Move it or lose it: interspecific variation in risk response of pond-breeding anurans

Philip Matich Corresp., 1, 2, Christopher M Schalk 3

1 Department of Marine Biology, Texas A&M University - Galveston, Galveston, Texas, United States
2 Texas Research Institute for Environmental Studies, Sam Houston State University, Huntsville, Texas, United States
3 Arthur Temple College of Forestry and Agriculture, Stephen F. Austin State University, Nacogdoches, Texas, United States

Corresponding Author: Philip Matich
Email address: pmatich@tamug.edu

Changes in behavior are often the proximate response of animals to human disturbance, with variability in tolerance levels leading some species to exhibit striking shifts in life history, fitness, and/or survival. Thus, elucidating the effects of disturbance on animal behavior, and how this varies among taxonomically similar species with inherently different behaviors and life histories is of value for management and conservation. We evaluated the risk response of three anuran species - southern leopard frog (Lithobates sphenocephalus), Blanchard’s cricket frog (Acris blanchardi), and green tree frog (Hyla cinerea) – to determine how differences in microhabitat use (arboreal vs ground-dwelling) and body size (small vs medium) may play a role in response to a potential threat within a human-altered subtropical forest. Each species responded to risk with both flight and freeze behaviors, however behaviors were species- and context-specific. As distance to cover increased, southern leopard frogs increased freezing behavior, green tree frogs decreased freezing behavior, and Blanchard’s cricket frogs increased flight response. The propensity of green tree frogs to use the canopy of vegetation as refugia, and the small body size of Blanchard’s cricket frogs likely led to greater flight response as distance to cover increased, whereas innate reliance on camouflage among southern leopard frogs may place them at greater risk to landscaping, agricultural, and transportation practices in open terrain. As such, arboreal and small-bodied species may inherently be better suited in human altered-landscapes compared to larger, ground-dwelling species. As land-use change continues to modify habitats, understanding how species respond to changes in their environment continues to be of importance, particularly in ecosystems where human-wildlife interactions are expected to increase in frequency.
Move it or lose it: interspecific variation in risk response of pond-breeding anurans

Philip Matich¹,², Christopher M. Schalk³

¹ Department of Marine Biology, Texas A & M University at Galveston, Galveston, TX, USA
² Texas Research Institute for Environmental Studies, Sam Houston State University, Huntsville, TX, USA
³ Arthur Temple College of Forestry and Agriculture, Stephen F. Austin State University, Nacogdoches, TX, USA

Corresponding Author:
Philip Matich
1001 Texas Clipper Road, Galveston, TX 77553, USA
Email address: pmatich@tamug.edu
Abstract

Changes in behavior are often the proximate response of animals to human disturbance, with variability in tolerance levels leading some species to exhibit striking shifts in life history, fitness, and/or survival. Thus, elucidating the effects of disturbance on animal behavior, and how this varies among taxonomically similar species with inherently different behaviors and life histories is of value for management and conservation. We evaluated the risk response of three anuran species - southern leopard frog (*Lithobates sphenoecephalus*), Blanchard’s cricket frog (*Acris blanchardi*), and green tree frog (*Hyla cinerea*) – to determine how differences in microhabitat use (arboreal vs ground-dwelling) and body size (small vs medium) may play a role in response to a potential threat within a human-altered subtropical forest. Each species responded to risk with both flight and freeze behaviors, however behaviors were species- and context-specific. As distance to cover increased, southern leopard frogs increased freezing behavior, green tree frogs decreased freezing behavior, and Blanchard’s cricket frogs increased flight response. The propensity of green tree frogs to use the canopy of vegetation as refugia, and the small body size of Blanchard’s cricket frogs likely led to greater flight response as distance to cover increased, whereas innate reliance on camouflage among southern leopard frogs may place them at greater risk to landscaping, agricultural, and transportation practices in open terrain. As such, arboreal and small-bodied species may inherently be better suited in human altered-landscapes compared to larger, ground-dwelling species. As land-use change continues to modify habitats, understanding how species respond to changes in their environment continues to be of importance, particularly in ecosystems where human-wildlife interactions are expected to increase in frequency.

Keywords: Amphibian; anthropogenic effects; behavioral ecology; edge habitat; human impacts
Introduction

Natural and anthropogenic disturbances continue to alter populations across terrestrial, freshwater, and marine ecosystems (Abatzoglou and Williams 2016; Hughes et al. 2017; Pecl et al. 2017). Often as a first response to perturbation, changes in behavior precede shifts in life history, fitness, and survival, which are of considerable interest for conservation in light of many imperiled species (Wong and Candolin 2015). Habitat and dietary generalists are inherently more adept at responding to disturbance (Devictor et al. 2008; Hamer and McDonnell 2008; Clavel et al. 2011), however species vary due to interspecific variability in morphology, physiology, and innate behavioral characteristics, regardless of being a specialists or generalist (McKinney 2006; Battisti et al. 2016; Legrand et al. 2017). As such, understanding how perturbations lead to changes in behavior, and how this may vary across taxonomic groups is important for developing a robust ecological paradigm for disturbance ecology (Caruso et al. 2016; Lany et al. 2017; Liu et al. 2017).

