2013) or non-native areas (Holway & Suarez, 1999; Chapple *et al.*, 2012; Sih *et al.*, 2012). If the behavioral types best suited for responding to urbanization and biological invasions conflict, then populations responding to one challenge will be at greater risk when facing the other. For instance, animals thriving in human-modified environments are commonly acknowledged to be bolder and more tolerant of humans (reviewed in Lowry *et al.*, 2013; Miranda *et al.*, 2013; Sol *et al.*, 2013). Animals with this behavioral type will save energy and increase feeding time when humans do not represent a significant threat. In contrast, the introduction of a non-native predator to an urban area could favor more cautious individuals if bolder animals are more easily detected and captured by predators (Sih *et al.*, 2003). At present, global change is shuffling ecological communities into new combinations of species. Consequently, nearby populations frequently interact with different competitors and predators, challenging their persistence in a mosaic of rapidly diverging ecological communities. Thus, different behavioral types could be favored in nearby populations of the same species as a response to distinct environmental challenges. The question of how different behavioral types are linked to ecological differences that facilitate dealing with different global change components remains poorly understood.

Moving from largely descriptive research toward more mechanistic studies is a major challenge for both urban ecology (Shochat *et al.*, 2006; Sol *et al.*, 2013; Alberti, 2014) and animal personality studies (Sih *et al.*, 2012; Dall & Griffith, 2014). Here, we assessed the association between behavioral and ecological differences that allow a common lizard (*Anolis sagrei*) to cope with two major components of global change:

urbanization and an invasive predator. We focused on the three main risk-taking behaviors predicted to play relevant roles in the responses of animals to global change: dealing with threats associated with environmental uncertainties, exploiting new resources such as food or refugia, and changing activity patterns to minimize risks such as invasive predators (Tuomainen & Candolin, 2011; Sih *et al.*, 2012; Sol *et al.*, 2013). By conducting replicated experiments in the wild and in captivity, we provide the first evidence of the existence of a behavioral syndrome in *Anolis* lizards. This syndrome integrates several measures of risk-taking behavior, and individuals show consistent differences in risk-taking across time and contexts (i.e., different behavioral types). Then, we show that the mean behavioral type of lizards differs consistently among replicated populations under different global change stressors. Finally, field experiments reveal a mechanistic link between the divergent behavioral types of free-ranging lizards and their ecology. Specifically, *A. sagrei* from populations under different predation regimes showed striking differences in foraging behavior as well as dramatic modifications in their daily patterns of activity. Overall, our study provides unprecedented evidence that ecologically relevant individual behavioral differences are favored in nearby populations exposed to different components of global change.

Methods

Study species and populations

The best way to obtain reliable measures of consistent, ecologically relevant individual variation in behavior (Bengston & Dornhaus, 2014) is to design standardized, repeatable experiments in well-studied biological systems (Dall & Griffith, 2014). Here, we used a set of novel experiments to measure risk-taking behavior in six populations of brown anoles (*A. sagrei*), one of the best studied vertebrate species in the fields of evolutionary ecology, invasion biology, and behavior (Losos, 2009). Specifically, we studied replicated populations of *A. sagrei* in South Florida differing in urbanization (i.e., urban or forest) and predation regime (i.e., presence or absence of invasive curly-tailed lizards, *Leiocephalus carinatus*, a well-known terrestrial predator of *A. sagrei*) (Schoener *et al.*, 1982, 2002; Losos *et al.*, 2004, 2006; López-Darias *et al.*, 2012). We studied adult males from two populations of forest-dwelling lizards, two urban populations with *L. carinatus*, and two urban populations without *L. carinatus* in April–July 2015 (coordinates indicated in S1 in Data S1). To our knowledge, there are no similar forested habitats with *L. carinatus* lizards present in the range of *A. sagrei* in South Florida. *Anolis sagrei* populations in our study areas were established between 1951 and 1964 (Florida Fish and Wildlife Conservation Commission; data obtained on December 2015), whereas *L. carinatus*

was first documented in the early 2000s (Smith & Engeman, 2004). An extended version of the Methods section can be found in the S1 in Data S1.

Fieldwork methods and escape behavior

After locating a lizard perched between 20 and 200 cm on vegetation, we measured its ESCAPE DISTANCE and quantified its AGGRESSIVENESS at capture (see further explanations of these methods in S1 in Data S1). Finally, we moved the lizard into an experimental cage and began the field-based experiment within 15 min after capture. Overall, we measured the behavior of 120 male lizards in the wild and in captivity (see below).

Experimental setup and field experiments

We used collapsible cages (68.5 × 68.5 × 122 cm) to conduct behavioral trials in the field. Cages had a transparent plastic front and three sides with mesh, which prevented small insects from entering the cages. We installed six 30 cm high, evenly distributed perches and a wooden refuge (25 × 23 × 18 cm) with an opening covered by a thick, dark cloth at one end of the cage. All trials were video-taped, and the researcher sat motionless at a distance of >5 m from the experimental cage, a sufficient distance for lizards to act normally (Sugerman, 1990; Shafir & Roughgarden, 1998).

Exploration experiment. We gently placed the lizard inside the refuge. After three minutes of habituation (Carazo *et al.,* 2014), we uncovered the opening of the refuge by gently pulling a string tied to the cloth covering the refuge. We measured the time for a lizard to poke its head out from the refuge (EXPLORATION START) and the time to move its entire body out (TIME BODY OUT). We obtained VISUAL EXPLORATION time as the difference between these two times. Once the full body of the lizard was outside the refuge, we allowed it to stay within the cage area for 15 min before terminating the experiment. We also measured the time each lizard took to climb to the first perch (TIME FIRST PERCH). Anoles were then individually kept in containers at room temperature until experiments in captivity were conducted.

