

SHORT NOTES

From forest to city: urbanization modulates relative abundance of anti-predator coloration

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Submitted: 5 February 2019; Received (in revised form): 17 July 2019. Accepted: 4 September 2019

Abstract

Increased urbanization has resulted in community changes including alteration of predator communities. Little is known, however, about how such changes affect morphological anti-predator traits. Given the importance of coloration in predator avoidance, this trait in particular is expected to be susceptible to novel selective environments in urban areas. Here, we investigate the coloration pattern of a Neotropical anuran species, the túngara frog (*Engystomops pustulosus*), along an urbanization gradient. Túngara frogs have two distinct color patterns (unstriped and striped) which we found to occur at different frequencies along an urbanization gradient. Striped individuals increased in frequency with urbanization. To assess the strength of selection imposed by predators on the two color morphs, we deployed clay models of túngara frogs in forest and semi-urban populations. In addition, we examined microhabitat selection by individuals of the different morphs. We found higher predation rates associated with urbanization than forested areas. In particular, frogs from forested habitats had lower number of attacks by avian predators. Contrary to our predictions, however, predation rates were similar for both color morphs independent of urbanization. Also, coloration of the frogs did not affect their microhabitat preference. Overall, túngara frogs are more likely to have a striped coloration pattern in semi-urban areas where predation by birds is higher than in the forest. Our findings suggest that factors other than predation pressure shape the coloration pattern of urban frogs and emphasize the complex nature of effects that anthropogenic changes in habitat and predator communities may have on prey morphology.

Key words: polymorphism, predation, mesopredators, *Physalaemus pustulosus*, urban ecology

Introduction

Understanding community assemblage and dynamics has long been of interest to ecologists. This interest, however, has increased due to recent trends in rapid urbanization around the globe. Urbanization is a complex phenomenon, especially when considering its role in altering and maintaining predator–prey interactions across the heterogeneous and dynamic landscapes within and surrounding a city (Grimm et al. 2008). Indeed, studies investigating these effects have revealed contradictory and unexpected results since predator abundance and predation pressure do not necessarily increase together in urban areas

(Fischer et al. 2012). While some urban habitats have increased predator abundance along with an expected increase in predation pressure (Sorace 2002; Prange et al. 2003; Shochat et al. 2004; Jokimäki et al. 2005), other urban habitats have lower predation pressure despite also having increased predator abundance (Warren et al. 2006; Rodewald and Kearns 2011). Low predation pressure in urban areas often results in higher prey survival and can thus decouple trophic interactions. Even though we lack clarity about the consequences of increased abundance of predators, there is consensus that urbanization decreases the diversity of both predators and prey, often

increasing the representation of foraging generalists rather than specialists (McKinney 2006; Sorace and Gustin 2009). Generalist foragers are possibly better suited for urban impacted habitats due to the lower diversity of prey species and/or the increase in anthropogenic subsidized food resources (e.g. trash, crops, bird feeders etc.) (Rodewald and Kearns 2011). Despite such drastic effects in urban predator communities and an increased interest in understanding how species thrive in altered environments (Shannon et al. 2014; Rebolo-Ifrán et al. 2017), relatively little is known about how changes in predator assemblage and abundance affect morphological traits of prey species that are able to persist in urban areas.

Novel predator communities are likely to result in changes in anti-predatory strategies in urban prey. Indeed, it is common for prey in urban environments to exhibit particular behavioral responses, such as altered reproductive and foraging strategies, to cope with altered predation pressure (e.g. Lowry et al. 2013). Similarly, given that the selective advantage conferred by cryptic coloration varies depending on the background (Cott 1940; Endler 1984) and the assemblage of visual predators at a given location (Endler 1980; Stuart-fox et al. 2003; Matthews et al. 2018), the unique, altered predatory communities and backgrounds in urban environments are likely to impose novel selective pressures on coloration morphs (Bateman et al. 2017). The specific outcome, however, is expected to depend on whether predation pressure is ultimately amplified or relaxed at a given urban area. If predation pressure is amplified in urban environments, for instance, we expect selection for color morphs that are more cryptic in the microhabitats they occupy in the city. In contrast, if predation pressure is relaxed, genetic drift, constraints and selection in other contexts could be major drivers of coloration pattern. Little is known, however, about how morphological anti-predator traits respond to urban predatory communities. In this study, we investigate whether individuals across an urbanization gradient differ in coloration pattern, a morphological trait critical for predator avoidance (Ruxton et al. 2018).