A variety of species have adjusted their behavior accordingly in response to a growing human footprint (e.g. Bateman and Fleming 2014; Wong and Candolin 2015; Caruso et al. 2016). For example, many birds and mammals have progressively increased their capacity to use human-altered habitats, and even thrive in some suburban and urban areas (e.g. Chace and Walsh 2006; Bateman and Fleming 2012; Meillère et al. 2015; Luscier 2018). Similarly, other species have significantly increased in population sizes in response to increased food availability and lower predation risk in agricultural areas and parks (e.g. Ganzhorn and Abraham 1991; Naughton-Treves 1998). Not all species, however, have responded positively to anthropogenic impacts. Habitat alterations have been particularly detrimental in many ecosystems, particularly for species that are less mobile and/or have stricter ecological and physiological requirements,
like amphibians (Hamer and McDonnell 2008; Crump 2009; Hughes et al. 2017; Tilman et al. 2017). Compared to endotherms, amphibians have limited mobility due to physiological constraints, which results in small home ranges (Wells 2007). Reduced mobility decreases the ability of amphibians to leave altered or degraded habitats, and our understanding of the proximate responses of amphibians (i.e. behavior) to land-use change is critical to inform conservation strategies focused on the long-term persistence of amphibian populations (Pechmann and Wilbur 1994; Gibbs 1998; Houlanah et al. 2000; Crump 2009).

Amphibians are among the most threatened taxonomic groups worldwide, with fungal infections and habitat degradation serving as leading causes of species declines (Stuart et al. 2004; Wake and Vredenburg 2008; Grant et al. 2016; Lips 2016). Approximately one third of amphibian species are threatened or endangered (IUCN; Collins and Storfer 2003; Stuart et al. 2004), highlighting the urgency of improving our understanding of their behavioral responses to perturbations, and their capacity to keep pace with human actions (Arroyo-Rodriguez et al. 2017; Lourenco et al. 2017; Tilman et al. 2017). Of concern beyond habitat availability is the response of amphibians to human-induced risk in altered habitats, because of the small body size and primary antipredator response of many species – camouflage. Remaining stationary is an effective antipredator response among many amphibians for natural predators that rely on visual cues (Crowshaw 2005; Ioannou and Krause 2009; Stevens and Merilaita 2011; Dodd 2013; Bulbert et al. 2017). However, remaining stationary may be detrimental in response to other risks, such as humans walking or driving vehicles that could lead to non-consumptive mortality (i.e. being stepped on or run over; sensu Andrews and Gibbons 2005; Beebee 2013; Heigl et al. 2017).
Here, we investigate the response of three anuran species with different body sizes, levels of mobility, and microhabitat use patterns - southern leopard frog (*Lithobates sphenoecephalus*), Blanchard’s cricket frog (*Acris blanchardi*), and green tree frog (*Hyla cinerea*) - to perceived risk at altered edge habitats in a subtropical forest, in order to improve our understanding of the effects of habitat alterations on amphibian response to perturbation. We predicted that in non-vegetated edge habitats, the arboreal species (green tree frog) would exhibit a greater risk response (i.e. flight) than the other species based on its propensity to be found in the canopy of vegetation (Dodd 2013). We also predicted that Blanchard’s cricket frogs would exhibit a greater risk response than southern leopard frogs, because of their smaller body size (Dodd 2013).

**Materials & Methods**

**Study site and species**

Our study took place at Sam Houston State University’s Center for Biological Field Studies (N 30°45′ W 95°25′), which is bordered by the Sam Houston National Forest to the south and east, and private ranching and timber holdings to the north and west. Within the Center for Biological Field Studies, pine-hardwood forest, open prairie, old-field succession, and riparian zones are the most abundant habitats (Dent and Lutterschmidt 2001), with amphibian monitoring conducted around ephemeral and permanent ponds.

Amphibians within the study area are locally abundant across much of their range and use a variety of altered and unaltered habitats (Pyburn 1958; Dodd et al. 2007; Dodd 2013), making them good model organisms for arboreal species (green tree frog) and semi-aquatic species (southern leopard frogs and Blanchard’s cricket frogs) spanning a range of small (Blanchard’s...
cricket frog) to medium body sizes (southern leopard frog). While all three species breed in
lentic aquatic habitats, Blanchard’s cricket frogs and green tree frogs breed in permanent aquatic
habitats, while southern leopard frogs breed in both temporary and permanent ponds. All three
species are primarily generalized invertivores that utilize a sit-and-wait foraging strategy (Dodd
2013). However, southern leopard frogs are also capable of consuming small vertebrates (e.g.,
fishes, other frogs; Dodd 2013). Southern leopard frogs call year-round in East Texas, while
calling activity is concentrated between April and August for both Blanchard’s cricket frogs and
green tree frogs (Saenz et al. 2006).

When immobile, the coloration patterns of Blanchard’s cricket frogs make them cryptic
on land, however, they are strong jumpers that can quickly change direction when approached
(Dodd 2013). Cricket frogs are also known to conceal themselves in vegetation. As such,
Blanchard’s cricket frogs may respond to an approaching threat initially through crypsis, and
then seek vegetative cover. The match between green tree frogs and surrounding vegetation
coupled with their reduced diurnal movement serves as the primary anti-predator strategy for
green tree frogs when in the canopy of vegetation (Dodd 2013). However, when disturbed,
individuals are capable of leaping long distances to evade predators (John-Alder et al. 1988).
Southern leopard frogs utilize multiple anti-predator strategies, and can remain motionless and
lower their body in a crouching position, or conceal themselves in vegetation (Marchisin and
Anderson 1978). The dorsal color and spot patterning enable individuals to match background
vegetation (Dodd 2013). Similar to Blanchard’s cricket frogs, leopard frogs likely respond first
through crypsis, and then seek vegetative cover. Southern leopard frogs also emit a warning
scream that functions to startle approaching predators, enabling individuals to escape.
Data collection