Experiments in captivity

Exploration and attack simulation (boldness) experiments. Exploration experiments were repeated in captivity 2 days after field experiments. In addition, at the end of the 15 min exploration time, a researcher (OL) slowly approached the cage and gently chased the lizard in the direction of the refuge by using the tip of a noose covered with a red cloth. We then measured the time it took the lizard to come out from the refuge (BOLDNESS). Lizards that did not emerge from the refuge during the exploration trial could not be tested for the attack simulation trial (*n* = 22). To assess the repeatability of behaviors in captivity, we repeated the full exploration and

attack simulation protocols 2 days later for lizards from three populations (one from each habitat type).

Foraging innovation experiment. In the experimental cage, we tested the willingness of lizards to feed in a novel context in captivity. We placed 10 mealworms in a new experimental feeding tray with a wooden base and 2 cm high, transparent Plexiglas® walls. We measured the latency to capture the first mealworm from the feeding tray (FEEDING INNOVATION) using lizards from one population replicate from each habitat type. A table including detailed information on the schedule of all experiments conducted in the study is indicated in S2 in Data S1.

Estimation of within-individual consistency and behavioral syndromes

Individual consistency in behavioral traits was estimated by using intra-class correlation indices (ICC) on log-transformed variables using the package {irr} (Gamer *et al.,* 2012) available in the R platform (R Development Core Team, 2013). Description of behavioral syndromes (i.e., the correlation among different behavioral traits estimated from different observational or experimental approaches) was based on a principal component analysis using a correlation matrix using the 'prcomp' function in R (R Development Core Team, 2013) after scaling the scores of all variables to have unit variance. PCA included escape distance and aggressiveness measured in the field, time to start exploring, time to get entire body out from the refuge (i.e., end exploration) and time to jump on the first perch visited, visual exploration, time exposed on the ground, boldness after the simulation of a predator attack and feeding innovation in captivity. Because this PCA included a single population of each habitat type for foraging behavior, we conducted an alternative PCA not including feeding innovation to increase sample size. This PCA provided virtually the same results (S3 in Data S1).

Daily patterns of activity

Visual encounter surveys (VES) were conducted to measure lizard activity and habitat use throughout the day. A VES was conducted in each half-hour time block from 0630 to 2030 for a total of 28 surveys in each of the six populations in June 2015. In each of these 168 surveys, the same observer (ZC) walked the same section of a habitat at a constant pace and used a stopwatch to standardize effective observation time to 10 min. During the surveys, we recorded the number, species, age category, and sex of lizards as well as their perch height and diameter. *Anolis sagrei* represented 95% of the observations across all populations (S4 in Data S1). No *L. carinatus* or any other terrestrial predators were observed during surveys at urban sites without predators or at forest sites. From the total number of observed lizards, we used the number of lizards on the ground as a surrogate of foraging activity.

Risk-taking assays in free-ranging lizards

To further assess the ecological relevance of the behaviors measured in captivity, we conducted an experiment in free-ranging *A. sagrei* that encompasses several components of risk-taking behavior (namely visual exploration, boldness to descend to the ground, and food innovation). We based our experiment on the fact that *A. sagrei* spend most of their time perched on vegetation while scanning the ground for potential prey, primarily arthropods (Stamps, 1977; Losos, 2009; Drakeley *et al.*, 2015). They tend to abandon this posture when fed to satiation (Stamps, 1977; Drakeley *et al.*, 2015). We tested the willingness of free-ranging lizards to feed from new resources by presenting a live mealworm on the ground at a distance of ~1 m from an *A. sagrei* perched in survey posture. We measured lizards' latency to descend to the ground and capture the mealworm (LATENCY TO FEED) as well as the time spent on the ground after first biting the prey (TIME ON GROUND). We conducted experimental trials at three different times

blocks: early morning (within two hours after dawn), midday-afternoon (1230–1600 h), and evening (within two hours before dusk). At least 30 trials were conducted during each time period at each of the four urban sites ($n = 384$ assays), and we noted whether a *L. carinatus* was present within 10 m of the focal lizard. The absence of *L. carinatus* in forest habitats in Florida prevented comparisons of predator effects in this habitat type.