We investigated frequency of color morphs in a cryptic Neotropical frog across an urbanization gradient. Specifically, we examined color morphs of the túngara frog (*Engystomops pustulosus*) along the Panama Canal to understand the potential role of predators at modulating frequency of color patterns in urban and forest environments. We aimed to assess abundance and microhabitat preference of the two color morphs in this tropical frog, and investigated changes in selective pressure imposed on the morphs by predators associated with urbanization. We expected differences in frequency of the color morphs from the forest to urban populations due to differential selection from predators. We also predicted that individuals from different color morphs would prefer microhabitats that increase their crypticity. Finally, following previous studies (Sorace 2002; Jokimäki et al. 2005), we predicted higher predation rates in urban areas. Our results contribute to our knowledge of the ecological effects of urbanization providing insights about this phenomenon in tropical communities, a region that has received limited attention relative to this topic.

Methods

Study system

The Panama Canal watershed is home to 93 amphibian species, 21 of which occur both in urban and forest habitats (Condit et al. 2001). Among these species, túngara frogs inhabit areas with diverse anthropogenic influences (McMahon et al. 2017).

Túngara frogs have two distinct coloration morphs that are not associated with sex: (i) 'unstriped', in which individuals are primarily one tone of brown with slight mottled patterning of various shades of brown layered on the dorsal side, and (ii) 'striped', in which individuals have light brown and black dorsolateral stripes (Fig. 1a). To determine color morph frequency, we sampled túngara frogs at 14 breeding sites in 3 populations representing different habitats: 3 urban sites (Panama City; 30.1599°N, -85.6604°E), 9 semi-urban sites (Gamboa, 9.1165°N, -79.7012°E) and 2 mature rainforest sites (Parque Nacional Soberania; 8.984°N, -79.5258°E). At each breeding site, we scored the morph type of all individual túngara frogs including calling males, females at the chorus and couples in amplexus. We sampled each site two times on different nights.

Predation experiment

To investigate the selective pressure imposed by predators on both coloration morphs, we used clay models of unstriped and striped morphs of túngara frogs. We deployed standard, non-hardening clay (Staedtler plastilin) models of the frogs to record predatory attack marks following widely used, established methods (Noonan and Comeault 2009; Shochat et al. 2010; Chouteau and Angers 2011; McElroy 2015; Casas-Cardona et al. 2018; Salvidio et al. 2019).

In total, 960 clay models were placed along 20 transects, 10 in a semi-urban area and 10 in the forest. Due to safety concerns, no models were deployed in the city. Transects were each 60 m long, with one station every 5 m, for a total of 12 stations per transect. At each station, models of each morph were placed side by side and pinned down with toothpicks on either soil or leaf litter (Fig. 1b), two naturally occurring backgrounds in which túngara frogs are commonly found. Therefore, per transect we deployed a total of 48 clay model frogs, 24 on each background.

All models were collected after 72 h and inspected for predatory attacks on site following McElroy (2015). Photos were also taken of each model. An attack was defined as any disturbance on the clay model, ranging from a model being bitten (avian: beak, or mammalian: teeth marks), flipped or moved off the substrate. Models with marks that could not be assigned to a particular type of predator were scored as unknown. Missing models and models attacked by ants were not included in the analysis. The sample size of this study is comparable to other studies investigating predation attacks using clay models (Noonan and Comeault 2009; Chouteau and Angers 2011; McElroy 2015; Casas-Cardona et al. 2018). In particular, the similarity in sample sizes between this study and another frog model predation experiment in Panama (McElroy 2015) suggests our sample size was appropriate to detect biologically relevant responses by predators in this community.