Four, ca. 1.5 m-wide belt transects (Amo et al. 2006) 250 m, 500 m, 750 m, and 750 m long were walked at or after dusk, four times monthly from June-November 2017 to conduct visual surveys (n = 96). Transects were paths and hatchery pond berms where vegetation had been cleared through mowing at the edges of forested habitat. The same belt transects were evaluated for each sampling event, in a randomly selected order, beginning <0.01 to 3.78 hours after sunset, depending on selection order (mean = 1.06 hrs after sunset ± 0.70 SD). Transects were divided into three sections - middle, edge, and boundary - to evaluate how the risk response of frogs to a potential threat (presence of a human) was influenced by proximity to cover/vegetation (Fig. 1). Middle sections were located within the interiors of belt transects, ca. 25 cm from cover with limited vegetation (i.e. low cut grass); edge sections were adjacent to middle section ca. 0-25 cm from cover with limited vegetation (i.e. low cut grass); and boundary sections were adjacent to edge sections at the boundary of transects, ca. 25 cm into vegetation (grasses, forbes, trees).

The same researcher walked slowly on each transect (<1 m/s) to detect anurans, and then moved more slowly (<0.5 m/s) upon encounters to simulate a threat, but effectively identify anurans (Cooper 2009). Once detected, study taxa were visually identified to species, location on transect was recorded (middle, edge, or boundary), and risk response was recorded - stationary (S; i.e. a freeze response), mobile (M - moving upon encounter; i.e. a flight response), or mobile-then-stationary (MS - mobile, then stationary after initial movement; i.e. a flight-then-freeze response). Research was conducted under Sam Houston State University IACUC #17-02-13-1034-3-01.
Data analysis

Data were organized by individual animal encounter. A generalized linear model using logistic regression was used to investigate the effects of species and transect section (middle, edge, boundary) on frog risk response. Due to the seasonal variability in environmental conditions within the subtropical study location, and habitat use patterns of the study species (Dodd 2013), monthly variability in frog behavior was considered as a predictor variable in addition to species and transect section. Friedman’s test was used to investigate the potential effects of sampling across different months, with significant results ($\chi^2 = 35.56, p < 0.01$). Therefore, sampling month was included as a factor in the model. Significant differences were not found across transects ($\chi^2 = 1.06, p = 0.90$), thus data were pooled. All main effects (species, section, month) and two-way interactions were included in the model:

$$H_{ijkl} = \mu + s_j + x_k + m_l + (sx)_{jk} + (sm)_{jl} + (xm)_{kl} + e_{ijkl}$$

Where $s$ is species, $x$ is transect section, $m$ is month, $i$ is the number of sampling events, $j$ is the number of species, $k$ is the number of sections, and $l$ is the number of months. Significance thresholds were corrected for multiple post-hoc comparisons. All analyses were conducted in IBM SPSS 22.

Results

From June-November 2017, 639 southern leopard frogs, 247 Blanchard’s cricket frogs, and 1800 green tree frogs were encountered during 24 nights of sampling across four belt transects (n = 96 total; Table 1). Leopard frogs and cricket frogs were more abundant in September-November, while green tree frogs were more abundant in July-September (Table 1).
Among southern leopard frogs, 217 encounters were in the middle of transects (34%), 179 were on transect edges (28%), and 243 were on transect boundaries (38%). Sixty-six Blanchard’s cricket frogs were encountered in the middle of transects (27%), 65 were on transect edges (26%), and 116 were on transect boundaries (47%). Among green tree frogs, 42 encounters were in the middle of transects (2%), 56 were on transect edges (3%), and 170 were on transect boundaries (95%).

The generalized linear model ($\chi^2 = 563.88, \text{df} = 73, p < 0.01$) indicated that species, transect section, and sampling month, as well as each two-way interaction were significant predictors of frog behavior (Table 2, 1S). Evaluation against an intercept-only model indicated the significance of the model ($\chi^2 = 2029.99, \text{df} = 33, p < 0.01$). Green tree frogs exhibited greater stationary behavior than Blanchard’s cricket frogs, which exhibited more mobile-then-stationary behavior ($\chi^2 = 1482.98, p < 0.01$). Green tree frogs also exhibited greater stationary behavior than southern leopard frogs compared to mobile ($\chi^2 = 282.21, p < 0.01$) and mobile-then-stationary behavior ($\chi^2 = 1325.34, p < 0.01$). Blanchard’s cricket frogs exhibited more mobile-then-stationary behavior than southern leopard frogs ($\chi^2 = 30.04, p < 0.01$).

In general, frogs were more mobile at transect edges ($\chi^2 = 6.13, p = 0.01$) and middles ($\chi^2 = 10.86, p < 0.01$) than boundaries, however this varied across species ($\chi^2 = 92.45, p < 0.01$). As distance from vegetation increased (i.e. boundary to edge to middle), southern leopard frogs increased stationary behavior ($\chi^2 = 101.68, p < 0.01$), switching from mobile and mobile-then-stationary behavior at transect boundaries, to mobile-then-stationary and stationary behavior at transect edges, to stationary and mobile-then-stationary behavior in the middle of transects (Fig. 2, Table 3). In contrast, Blanchard’s cricket frogs exhibited increased mobility from transect
boundary to middle ($\chi^2 = 40.05, p < 0.01$), while green tree frogs decreased stationary behavior from transect boundary to middle ($\chi^2 = 353.79, p < 0.01$; Fig. 2, Table 3).

Temporally, green tree frogs and Blanchard’s cricket frogs exhibited limited seasonal trends in behavior, while southern leopard frogs exhibited a decrease in stationary behavior from June to November (Fig. 3, Table 4). Southern leopard frogs and Blanchard’s cricket frogs were more mobile in June (17% and 20%, respectively) and July (23% and 26%, respectively) compared to the rest of the sampling period (1% and 4%, respectively; Fig. 3). All three species exhibited less mobile-then-stationary behavior than expected at the beginning of the sampling period (June and July), and more mobile-then-stationary behavior than expected at the end of the sampling period (October and November; Table 4).