Statistical analyses

Experimental differences among populations were tested using ANOVA and Tukey's honestly significant difference (HSD) *post hoc* tests when data were normally distributed. We used {survival} R package (Therneau & Lumley, 2015) to analyze right censored data obtained from experiments in which a maximum time limit was set. The Kaplan–Meier nonparametric method allowed us to estimate the survival function
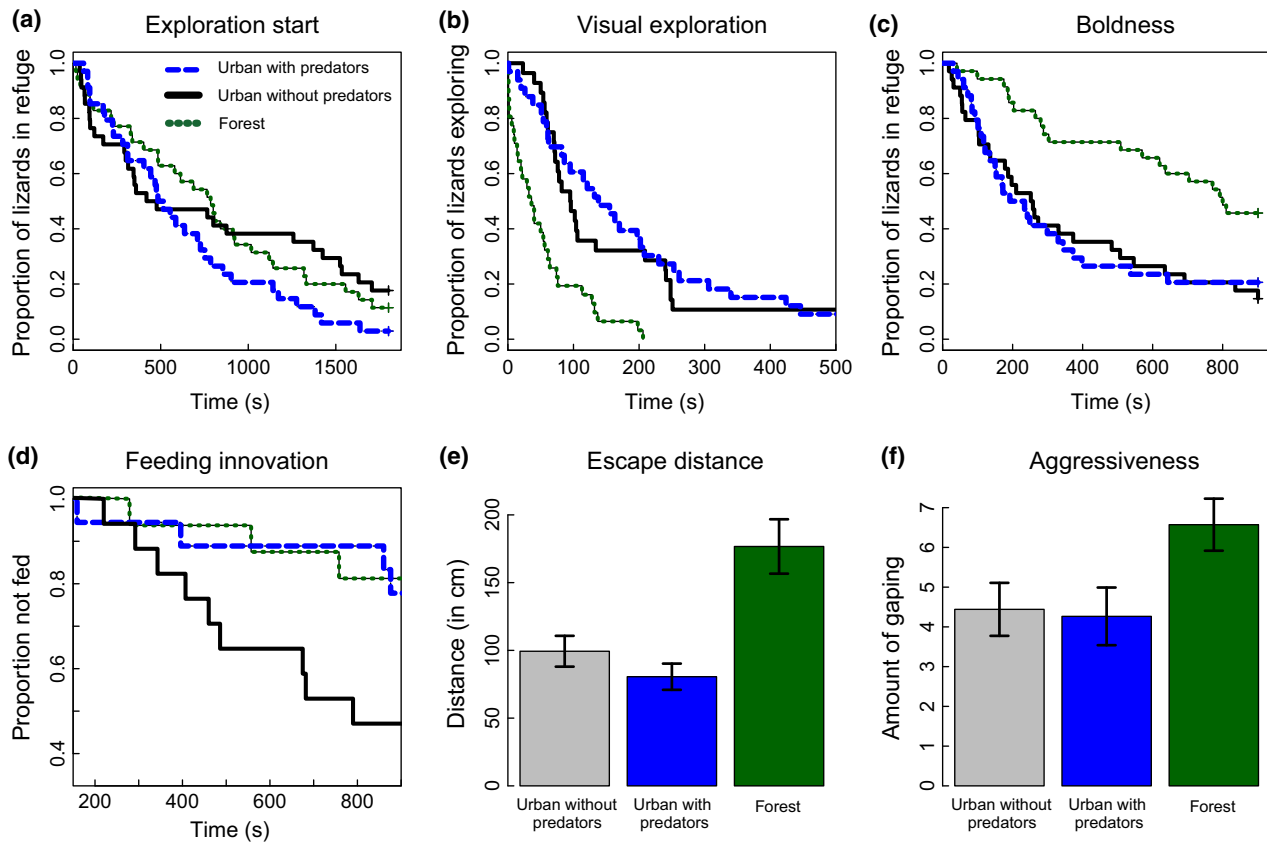
Fig. 1 Mean differences in behavioral traits measured for *Anolis sagrei* from three habitat types: forest, urban without predators, and urban with predators. Results from habitat type replicates are pooled together for simplification. (a) *A. sagrei* started exploring from inside the refuge at similar times in all populations (Log-rank test: $\chi^2 = 3.7$, 2 df, $P = 0.16$). (b) Urban lizards (with and without predators) spent more time exploring visually before emerging into the novel environment compared to forest lizards (Log-rank test: $\chi^2 = 29.8$, 2 df, $P < 0.0001$). (c) Forest lizards took more time to emerge from their refuge after a simulated predator attack in captivity (Log-rank test: $\chi^2 = 13.3$, 2 df, $P = 0.001$). (d) *A. sagrei* from urban sites lacking predators had a higher tendency to exploit a new foraging resource than both *A. sagrei* from urban areas with predators present and forest-dwelling individuals (Log-rank test: $\chi^2 = 6.2$, 2 df, $P = 0.04$). (e) Lizards from urban habitats had shorter escape distances than forest-dwelling lizards ($F = 12.3$, 2 df, $P < 0.0001$) and (f) were less aggressive when captured ($F = 3.8$, 2 df, $P = 0.03$).

and build survival curves for each condition (e.g., habitat type or time blocks). We tested the significance of different survival curves by using the G-rho family rank test for censored survival data (Harrington & Fleming, 1982). We investigated whether body size or morphology (SVL, body mass, and body condition) played a role in determining behaviors of *A. sagrei* (see S5 in Data S1). Finally, two-sample nonparametric Kolmogorov–Smirnov tests were used to evaluate whether the patterns of activity of lizards on the ground differed throughout the day among habitat types.