Color measurement and visual modelling

Reflectance spectra of clay models and wild-caught frogs from both morphs projected on an avian vision model (Maia et al. 2013a,b; McElroy 2015) confirmed high degree of similarity among frogs and models. We used a photospectrometer (StellarNet, Inc. Black Comet Spectrometer) to measure reflectance spectra from five unstriped and five striped frogs along with one of each clay model morph (Fig. 2). Neither the frogs nor the models reflect in the UV range so we focused on estimates in the visual range (300–700 nm). To examine the similarity of the frogs and the clay models we used, we projected the reflectance spectra of both frogs and models into an avian

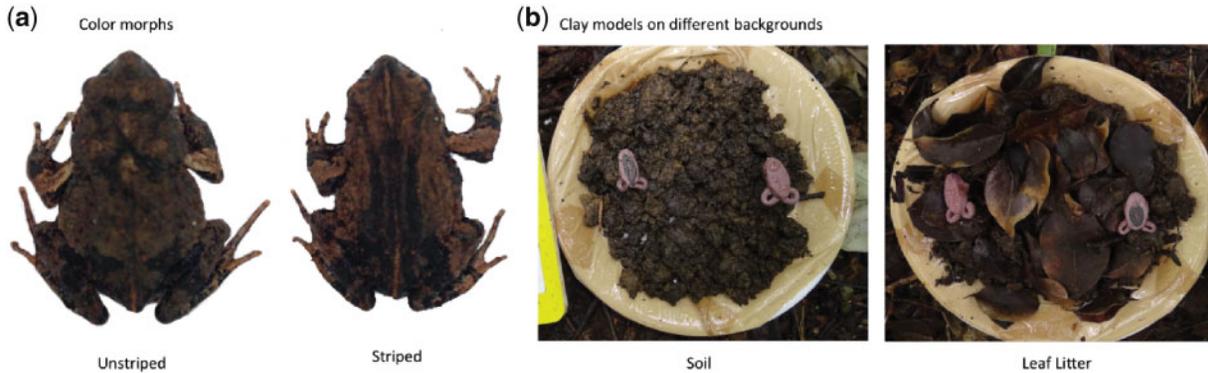


Figure 1: Coloration morphs in túngara frogs in live individuals (a) and as presented using clay models on different backgrounds (b).

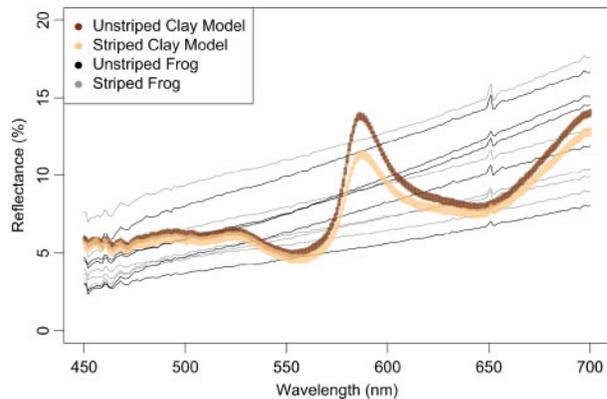


Figure 2: Reflectance values of both morphs of clay models and wild-caught túngara frogs. Average reflectance spectra of unstriped and striped clay models are shown in bold and colored lines (\pm SE). For wild-caught individuals, reflectance values for each individual are presented for unstriped (black lines, $n=5$) and striped (gray lines, $n=5$) frogs.

visual model. We used the blue tit model of avian vision in the R package ‘pavo’ (Maia et al. 2013b), which has been successfully used to assess the degree of variation between anurans and clay models (McElroy 2015). We projected the reflectance into avian UV tetrahedral color space to visualize the degree of variation between our clay models and wild caught frogs (Maia et al. 2013a,b; Fig. 3).