**Discussion**

As human impacts continue to alter ecosystems, understanding animal behavior and species abilities to adjust to changing landscapes is of importance for wildlife and habitat management to ensure the maintenance of ecological communities (Becker et al. 2007; Battisti et al. 2016; Legrand et al. 2017; Pecl et al. 2017). Our study shows that the risk response of frogs in an altered forest ecosystem is both species- and context-specific, with some species (i.e. southern leopard frogs) at potentially greater risk to human actions in open terrain than others (i.e. green tree frog). As mobile species, frogs are able to avoid predators and other risks through both flight and camouflage (Marchisin and Anderson 1978). However, the efficacy of risk responses may differ based on characteristics of habitat (open or covered) and risk (visual, olfactory, heat sensing, non-consumptive, natural vs unnatural; Gregory 1979; Wells 2007; Bulbert et al. 2015). Our results suggest that morphology, including the ability to use trees and
other vegetation as refuge, and body size can potentially lead to important differences in the response of animals to risk factors.

As predicted, arboreal green tree frogs decreased stationary behavior as the distance to vegetative cover increased, likely due to their propensity to use the canopy of vegetation for refuge (Dodd 2013). Similarly, Blanchard’s cricket frogs, a ground-dwelling species, increased mobility as distance to cover increased, which could be attributed to the inherent risk faced by this species based on its small body size (Werner and Gilliam 1984). Supportive of our second hypothesis, southern leopard frogs exhibited the greatest likelihood to freeze in more open terrain (i.e. middle sections of transects), with increased stationary behavior as distance to cover increased. Movement may serve as an indicator to visual predators (Ioannou and Krause 2009), and therefore some ground dwelling frogs may remain stationary, and even flatten themselves against the substrate to avoid detection by predators, such as snakes, birds, and mammals (Marchisin and Anderson 1978). Species-specific differences in risk responses may also be innate - some amphibians actively evade predators (e.g. Tollrian and Harvell 1999), some species engage or scare predators (e.g. Altig 1974), and many remain motionless and use camouflage to blend in to their environments to avoid detection (e.g. Marchisin and Anderson 1978; Stevens and Merilaita 2011).

Yet, species with greater tendencies to remain stationary in open but risky habitats may face greater challenges adjusting to human-altered landscapes, with larger-bodied, ground dwelling animals (e.g., leopard frogs) potentially at greater risk of human-induced injury or mortality in unvegetated habitats compared to tree dwelling species (Beebee 2013; Sosa and Schalk 2016). Camouflage is a primary antipredator response of many frogs (Marchisin and Anderson 1978), and all three study species exhibited stationary behavior (98%, 30%, and 13%,
respectively for green tree frogs, southern leopard frogs, and Blanchard’s cricket frogs), overall with more frequent freeze responses in more vegetated transect sections (boundary, edge). In terrestrial habitats, species at risk may be more vigilant as terrain becomes less protected by vegetation or landscape features, and flee into more covered habitat when risk exceeds a threshold in open habitats (Edut and Eilam 2003; Stankowich 2008). Green tree frogs and Blanchard’s cricket frogs followed this model, while southern leopard frogs did not, exhibiting an inverse relationship between distance to cover and flight (Takada et al. 2018).

Across human-altered ecosystems, some innate behaviors remain beneficial, and the plasticity of other behaviors make them more advantageous in disturbed ecosystems (Chace and Walsh 2006; McKinney 2006; McCleery 2009). For example, the scavenging nature of some predators increases their foraging efficiency in urban and suburban environments where discarded human food is nutritionally beneficial and widely available, reducing energetic costs (e.g. Fedriani et al. 2001; Merkle et al. 2013). Similarly, human structures can be readily incorporated and utilized by species that rely on camouflage for protection (Merilaita 2003; Banos-Villaba et al. 2018). However, camouflage in ecosystems used by humans is likely most effective for species that blend-in with elevated structure, both natural and man-made. Indeed, camouflage and freeze responses among ground-dwelling species likely provide little protection from agricultural, landscaping, and transportation practices, each presenting lethal risk (Trombulak and Frissell 2000; Kirk et al. 2001; Carvalho et al. 2017). For many species, humans present unnatural conditions and perturbations that heighten risk (Cushman 2006; Wong and Candolin 2015; Li et al. 2017). Yet while camouflage may be the primary risk response of many frogs, this behavior is apparently not ubiquitous among all species, enabling some taxa to thrive in urban and suburban environments (Rubbo and Kiesecker 2005; Hamer and McDonnell
274 2008; Scheffers and Paszkowski 2012). Identifying species at greater risk and greater
275 adaptability is of importance moving forward in urban and disturbance ecology, as well as
276 conservation, in which identifying general behavioral patterns may be of great value (Lima and
277 Dill 1990; Wong and Candolin 2015; Battisti et al. 2016). Our data suggest that arboreal and
278 small-bodied species may be more able to adjust to human impacts than larger-bodied, ground-
279 dwelling species, however more refined study designs are needed to test this hypothesis.
280
281 Caveats
282 In light of the observed behavioral patterns and the extensive use of stationary/freeze
283 responses by all three study species, observations may have been biased based on the
284 researcher’s ability to detect immobile frogs near or in vegetation (boundary and edge habitats).
285 Yet, substantially more individuals were detected along the boundaries of transect (n = 2062)
286 compared to transect edges (n = 300) and middles (n = 325). Thus, detection bias was an
287 unlikely factor in shaping the observed trends, and was uniform across all sampling events,
288 because the same observer collected all sampling data.
289 Seasonal variability in environmental conditions and reproduction often shape animal
290 behavior in subtropical latitudes (e.g. Matich et al. 2017), and frogs exhibited monthly
291 differences in behavior. Yet, temporal trends in behavior were limited among the study species.
292 Frogs became more mobile from Summer to Autumn, which could be due to decreased
293 vegetation on transects as air temperature decreased, reducing the effectiveness of camouflage,
294 and/or differences in ground and air temperatures, food availability, or breeding cycles (Saenz et
295 al. 2006; Wells 2007). Seasonal variability in predation risk could also lead to seasonal patterns
in activity levels and behavior of frogs (Lode 2000; Sperry et al. 2008), however more controlled experiments are needed to test these hypotheses.