Results

Risk-taking behavior is associated with urbanization and predation in A. sagrei

Urban and forest-dwelling *A. sagrei* showed different behavioral types when assessing escape behavior, exploration, and boldness after an attack simulation (see legend of Fig. 1 for statistical details). Although lizards started exploring from inside the refuge at similar times in all populations (Fig. 1a), urban lizards spent more time exploring visually before emerging into the novel environment compared to forest lizards (Fig. 1b). Forest lizards took more time to emerge from their refuge after a simulated predator attack in captivity (Fig. 1c). Finally, lizards from urban habitats had shorter escape distances compared to forest-dwelling lizards (Fig. 1e) and were less aggressive when captured (Fig. 1f). Effect sizes are shown in S6 in Data S1. Significant differences in behavior were not associated with morphological

Table 1 PCA loadings for each behavioral trait built from a correlation matrix (see Methods). The first four axes are shown

	PC1	PC2	PC3	PC4
Escape distance	−0.1978	−0.4090	−0.4266	−0.1637
Aggressiveness	−0.1769	−0.2832	0.3879	−0.5586
Start exploration	−0.5518	0.1705	−0.1296	−0.1932
End exploration	−0.5021	0.2781	−0.0786	−0.1144
Visual exploration	0.0345	0.5941	0.1407	0.2720
Exposed time	−0.0712	−0.2007	0.7608	0.1553
First perch	−0.4792	0.2547	0.1708	−0.0098
Boldness	−0.3271	−0.3574	0.0636	0.3974
Feeding innovation	−0.2696	−0.2456	−0.1129	0.5954
Importance of components				
Standard deviation	1.815	1.3177	1.1127	0.92046
Proportion of variance	0.366	0.1929	0.1376	0.09414
Cumulative proportion	0.366	0.559	0.6965	0.79066

differences among populations from different habitat types (Table in S5 in Data S1).

Risk-taking behavior differed between individuals living under different predation regimes. Specifically, *A. sagrei* from urban sites lacking *L. carinatus* had a higher tendency to exploit a new foraging resource compared to both *A. sagrei* from urban areas with *L. carinatus* present and forest-dwelling individuals (Fig. 1d).

Suites of correlated risk-taking behaviors in A. sagrei: behavioral syndromes
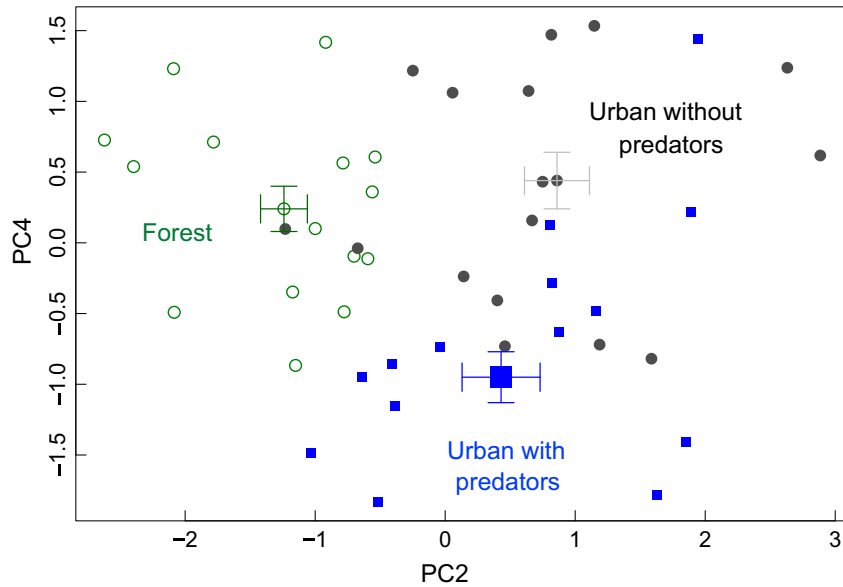
Behavioral syndromes are relevant because they imply that multiple behavioral traits exert a combined effect on the fitness of an animal, increasing the relevance of individual variation in behavior under divergent selective regimes. We conducted a PCA to obtain a more integrative comparison of risk-taking behavior among habitats and predator regimes. Results confirmed that several independent risk-taking behaviors constitute a behavioral syndrome (Table 1), and lizards living under these different selective regimes showed different behavioral types. Specifically, we found significant differences in PC2 scores between forest-dwelling lizards and both types of urban populations ($F = 16.71$; $P < 0.001$). Differences in PC2 show that urban lizards had shorter escape distances, were less aggressive, and spent more time visually exploring new environments as compared to forest-dwelling lizards (Table 1; Fig. 2). PC4 showed that lizards living in absence of the predator *L. carinatus* had higher food innovation tendencies ($F = 10.86$; $P < 0.001$; Fig. 2). Altogether, these results show that behavioral types differ in nearby populations diverging in urbanization and the presence of an invasive predator. A PCA excluding food innovation conducted to increase the sample size provided very similar axes of variation (see details in S3 in Data S1). Importantly, risk-taking behaviors of *A. sagrei* individuals were consistent over time (i.e., on experimental days 1, 3, and 5) and in different contexts (i.e., in semi-natural conditions in the field and in captive laboratory conditions; Table 2).

Daily activity patterns in populations with different behavioral types

After showing that urbanization and invasion by a novel predator are associated with differences in how *A. sagrei* deal with novel environmental uncertainties and exploitation of new resources, we assessed a third behavioral response important for responding to global change: modifications in activity patterns to minimize risks (Tuomainen & Candolin, 2011; Sih *et al.*, 2012; Sol

Fig. 2 PCA of behavioral traits measured in free-ranging lizards as well as during experiments in captivity. PC2 and PC4 separate the three populations and account for 19% and 9% of variation, respectively. Mean PCA scores +/- 1SE are shown for each population.