We calculated achromatic color contrasts to determine if the wild-caught frogs and our clay models were perceived differently from one another. We calculated ‘just-noticeable-differences’ (JNDs) and followed standard criteria in which a value of 1 or less is considered indistinguishable while comparisons become more distinguishable as JND values increase past 1 (Siddiqi et al. 2004; Stoddard et al. 2011; McElroy 2015). We found that individual frogs were easily distinguishable among (average \pm SD: Unstriped = 3.30 ± 2.16 ; Striped = 3.43 ± 2.09) and between (3.15 ± 2.04) color morphs. Similarly, frogs and our clay models were distinguishable (2.17 ± 1.43). Our clay models, however, were more similar to each other than the average values for all other comparisons (JND = 1.09). Overall, JND values were highly variable among individual frogs of both color morphs (CV = 64.6%) and between frogs and our clay models (CV = 65.8%).

Microhabitat preference experiment

An experimental circular arena (71 cm diameter) was used to test microhabitat preference between striped and unstriped

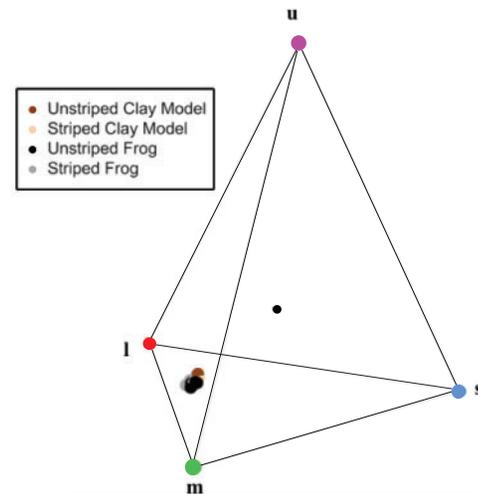


Figure 3: Perception of clay models and wild-caught frogs in the tetrahedral model for avian VS vision. Vertices represent maximal excitation of the ultraviolet (u), blue (s), green (m) and red (l) photoreceptors of avian VS vision. The black point represents equal excitation of each photoreceptor.

individuals. Each side of the arena was illuminated using an ExoTerra 13W Reptile UVB 100 bulb to replicate natural light and eliminate shadows. The bottom of the arena was equally divided into two backgrounds, soil and leaf litter, separated by a white stripe (Fig. 4). Using a temperature gun (Tool Shop CW1250), we confirmed there were no differences in temperature between the two substrates at the beginning of each trial. A trial consisted of 15 min in which we remotely tracked the frog using an AXIS P1343 camera with AXIS Camera Station Client. Initial orientation, first and last substrate chosen as well as time spent on each substrate were documented. Frogs used in trials were from our colony of túngara frogs at Purdue University in which we had both wild caught and lab reared. Wild caught individuals were both striped and unstriped and the laboratory reared individuals were all unstriped. After the trials, all individuals were returned to their corresponding aquariums in the colony.

Statistical analysis

To examine differences in the proportion of striped to unstriped morphs across the urbanization gradient, we performed a Kruskal–Wallis test followed by a post hoc Tukey test. To determine whether morph, habitat or substrate predicted attack