Conclusions

Habitat degradation continues to pose important conservation concerns across all ecosystems, including forests harvested for timber and converted to agricultural and ranch lands (Arroyo-Rodriguez et al. 2017; Lourenco et al. 2017; Tilman et al. 2017). Amphibians rely on tropical, subtropical, and temperate forests for habitat and food resources, and in strongholds where diseases have not infected populations, habitat management and conservation is of great importance (Stuart et al. 2004; Grant et al. 2016). Our results suggest that differences in distance to cover, habitat use patterns, and body size may affect frog behavior, with a greater propensity for flight responses to risk by arboreal frogs in open terrain (green tree frogs), and a greater propensity for freeze responses to risk by larger, ground-dwelling frogs (southern leopard frogs). With growing perturbations to many forested regions, these context-specific behaviors are of important consideration for future conservation and management in human-altered systems.

Acknowledgments

We thank the Center for Biological Field Studies and Alan Byboth for providing logistical support during data collection, and the many volunteers that helped survey frogs, including Kaya Moore, Demtri Payblas, Monica Anderson, and Kayla Hankins. We also thank the Texas Research Institute for Environmental Studies for providing logistical support in preparation of the manuscript.
References

Abatzoglou, J.T. & Williams, A.P. (2016) Impact of anthropogenic climate change on wildfire across western US forests. *PNAS* **113**, 11770-11775.

Altig, R. (1974) Defense behavior in *Rana areolata* and *Hyla avivoca*. *Quar. J. Florida. Acad. Sci.* **35**, 212-216.

Amo, L., Lopez, P., & Martin, J. (2006). Nature-based tourism as a form of predation risk affects body condition and health status of *Podarcis muralis* lizards. *Biol. Conserv.* **131**, 402-409.

Andrews, K.M. & Gibbons, J.W. (2005) How do highways influence snake movement? Behavioral responses to roads and vehicles. *Copeia* **2005**, 772-782.

Arroyo-Rodriguez, V., Melo, F.P.L., Martinez-Ramos, M., Bongers, F., Chazdon, R.L., Meave, J.A., Norden, N., Santos, B.A., Leal, I.R. & Tabarelli, M. (2017) Multiple successional pathways in human-modified tropical landscapes: new insights from forest succession, forest fragmentation and landscape ecology research. *Biol. Rev.* **92**, 326-340.

Banos-Villabla, A., Quevedo, D.P., & Edelaar, P. (2018). Positioning behavior according to individual color variation improves camouflage in novel habitats. *Behav. Ecol.* **29**, 404-410.

Bateman, P. W., & Fleming, P. A. (2012). Big city life: carnivores in urban environments. *J. Zool.* **287**, 1-23.

Bateman, P. W., & Fleming, P. A. (2014). Does human pedestrian behaviour influence risk assessment in a successful mammal urban adapter? *J. Zool.*, **294**, 93-98.

Battisti, C., Poeta, G. & Fanelli, G. (2016) *An introduction to disturbance ecology. A road map for wildlife management and conservation*. Springer. P. 178.
Becker, C.G., Fonseca, C.R., Haddad, C.F.B., Batista, R.F. & Prado, P.I. (2007) Habitat split and the global decline of amphibians. *Science* **318**, 1775-1777.

Beebee, T.J.C. (2013) Effect of road mortality and mitigation measures of amphibian populations. *Conserv. Biol.* **27**, 657-668.

Bulbert, M.W., Page, R.A. & Bernal, X.E. (2015) Danger comes from all fronts: predator-dependent escape tactics of Túngara frogs. *PLoS ONE* **10**, e0120546.

Bulbert, M.W., White, T.E., Saporito, R.A. & Kraus, F. (2017) Ontogenetic colour change in *Oreophryne ezra* (Anura: Microhylidae) reflects an unusual shift from conspicuousness to crypsis but not in toxicity. *Biol. J. Linn. Soc.* **12**, 12-20.

Caruso, N., Lucherini, M., Fortin, D. & Casanave, E.B. (2016) Species-specific responses of carnivores to human-induced landscape changes in central Argentina. *PLoS ONE* **11**, e0150488.

Carvalho F., Santos S.M., Mira A., & Lourenço R. (2017) Methods to Monitor and Mitigate Wildlife Mortality in Railways. In: Borda-de-Água L., Barrientos R., Beja P., Pereira H. (eds) Railway Ecology. Springer. P. 23-42.

Chace, J.F. & Walsh, J.J. (2006) Urban effects on native avifauna: a review. *Landsc. Urban Plan.* **74**, 46-69.

Clavel, J., Julliard, R., & Devictor, V. (2011). Worldwide decline of specialist species: toward a global functional homogenization? *Frontiers Ecol. Environ.* **9**, 222-228.

Collins, J.P. & Storfer, A. (2003) Global amphibian declines: sorting the hypotheses. *Diver.* **9**, 89-98.