Table 2 Intra-class correlation coefficient scores describing the within-individual repeatability of log-transformed behavioral traits at different times and in different contexts

Behavioral trait	N assays	ICC score	P-value	Populations
Start exploration	3	0.359	<0.001	3
End exploration	3	0.297	<0.001	3
First perch	3	0.293	<0.001	3
Visual exploration	2	0.198	0.051	6
Exposed time	2	0.282	0.010	6
Boldness	2	0.350	0.040	3
Time to hide	2	0.308	0.029	3
Spatial exploration	2	0.470	0.002	3

'N assays' refers to the number of experimental sessions for which repeatability data were available for this analysis. 'N assays' = 3 means that data are included from assays in the wild (day 1), in captivity (day 3), and a repeated assay in captivity (day 5). 'Populations' is the number of populations available for each comparison. Two additional variables were included here for comparison: time it took lizards to hide in the refuge in two different simulations of attack by the researcher (time to hide) as well as for the number of perches visited by each lizard in 15 min of experimental time (spatial exploration). As it was an innovation experiment, the feeding innovation experiment was conducted only once so there is no repeatability data available for this behavioral trait

et al., 2013). During visual encounter surveys, we observed a total of 5,576 *Anolis* and 425 *L. carinatus* with a mean of 31.4 *A. sagrei* observed per survey (see details in S4 in Data S1). Populations from different habitats showed strikingly different daily patterns of activity (Fig. 3). In particular, *A. sagrei* from urban populations with predators were almost exclusively active on the ground right after dawn and before dusk. These activity patterns significantly differed from those found in populations from the forest ($D = 0.385$; $P < 0.0001$) and urban populations without predators ($D = 0.317$; $P < 0.0001$), which lacked this midday reduction in activity. In addition, the activity patterns of *A. sagrei* and *L. carinatus* in both urban sites with predators showed a strong negative correlation (Fig. 3c; Pearson's coefficient $r = -0.68$, $P < 0.001$ and $r = -0.43$, $P = 0.02$). These results strongly suggest that *A. sagrei* modified their daily activity patterns in response to the presence of *L. carinatus*, which are only active during midday in these populations (Fig. 3c).

Ecological consequences of behavioral types under different predation regimes

To assess whether different behavioral types and patterns of activity are mechanistically associated with ecologically relevant aspects of the biology of free-ranging *A. sagrei*, we conducted an integrative risk-taking experiment in the field. Consistent with results from experiments conducted in captivity (Fig. 1d), free-ranging *A. sagrei* from populations with predators had a lower tendency to exploit new food resources as compared with individuals from populations without *L. carinatus* (Fig. 4a). Importantly, this difference between habitat types was exclusively detected during the midday-afternoon period ($\chi^2 = 5.0$, $P = 0.02$; Fig. 4),
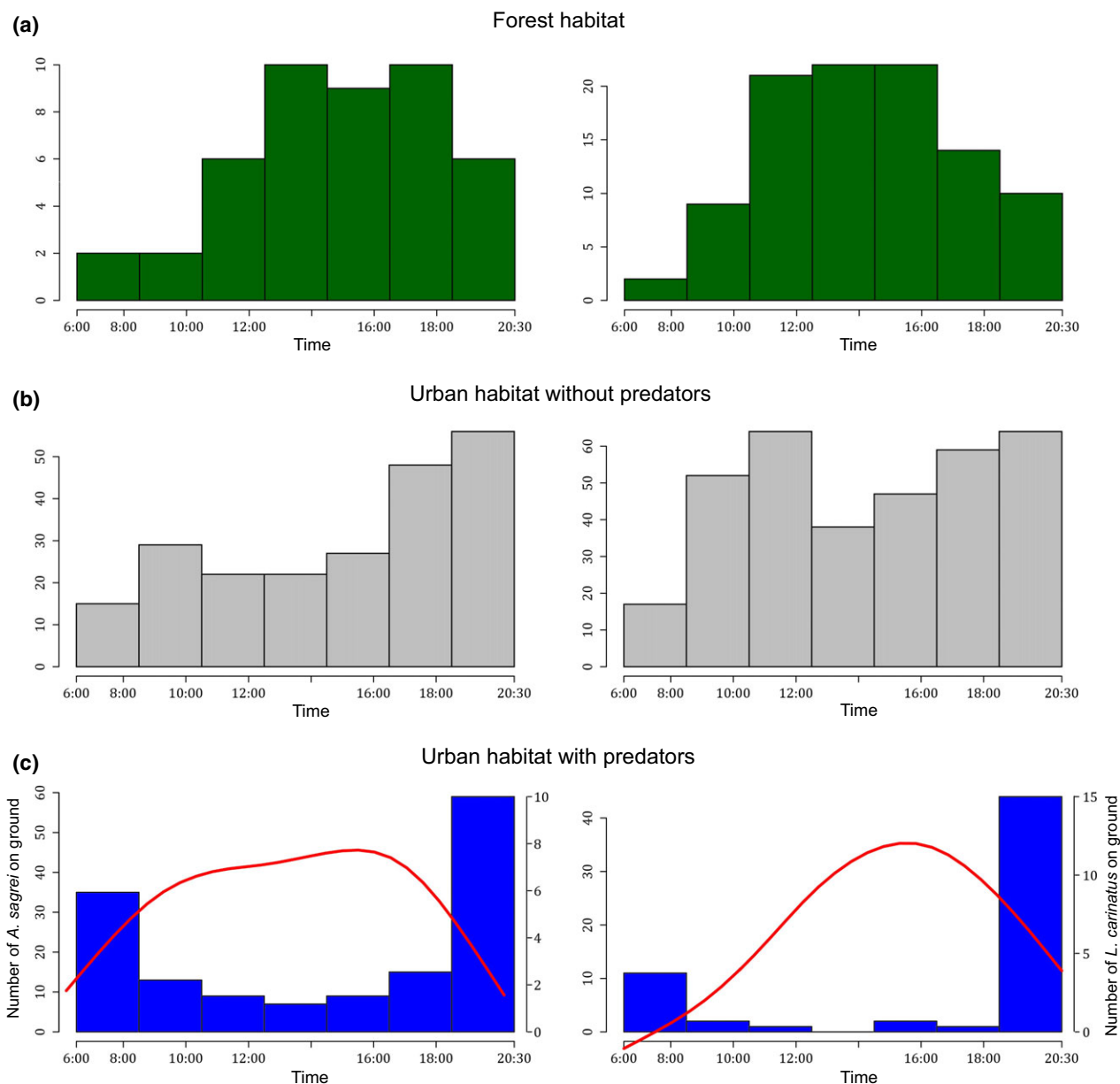
Fig. 3 Daily patterns of activity for *Anolis sagrei* at each study site obtained from observations conducted during visual encounter surveys. Histograms show the number of *A. sagrei* on the ground pooled into one-hour time blocks in (a) two urban habitats without *Leiocephalus carinatus* present, (b) two urban sites where *L. carinatus* was present, and (c) two forest sites. *Y*-axis scales differ between habitat types to facilitate visualization. In (b), we include an overlaid representation of the number of *L. carinatus* observed in these two urban sites with scale represented in the right axis. Note *y*-axis scales differ for the two species to facilitate visualization of the patterns. The foraging patterns of activity of lizards from urban populations with the predator *L. carinatus* differed from those of both urban populations without predators and forest populations ($D = 0.317$; $P < 0.0001$ and $D = 0.385$; $P < 0.0001$, respectively). Urban populations without *L. carinatus* also differed from forest populations, although differences between these distributions were not as striking ($D = 0.147$; $P = 0.014$). Finally, in populations with predators, there was a strong negative correlation between the patterns of activity of *A. sagrei* and *L. carinatus* (Pearson's coefficient $r = -0.68$, $P < 0.001$ and $r = -0.43$, $P = 0.02$, respectively).