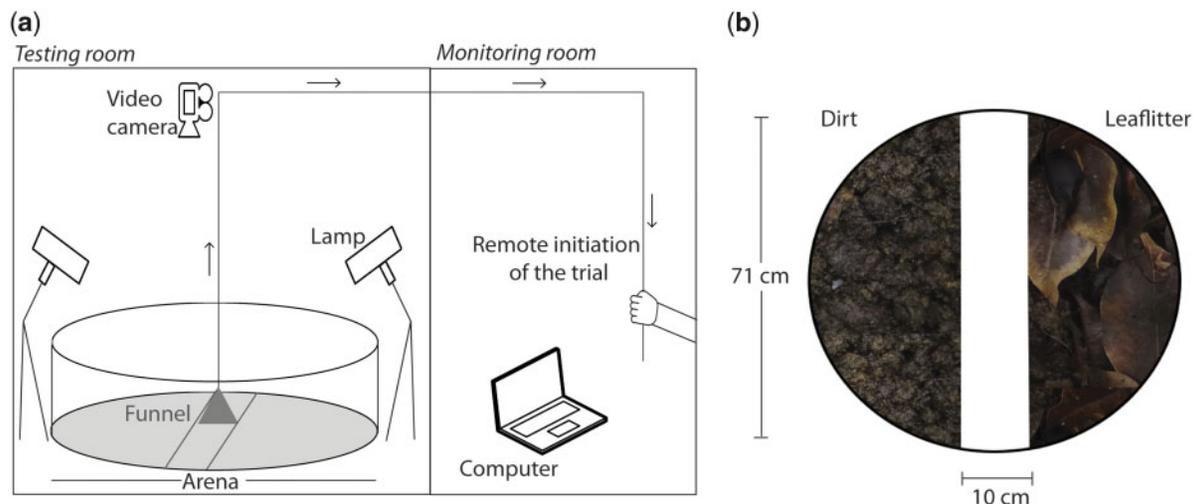


Figure 4: Experimental set-up used in the background choice experiment (a), with a close up view of the arena showing the two backgrounds available to the frogs (b).

rates, we used the *lme4* package (Bates et al. 2014) in R (R Core Team 2018) to perform a generalized linear mixed model (GLMM) using a binomial distribution. We treated morph, habitat, substrate and the interaction between morph and habitat as fixed effects and transect as a random effect. We further evaluated whether predators preferentially attacked models from a given morph by considering only the data in which only one of the two models that were placed next to each other was attacked. We thus ran the same GLMM model described above using the subset of data that excluded attacks on both ‘neighbor’ models.

We were also interested in evaluating potential differences in attack rates between different predators. Given the small sample size when the attacks were divided by the type of predator, however, including this variable resulted in an overfitted model. Therefore, we investigate potential differences in attacks by type of predator (avian vs mammalian) in the forest and semi-urban area performing a χ^2 test using a 2×2 contingency table.

Finally, we examined the behavior of the frogs when presented with the two backgrounds using a two-way ANOVA (Rohlf and Sokal 1995) with morph and initial orientation as factors. To perform the ANOVA, we calculated and arcsine transformed the relative amount of time spent on one background (soil). Two contingency tables were also performed to compare initial and final substrate chosen by both striped and nonstriped frogs.

Results

The proportion of striped to unstriped túngara frogs significantly changes along the urbanization gradient from the forest to the city ($H = 7.600$, $P = 0.022$; Tukey’s test, $P < 0.050$ for all comparisons; Fig. 5a). Striped individuals are more common in the city where they are almost as frequent as unstriped frogs. In the forest, striped frogs are rare, representing $<10\%$ of the individuals. In contrast, striped frogs are more likely to be found at semi-urban sites than in the forest but not as common as in the city.

Out of 960 models deployed, a total of 64 models were attacked (6.7%; 33 unstriped and 31 striped models). There were no significant differences in the number of attacks on different substrates ($z = 0.796$, $P = 0.787$) or between color morphs in different habitats ($z = 0.269$, $P = 0.394$). The overall number of attacks, however, was significantly lower in the forest than in the semi-urban area

(Fig. 5b; $z = 1.787$, $P = 0.037$). In addition, there was a difference in the proportion of attacks by avian and mammalian predators between the forest and semi-urban habitat (Fig. 5c; $\chi^2 = 6.09$; $P = 0.020$). When considering attacks on a single frog model by substrate, there was no preference from the predator to attack models of a given morph more than the other ($z = 0.786$, $P = 0.216$). As in the previous model, habitat was the only significant predictor of which models were attacked ($z = 1.825$, $P = 0.034$). Details of the GLMM estimates are reported in Supplementary Material.