Cooper, W.E. Jr. (2009) Fleeing and hiding under simultaneous risks and costs. *Behav. Ecol.* **20**, 665-671.
Crowshaw, D.A. (2005) Cryptic behavior is independent of dorsal color polymorphism in juvenile northern leopard frogs (*Rana pipiens*). *J. Herpet.* **29**, 125-129.

Crump, M.L. (2009) Amphibian diversity and life history. Amphibian Ecology and Conservation. *A Handbook of Techniques*, 3-20.

Cushman, S.A. (2006) Effects of habitat loss and fragmentation on amphibians: a review and prospectus. *Biol. Conserv.* **128**, 231-240.

Dent, L. & Lutterschmidt, W.I. (2001) The ichthyofauna of Harmon and Wynne Creeks sampled within the Center for Biological Field Studies, Walker County, Texas. *Texas. J. Sci.* **53**, 139-146.

Devictor, V., Julliard, R., & Jiguet, F. (2008). Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. *Oikos* **117**, 507-514.

Dodd, C.K. (2013) Frogs of the United States and Canada, 2-vol. set (Vol. 1&2). JHU Press.

Dodd, C.K. Jr., Barichivich, W.J., Johnson, S.A. & Staiger, J.S. (2007) Changes in a northwestern Florida gulf coast herpetofaunal community over a 28-y period. *Am. Mid. Nat.* **158**, 29-48.

Edut, S. & Eilam, D. (2003). Rodents in open space adjust their behavioral response to the different risk levels during barn-owl attack. *BMC Ecology* **3**, 10.

Fedriani, J.M., Fuller, T.K., & Sauvajot, R.M. (2001). Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California. *Ecography* **24**, 325-331.

Ganzhorn, J. U. & J.-P. Abraham. (1991). Possible role of plantations for lemur conservation in Madagascar: food for folivorous species. *Folia Primatologica* **56**, 171-176.
387 Gibbs, J. P. (1998). Genetic structure of redback salamander *Plethodon cinereus* populations in continuous and fragmented forests. Biol. Conserv. **86**, 77-81.

389 Grant, E.H.C., Miller, D.A., Schmidt, B.R., Adams, M.J., Amburgey, S.M., Chambert, T., et al. (2016) Quantitative evidence for the effects of multiple drivers on continental-scale amphibian declines. *Sci. Rep.* **6**, 25625.

392 Gregory, P.T. (1979) Avoidance behavior of the red-legged frog (*Rana aurora*). *Herpetologica* **35**, 175-184.

394 Hamer, A.J., & McDonnell, M.J. (2008) Amphibian ecology and conservation in the urbanizing world: A review. *Biol. Conserv.* **10**, 2432-2449.

396 Heigl, F., Horvath, K., Laaha, G. & Zaller, J.G. (2017) Amphibian and reptile road-kills on tertiary roads in relation to landscape structure: using a citizen science approach with open-access land cover data. *BMC Ecology* **17**, 24.

399 Houlahan, J.E., Findlay, C.S., Schmidt, B.R., Meyer, A.H., & Kuzmin, S.L. (2000) Quantitative evidence for global amphibian population declines. *Nature* **404**, 752-755.

401 Hughes, T.P., Barnes, M.L., Bellwood, D.R., Cinner, J.E., Cumming, G.S., Jackson, J.B.C., Kleypas, J., van de Leemput, I.A., Lough, J.M., Morrison, T.H., et al. (2017) Coral reefs in the Anthropocene. *Nature* **546**, 82-90.

404 Ioannou, C.C. & Krause, J. (2009) Interactions between background matching and motion during visual detection can explain why cryptic animals keep still. *Biol. Lett.* **5**, 191-193.

406 John-Alder, H.B., Morin, P.J. & Lawler, S. (1988) Thermal physiology, phenology, and distribution of tree frogs. *Am. Nat.* **132**, 506-520.

408 Kirk, D. A., Lindsay, K. E., & Brook, R. W. (2011). Risk of agricultural practices and habitat change to farmland birds. *Avian Conserv Ecol* **6**, 5.
Lany, N.K., Zarnetske, P.L., Gouhier, T.C. & Menge, B.A. (2017) Incorporating context dependency of species interactions in species distribution models. *Int. Compar. Biol.* **57**, 159-167.

Legrand, D., Cote, J., Fronhofer, E.A., Holt, R.D., Ronce, O., Schtickzelle, N., Travis, J.M.J. & Clobert, J. (2017) Eco-evolutionary dynamics in fragmented landscapes. *Ecography* **40**, 9-25.

Li, D., Liu, Y., Sun, X., Lloyd, H., Zhu, S., Zhang, S., Wan, D., & Zhang, Z. (2017) Habitat-dependent changes in vigilance behavior of Red-crowned Crane influenced by wildlife tourism. *Sci. Rep.* **7**, 16614.

Lima, S. L. & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* **68**, 619-640.

Lips, K.R. (2016) Overview of chytrid emergence and impacts on amphibians. *Phil. Trans. Royal. Soc. B* **371**, 20150465.

Liu, X.P., Liang, X., Li, X., Xu, X.C., Ou, J.P., Chen, Y.M., Li, S.Y., Wang, S.J. & Pei, F.S. (2017) A future land use simulation model (FLUS) for simulating multiple land use scenarios by coupling human and natural effects. *Landscape Urban Plan.* **168**, 94-116.

Lode, T. (2000) Functional response and area-restricted search in a predator: seasonal exploitation of anurans by the European polecat, *Mustela putorius*. *Aust. Ecol.* **25**, 223-231.