which is the period of high *L. carinatus* activity. We found no significant differences during the other two time periods (morning: $\chi^2 = 2.6$, $P = 0.10$; evening: $\chi^2 = 0.6$, $P = 0.44$). In addition, lizards from

populations with predators spent much less time on the ground (where they are more vulnerable to predation) after capturing the prey item. Again, this was only significant in the period of high *L. carinatus* activity

(a) Latency to feed
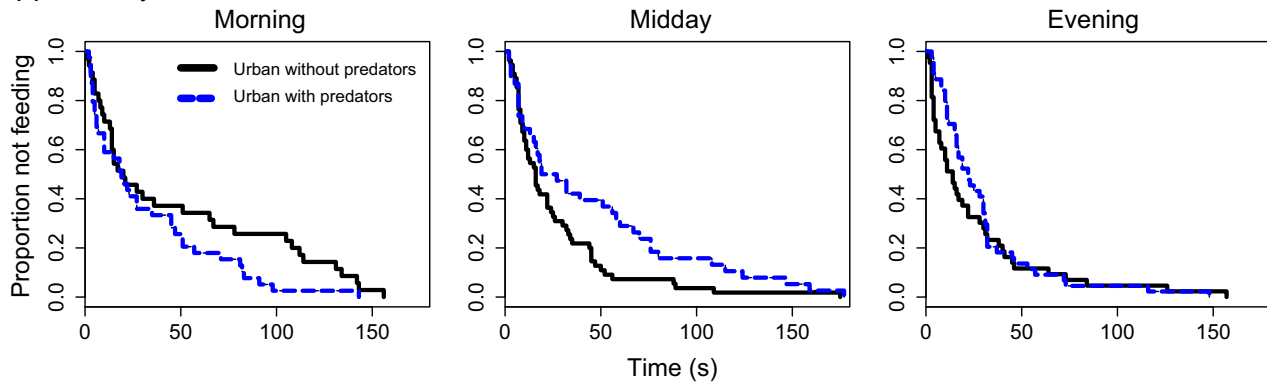
(b) Time on ground
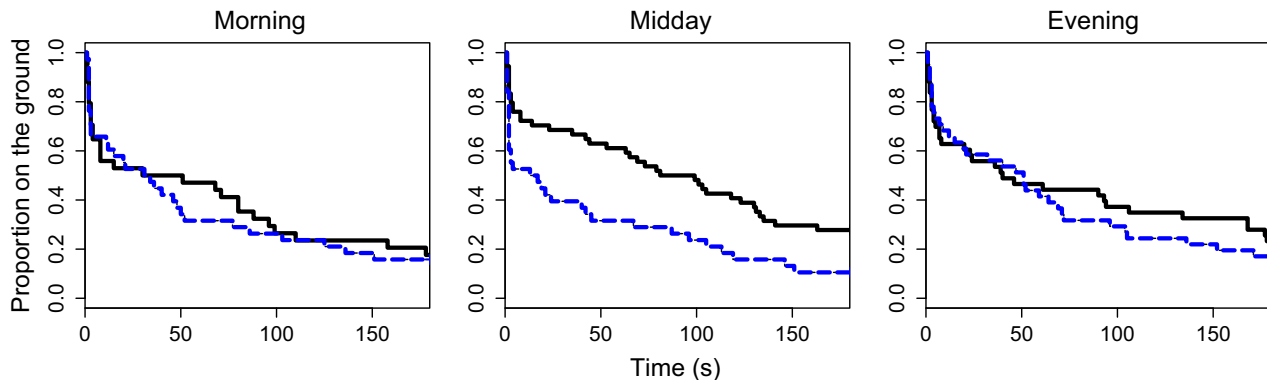
Fig. 4 Survival curves comparing urban populations with (blue) or without predators (black) in the time to capture an experimental prey item (top) and time on the ground after capturing the prey (bottom). Results are shown for three experimental time blocks (morning, middy-afternoon, and evening).