Contrary to our predictions for the microhabitat preference experiment, striped and unstriped frogs were equally likely to choose soil as the first substrate they used ($\chi^2 = 0.01$, $P = 0.92$, effect size = 0.0127). Similarly, both morphs were likely to end trials on soil substrate ($\chi^2 = 3.24$, $P = 0.07$, effect size = 0.229) and individuals of both morphs spend about the same amount of time on each background [two-way ANOVA $F_{(1, 62)} = 0.436$, $P = 0.649$].

Discussion

We found that túngara frog color morphs occur in different frequencies along the urbanization gradient following the Panama Canal. In particular, the striped color morph is more abundant in the city than the forest, with the semi-urban sites having intermediate frequencies. These findings reveal a change in color morph frequency associated with urbanization. Anthropogenic associated changes in coloration were recognized in the Peppered moth (*Biston betularia*) after the industrial revolution (Kettlewell 1959), and this type of human-driven morphological change has received more attention since, specifically in the contemporary context of urbanization (Jones et al. 2010; Récapet et al. 2013; Hutton and McGraw 2016). Our study sheds new light on this topic describing changes in prey color morph frequency associated with urbanization.

It is possible that higher frequency of striped frogs is driven by different predator communities and predation pressure in the city. When we considered the potential role of altered predator communities on color polymorphism in the túngara frog, we found uneven predation pressures between the forest and semi-urban habitat. Our frog models had a higher number of attacks in the semi-urban area than the forest. This increase in attacks is consistent with the high abundance of predators characteristic of urban areas (Sorace 2002; Jokimäki et al. 2005)