Lourenco, A., Alvarex, D., Wang, I.J. & Velo-Anton, G. (2017) Trapped within the city: integrating demography, time since isolation and population-specific traits to assess the genetic effects of urbanization. *Molec. Ecol.* **6**, 1498-1514.
Luscier, J.D. (2018). Effects of urbanization on great-tailed grackle habitat use and nest success in Sherman, Texas. *Urban Nat.* **15**, 1-14.

Marchisin, A. & Anderson, J.D. (1978) Strategies employed by frogs and toads (Amphibia, Anura) to avoid predation by snakes (Reptilia, Serpentes). *J. Herp.* **12**, 151-155.

Matich, P., Ault, J. S., Boucek, R. E., Bryan, D. R., Gastrich, K. R., Harvey, C. L., ... & Rosenblatt, A. E. (2017). Ecological niche partitioning within a large predator guild in a nutrient-limited estuary. *Limnol. Oceanog.* **62**, 934-953.

McCleery, R.A. (2009). Changes in fox squirrel anti-predator behaviors across the urban–rural gradient. *Landsc. Ecol.* **24**, 483.

McKinney, M.L. (2006) Urbanization as a major cause of biotic homogenization. *Biol. Conserv.* **127**, 247-260.

Meillère, A., Brischoux, F., Parentseau, C., & Angelier, F. (2015). Influence of urbanization on body size, condition, and physiology in an urban exploiter: a multi-component approach. *PloS one* **10**, e0135685.

Merkle, J.A., Robinson, H.S., Krausman, P.R., & Alaback, P. (2013) Food availability and foraging near human developments by black bears. *J. Mamm.* **94**, 378-385.

Merilaita, S. (2003). Visual background complexity facilitates the evolution of camouflage. *Evolution*, **57**: 1248-1254.

Naughton-Treves, L. (1998). Predicting patterns of crop damage by wildlife around Kibale National Park, Uganda. *Conserv. Biol.* **12**, 156-168.

Pechmann, J.H.K. & Wilbur, H.M. (1994) Putting declining amphibian populations in perspective – natural fluctuations and human impacts. *Herpetologica* **50**, 65-84.
Pecl, G.T., Araujo, M.B., Bell, J.D., Blanchard, J., Bonebrake, T.C., Chen, I.C., Clark, T.D., et al. (2017) Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. *Science* **355**, eaai9214.

Pyburn, W.F. (1958) Size and movements of a local population of cricket frogs (*Acris crepitans*). *Texas. J. Sci.* **10**, 325-342.

Rubbo, M.J. & Kiesecker, J.M. (2005). Amphibian breeding distribution in an urbanized landscape. *Conserv. Biol.* **19**, 504-511.

Saenz, D., Fitzgerald, L.A., Baum, K.A. & Conner, R.N. (2006) Abiotic correlates of anuran calling phenology: the importance of rain, temperature, and season. *Herp. Monogr.* **20**, 64-82.

Scheffers, B. R., & Paszkowski, C. A. (2012). The effects of urbanization on North American amphibian species: identifying new directions for urban conservation. *Urban Ecosys.* **15**, 133-147.

Sosa, R. & Schalk, C.M. (2016) Seasonal activity and species habitat guilds influence road–kill patterns of Neotropical snakes. *Trop. Conserv. Sci.* **9**, 1-12.

Sperry, J.H., Peak, R.G., Cimprich, D.A., & Weatherhead, P.J. (2008) Snake activity affects seasonal variation in nest predation risk for birds. *J. Avian. Biol.* **39**, 379-383.

Stankovich, T. (2008) Ungulate flight responses to human disturbance: A review and meta-analysis. *Biol. Conserv.* **141**, 2159-2173.

Stevens, M. & Merilaita, S. (2011) *Animal Camouflage. Mechanisms and Function*. Cambridge University Press. P. 357.
Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S., Fischman, D.L. & Waller, R.W. (2004) Status and trends of amphibian declines and extinctions worldwide. Science 306, 1783-1786.

Takada, H., Nakamura, K., Takatsuki, S., & Minami, M. (2018). Freezing behavior of the Japanese serow (Capricornis crispus) in relation to habitat and group size. Mamm. Res. 63, 107-112.

Tilman, D., Clark, M., Williams, D.R., Kimmel, K., Polasky, S. & Packer, C. (2017) Future threats to biodiversity and pathways to their prevention. Nature 546, 73-81.

Tollrian, R. & Harvell, C.D. (eds.) (1999). The ecology and evolution of inducible defenses. Princeton University Press

Trombulak, S.C. & Frissell, C.A. (2000). Review of ecological effects of roads on terrestrial and aquatic communities. Conserv. Biol. 14, 18-30.

Wake, D.B. & Vredenburg, V.T. (2008) Are we in the midst of the sixth mass extinction? A view from the world of amphibians. PNAS 105, 11466-11473.

Wells, K.D. (2007) The ecology and behavior of amphibians. Chicago: The University of Chicago Press

Werner, E.E., & Gilliam, J.F. (1984) The ontogenetic niche and species interactions in size-structured populations. An. Rev. Ecol. System. 15, 393-425

Wong, B.B.M. & Candolin, U. (2015) Behavioral responses to changing environments. Behav. Ecol. 26, 665-673.
Table 1 (on next page)

Sample sizes of study species observed during sampling period.