(morning: $\chi^2 = 0.1$, $P = 0.73$; midday-afternoon: $\chi^2 = 7.8$, $P < 0.01$; evening: $\chi^2 = 0.3$, $P = 0.57$; Fig. 4b).

Finally, in the habitat with predators, lizards took longer to feed when there was a *L. carinatus* within 10 m (nonparametric Wilcoxon rank test: $W = 370$; $P < 0.001$; S7 in Data S1). There were no differences in feeding time between habitat types after restricting the dataset to trials with no *L. carinatus* within a 10-m radius ($W = 940$, $P = 0.43$). In contrast, lizards spent much less time on the ground in the habitats with predators (Wilcoxon rank test: $W = 939$, $P < 0.01$; Data S3) irrespective of whether *L. carinatus* were within 10 m or not ($W = 426.5$, $P = 0.29$). Overall, our results provide a link between the existence of different behavioral types and ecological differences that allow *A. sagrei* to deal with new selective pressures associated with different components of global change.

Discussion

Although behavior has long been considered crucial for determining the fate of animals in new environments (Baldwin, 1896; Bogert, 1949; Mayr, 1963; Wyles *et al.*, 1983; West-Eberhard, 1989; Duckworth, 2009; Lapiedra *et al.*, 2013), behavioral ecology has been slower than other ecological disciplines to study the consequences of human-induced environmental changes (Caro & Sherman, 2011). There is a lack of empirical evidence for the link between behavioral differences and their ecological implications in studies of global change (Sih *et al.*, 2012). To address this major gap, we adopted a behavioral syndrome approach to study individual variation in the behavior of *A. sagrei* in populations experiencing different components of global change. Our analyses provide the first evidence that urbanization and biological invasion favor the emergence of divergent behavioral types in nearby populations. These behavioral types are consistent across time and contexts and constitute a risk-taking behavioral syndrome. Importantly, we provide a link between the existence of different animal personalities and ecologically relevant dimensions of their niche. These include differences in the way *A. sagrei* obtain

food resources as well as strong modifications of their daily patterns of activity.

Effect of urbanization on the behavior of A. sagrei populations

A common finding in urbanization studies is that urban animals are more tolerant to approaching humans (e.g., Miranda *et al.*, 2013; Samia *et al.*, 2015 and references therein). This finding has frequently led to the conclusion that urban populations are bolder than those inhabiting natural areas. By measuring several independent components of risk-taking behavior, our results challenge the idea that escape distance measurements should be interpreted as a surrogate of a general boldness domain. For instance, although *A. sagrei* indeed had shorter escape distances in urban areas, they also spent more time collecting information before making potentially risky decisions (i.e., visual exploration). This suggests that being cautious favors persistence of lizards in novel, potentially risky, environments such as urban habitats (Marzluff *et al.*, 2001; McKinney, 2006; Sol *et al.*, 2016), whereas this is not necessarily beneficial in more predictable natural forest habitats. In fact, in a foraging context, *Anolis cristatellus* (a species ecologically similar to *A. sagrei*) follow a decision-making process in which they balance the potential costs and benefits of intraspecific competition and predation (Drakeley *et al.*, 2015). Our findings suggest that, by being more tolerant of humans but more cautious when faced with new challenges, urban lizards may be more likely to successfully respond to changes in the environment. This agrees with conclusions drawn from both comparative (Sol *et al.*, 2014) and empirical studies (Miranda *et al.*, 2013; Audet *et al.*, 2015) comparing rural and urban birds.

Effect of the presence of an invasive predator on the behavior of A. sagrei

Our findings suggest that different behavioral types are associated with relevant ecological differences in free-ranging *A. sagrei* living under different predation regimes. Several lines of evidence not only support that behavioral differences are the consequence of predation risk, but also that these differences facilitate persistence of *A. sagrei* in these populations. First, in a foraging innovation test conducted in captivity, we showed that urban lizards that share their habitat with *L. carinatus* were intrinsically less willing to take the risks associated with exploiting a new food resource. However, these results were based on a small sample size. Therefore, we secondly designed a field experiment to obtain more integrative evidence of the association of population-level behavioral

types with relevant ecological differences in free-ranging *A. sagrei*. Results were consistent with those obtained in captivity. As predicted, *A. sagrei* from populations with *L. carinatus* showed a reduced foraging response and spent less time on the ground after capturing a prey item, showing that invasive predators can rapidly modify population-level behavioral patterns of their prey (Holway & Suarez, 1999; Sih *et al.*, 2011; Tuomainen & Candolin, 2011; Sol *et al.*, 2013). Third, *A. sagrei* were almost exclusively found on the ground in the early morning and evening at sites with predators. This pattern was strikingly different from urban populations without this predator. Further evidence that predation leads to changes in the daily activity pattern of *A. sagrei* derives from the strong negative correlation in the abundance of both species on the ground. Finally, previous studies have reported how *A. sagrei* change their habitat use in response to the presence of *L. carinatus*. Specifically, *A. sagrei* has been shown to move higher in the vegetation when *L. carinatus* is present (Schoener *et al.*, 2002; Losos *et al.*, 2004, 2006; López-Darias *et al.*, 2012). Indeed, increased antipredatory behavior has costs (Lima & Bednekoff, 1999) and should therefore only be justified by an increase in predation pressures (Brock *et al.*, 2014). Although direct consumption of *A. sagrei* by *L. carinatus* has been shown (Schoener *et al.*, 1982), non-consumptive effects (Preisser *et al.*, 2005) are also compatible with our results. We predict that, by being more cautious, lizards minimize predation risk in sites where predation pressures are higher.