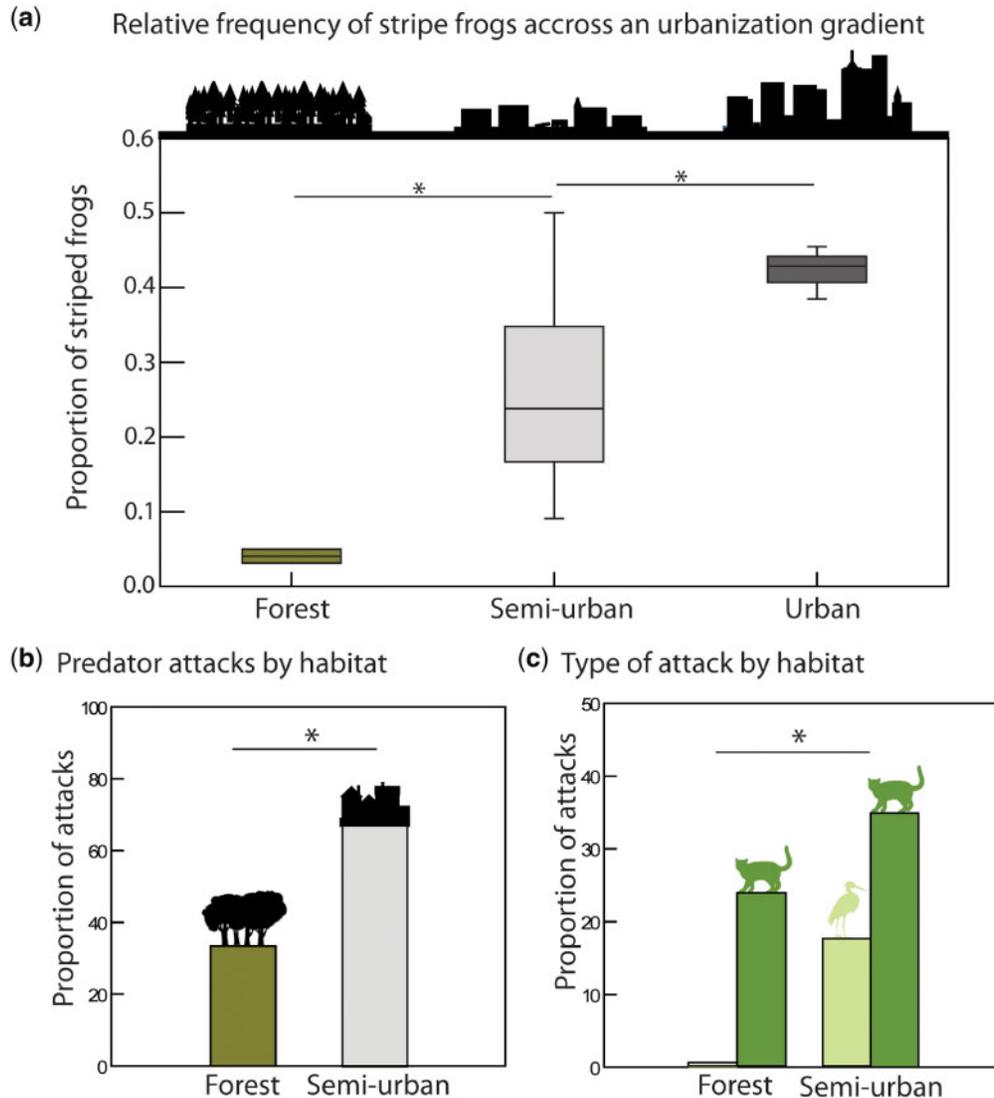


Figure 5: Relative frequency of striped color morph túngara frogs across an urbanization gradient along the Panama Canal (a). The lower panels display the proportion of predator attacks in forested and semi-urban sites (b) and by type of predator attacks (bird=avian; cat=mammalian) across such habitats (c). Asterisks represent statistically significant differences from contingency tables (a, c) or GLMM (b), details in the Methods section.

that sometimes, but not always, results in higher predation pressure (Fischer et al. 2012). Our results also revealed a higher number of attacks by avian predators in the semi-urban habitat compared with the forest, where mammals inflicted all of the attacks. This increase in urban visual predators parallels general trends described for urban wildlife communities (Rodewald et al. 2011). It also adds to the known decrease in nocturnal, acoustically oriented predators at this specific urban area in Panama compared with the surrounding forests (McMahon et al. 2017; Halfwerk et al. 2018). Túngara frogs in the city thus survive and reproduce in areas with more avian predators and less nocturnal predators that eavesdrop on their mating calls compared with their forest counterparts.

Despite an increase in visually oriented predators in semi-urban areas, our findings suggest striped and unstriped túngara frogs are equally likely to be attacked in forest and semi-urban habitat. Higher abundance of avian attacks on semi-urban frogs thus does not explain the higher frequency of the striped coloration pattern. This result is surprising given that coloration affects susceptibility to visually oriented predators (Bond and Kamil

2002), and predation influences the evolution of color patterns (Bond 2007). The similarity in attacks between morphs may be due to the limitations involved with clay models (Bateman et al. 2017; Rößler et al. 2018). This methodology, for instance, only addresses the first stage of the predatory process, prey detection, and it is limited to nonmoving visual cues. Common predators of túngara frogs such as bats, opossums, snakes and spiders depend on a variety of nonvisual cues or movement to attack túngara frogs (Page et al. 2014) and therefore were not among the predators attacking our models. Since there are no known differences in behavior between the morphs, it seems unlikely that these nonvisual predators affect color morph frequency. It is possible, however, that both morphs are equally cryptic in the backgrounds they use in semi-urban habitat during the day, minimizing the potential for predators to impose differential selection. Little is known, however, about the diurnal habits of túngara frogs in nature to evaluate this potential explanation. Finally, the use of clay models also excludes potential differences in escape behavior. While frogs from both morphs seem to use the same escape responses (Bulbert et al. 2015), stripe frogs could enjoy an

additional advantage by reducing the ability of observers to judge the speed and direction of moving prey (Thayer 1909; Stevens et al. 2008; Hämäläinen et al. 2015). Further studies that consider movement of the frogs after detection could provide valuable insights given the potential role of prey's longitudinal stripes on escape success.