Sample sizes of study species observed during sampling period from June – November 2017.
Table 1: Sample sizes of study species observed during sampling period from June – November 2017.

| Species          | Month | N  |
|------------------|-------|----|
| *L. sphenoecephalus* | June  | 54 |
|                  | July  | 46 |
|                  | August | 36 |
|                  | September | 170 |
|                  | October | 163 |
|                  | November | 170 |
| *A. blanchardi*   | June  | 18 |
|                  | July  | 13 |
|                  | August | 39 |
|                  | September | 45 |
|                  | October | 30 |
|                  | November | 102 |
| *H. cinerea*      | June  | 166 |
|                  | July  | 777 |
|                  | August | 340 |
|                  | September | 268 |
|                  | October | 151 |
|                  | November | 98 |
Test statistics for the generalized linear model investigating the effects of species, location on transection (i.e. section), and sampling month on the risk response of *A. blanchardi*, *H. cinerea*, and *L. sphenocephalus*.

**Table 2 (on next page)**

Test statistics for the generalized linear model.
Table 2: Test statistics for the generalized linear model investigating the effects of species, location on transection (i.e. section), and sampling month on the risk response of *A. blanchardi*, *H. cinerea*, and *L. sphenoscephalus*.

| Factor          | $\chi^2$ | df | p-value |
|-----------------|----------|----|---------|
| Species         | 139.59   | 2  | <0.01   |
| Transect section| 10.71    | 2  | <0.01   |
| Month           | 24.57    | 5  | <0.01   |
| Species*Section | 140.64   | 4  | <0.01   |
| Species*Month   | 31.76    | 10 | <0.01   |
| Section*Month   | 33.06    | 10 | <0.01   |
Table 3 (on next page)

Post hoc results for chi squared test of location-specific differences in risk behavior.

Post hoc results for chi squared test of location-specific differences in risk behavior. M indicates mobile behavior, MS indicates mobile-then-stationary behavior, S indicates stationary behavior, and ND indicates no difference between behaviors.
Table 3: Post hoc results for chi squared test of location-specific differences in risk behavior. M indicates mobile behavior, MS indicates mobile-then-stationary behavior, S indicates stationary behavior, and ND indicates no difference between behaviors.

|                | Boundary         | Edge            | Middle          |
|----------------|------------------|-----------------|-----------------|
| *L. sphenocephalus* | M & MS > S       | MS & S > M      | S & MS > M      |
| *A. blanchardi*   | MS > S > M       | MS > M & S      | M & MS > S      |
| *H. cinerea*      | S > MS > M       | S > M & MS      | ND              |
Table 4 (on next page)

Post hoc results for chi squared test of month-specific differences in risk behavior.

Post hoc results for chi squared test of month-specific differences in risk behavior. M indicates mobile behavior, MS indicates mobile-then-stationary behavior, and S indicates stationary behavior. A plus (+) indicates a behavior exhibited more frequently than expected, a minus (-) indicates a behavior exhibited less frequently than expected, and ND indicates no difference between behaviors.
Table 4: Post hoc results for chi squared test of month-specific differences in risk behavior. M indicates mobile behavior, MS indicates mobile-then-stationary behavior, and S indicates stationary behavior. A plus (+) indicates a behavior exhibited more frequently than expected, a minus (-) indicates a behavior exhibited less frequently than expected, and ND indicates no difference between behaviors.

| Species          | Jun  | Jul  | Aug  | Sep  | Oct  | Nov  |
|------------------|------|------|------|------|------|------|
| *L. sphenoecephalus* | -MS  | -MS, +M | -MS, -M | ND  | +MS  | +MS  |
| *A. blanchardi*   | -MS  | +M   | ND   | +MS  | +MS  | +MS  |
| *H. cinerea*      | ND   | -MS  | ND   | ND   | +MS  | +MS  |
Transect sections used to evaluate how the risk response of frogs was influenced by proximity to cover.

Transect sections used to evaluate how the risk response of frogs was influenced by proximity to cover. Middle sections were located ca. 25 cm from cover; edge sections were ca. 0-25 cm from cover; and boundary sections were adjacent to edge sections at the boundary of transects, ca. 25 cm into vegetation. In the figure, black frogs are in boundary sections, light gray frogs are in edge sections, and dark gray frogs are in the middle section.
Figure 1: Transect sections used to evaluate how the risk response of frogs was influenced by proximity to cover. Middle sections were located \textit{ca.} 25 cm from cover; edge sections were \textit{ca.} 0-25 cm from cover; and boundary sections were adjacent to edge sections at the boundary of transects, \textit{ca.} 25 cm into vegetation. In the figure, black frogs are in boundary sections, light gray frogs are in edge sections, and dark gray frogs are in the middle section.
Figure 2 (on next page)

Spatial patterns in frog behavior

Proportion of encounters among study species in transect sections that remained stationary (S; light gray), mobile-then-stationary (MS; dark gray), and mobile (M; black) among southern leopard frogs (L. sphencephalus), Blanchard’s cricket frogs (A. blanchardi), and green tree frogs (H. cinerea).
Figure 2: Proportion of encounters among study species in transect sections that remained stationary (S; light gray), mobile-then-stationary (MS; dark gray), and mobile (M; black) among southern leopard frogs (*L. sphenocephalus*), Blanchard’s cricket frogs (*A. blanchardi*), and green tree frogs (*H. cinerea*).
**Figure 3** (on next page)

Monthly patterns in frog behavior

Monthly patterns in behavior [stationary (S; light gray), mobile-then-stationary (MS; dark gray), and mobile (M; black)] among southern leopard frogs (L. sphenocephalus), Blanchard’s cricket frogs (A. blanchardi), and green tree frogs (H. cinerea).
Figure 3: Monthly patterns in behavior [stationary (S; light gray), mobile-then-stationary (MS; dark gray), and mobile (M; black)] among southern leopard frogs (*L. sphenocephalus*), Blanchard’s cricket frogs (*A. blanchardi*), and green tree frogs (*H. cinerea*).