Behavioral syndromes and behavioral types in A. sagrei

Consistent inter-individual variation is crucial to studies of adaptation in behavioral traits because this variation is the raw material by which natural selection can favor some behavioral types over others. *Anolis* lizards are one of the most well-studied model systems in ecology and evolution (Losos, 2009). To our knowledge, however, evidence for consistency in their behaviors at different times and in different contexts (i.e., 'animal personalities') had not been reported previously. In addition, we validated the rarely tested assumption that behaviors measured in captivity correlate with behavior in the wild, an assumption that is not necessarily true (see Fisher *et al.*, 2015). Furthermore, our results provided the first evidence of behavioral syndromes – defined here as the correlation among suites of different behavioral dimensions – in *A. sagrei*. For instance, lizards that more readily escaped from approaching humans in the wild took more time to start exploring a novel experimental setting and had a lower tendency to emerge from their refuges after the simulation of a predator attack. Behavioral syndromes play a relevant role in the

maintenance of individual behavioral variation (Sih *et al.*, 2004), which can promote fitness differences among individuals under different ecological scenarios. To explicitly investigate whether the existence of different behavioral patterns is the consequence of evolutionary change, future studies will need to address whether these components of behavior are heritable. Indeed, heritable variation in behavioral traits has been shown in captive breeding studies (see Table 5 in Réale *et al.*, 2007 for a summary) including those specifically designed to test for the heritability of risk-taking behaviors in *Parus major* and *Turdus merula* (van Oers *et al.*, 2004; Miranda *et al.*, 2013). In a recent meta-analysis from published literature, Dochtermann *et al.* (2015) showed that 52% of personality variation found in published studies could be attributed to additive genetic variation. The repeatability scores found in our study (Table 2), which set an upper limit for heritability, fall well within the range of those found in studies in other vertebrate species (Réale *et al.*, 2007). By providing evidence for repeatability of behavioral types and their association with ecological patterns, our results suggest that risk-taking behavior could be a relevant target of natural selection in a rapidly changing planet.

Implications for ecology, evolution, and conservation

Our ability to test whether natural selection acts on behavioral traits in the context of human-induced environmental changes has been limited by the lack of empirical studies showing the ecological consequences of these behaviors (Smith & Blumstein, 2007; Sih *et al.*, 2012). Our results show that different components of global change – urbanization and biological invasions – are favoring different behaviors in nearby populations. This paves the way to study natural selection on behavior in a global change context. For instance, the behavioral patterns described suggest that anoles spending more time on the ground or feeding in the middle of the day are more exposed to *L. carinatus* predation attempts. The hypothesis that differences in risk-taking behaviors are an adaptive response to new environments is supported by previous ecological information in this study system. Indeed, in field experiments on small islands in the Bahamas, the presence of *L. carinatus* forced *A. sagrei* to climb higher on perches to avoid predation, generating new selective pressures associated with limb morphology (Losos *et al.*, 2004, 2006). Finally, behavioral differences could have important implications for conservation biology because they can determine the success of animals intentionally (Bremner-Harrison *et al.*, 2004) or unintentionally (Chapple *et al.*, 2012) introduced into new environments.

The existence of locally divergent behavioral types is relevant because it entails differences in the way animals interact with their environment. Consequently, individuals with different behaviors could have different ecological roles in the ecosystem, facilitating the adjustment of eco-evolutionary dynamics to prevailing human-induced environmental conditions (Bolnick *et al.*, 2011; Alberti, 2014). As global change shuffles combinations of different species together into novel ecological communities, animals will frequently encounter novel competition and predation regimes that can drive changes in how they exploit resources. Because selective forces can significantly differ even over small spatial scales (Richardson *et al.*, 2014), we suggest that the combined action of different components of global change holds the potential to promote adaptive behavioral divergence, generating a mosaic of behavioral phenotypes in nearby populations. Therefore, we underscore that incorporating animal personalities can provide great insight into our understanding of the ecological and evolutionary consequences of global change.

Author contributions

OL conceived and designed the study, designed the experiments, carried out fieldwork, carried out data analysis, and wrote the manuscript; ZC carried out fieldwork, contributed to the experimental design, and contributed to writing the manuscript. JJK conceived and coordinated the study, contributed to statistical analyses, and wrote the manuscript. All authors gave final approval for publication.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. S1. Extended version of Methods section; S2. Timing of the experiments conducted in each of the studied populations; S3. PCA excluding data from feeding innovation experiment to increase sample size; S4. Table describing observations from the VES; S5. Body size, body condition, and behavioral traits; S6. Effect sizes; S7. Effects of the presence of *L. carinatus* on foraging behavior of *A. sagrei.*
Data S2. Database of results from the behavioral experiments
Data S3. Database of the risk-taking behavioral assays conducted in free-ranging lizards