Contrary to our predictions, we found no evidence of túngara frogs preferentially choosing to be on a given substrate. While such lack of preferences for particular substrates was surprising given that this phenomenon is common and widespread across taxonomic groups (Kang et al. 2013; Siegenthaler et al. 2018), it is consistent with the similarity in predation rates we observed between the morphs on those backgrounds in the field. We recognize that background preferences by frogs of different color morphs can be complex due to the presence of color-changing individuals and potential differences in habitats used at different color stages (Morey 1990; Wente and Phillips 2005; Brattstrom et al. 2017). Even though in túngara frogs the color morphs are not known to be plastic, little is known about habitat use by the two morphs or potential changes in this behavior or susceptibility to predation during development.

In general, our results suggest that predation is not the main driver behind the differences in abundance of the two color morphs in túngara frogs in forest and semi-urban habitat. Thus there may be other selective pressures in urban habitats driving a higher proportion of striped túngara frogs at those areas. Urban environments present diverse environmental stressors including different types of pollution (chemical, noise and artificial light), infectious disease and diet quality (Isaksson 2015). Urban environments, like Panama City, also present higher temperatures than their surrounding forests (McMahon et al. 2017). Urban environmental stressors and temperature may play a role in influencing proportions of color morphs in polymorphic species, if individuals of different morphs vary in exposure and susceptibility to stressors (e.g. Jacquin et al. 2013) or their thermal physiology (e.g. Matthews et al. 2018). Urban túngara frogs live in areas with few or no eavesdropping frog-biting midges (McMahon et al. 2017; Halfwerk et al. 2018), a vector of anuran trypanosomes (Johnson et al. 1993; Bernal and Pinto 2016). Presence of this vector and blood parasite could disrupt gene-by-environment interactions modulating the relative abundance of the color morphs. Future studies that address parasites as well as other factors that may vary between color morphs like dispersal behavior (Grant and Liebgold 2017) and competitive strategies (Dijkstra et al. 2009) are necessary to better understand relative abundance of color morphs in túngara frogs. In general, closer examination of the specific differences in predator communities between urban, semi-urban and forest habitats following the Panama Canal is necessary to better understand the selective landscape on the color morphs (e.g. Valkonen et al. 2012; Nokelainen et al. 2014).

Overall, we found that túngara frogs are more likely to have a striped coloration pattern in semi-urban areas where predation by birds is higher than in the forest. While increased urbanization trends worldwide result in striking effects such as biodiversity loss (McDonald et al. 2008), more subtle effects of urbanization like the one described here can provide valuable insights into the complex, cascading effects that human-driven changes can have through species interactions. Subtle effects on species which are able to thrive in cities can provide valuable insights about how urbanization-driven ecological changes could lead to evolutionary change (Rivkin et al. 2018). Our study emphasizes the complex nature of effects that urbanization can have on ecological interactions by revealing differences in

urban prey coloration, that are not explained by the altered predator community in this urban area.

Data availability

The data used in this study are archived at the Dryad Digital Repository (doi:10.5061/dryad.m2d1h37).

Supplementary data

Supplementary data are available at JUECOL online.

Acknowledgements

We thank A.J. Vargas, T. Vargas-Bernal and M.E. Mattos for their endless support and encouragement throughout this endeavor. We greatly appreciate the help of E. Rubin, R. Lim and E. Shank who provided valuable support running behavioral trials. P. Baumhardt and D. Pita kindly helped collect reflectance spectra data. G. Kvifte and H. Legett provided valuable comments on early versions of this manuscript. Approval for the use of live animals for the habitat selection experiments was provided by the Animal Care Use Protocol at Purdue University (PACUC #1609001478). Feedback from three anonymous reviewers and J. Chad Johnson helped improve the clarity and strength of the study. M. McElroy kindly provided access to his data from a previous study to calculate the effect size. We are also grateful to the Smithsonian Tropical Research Institute for their logistic support.

Funding

This research was funded by the National Science Foundation (IOS#1433990 to X.E.B).

Conflict of interest statement. None declared.

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