

Stephen F. Austin State University  
**SFA ScholarWorks**

---

Faculty Publications

Forestry

---


2019

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

Philip Matich  
*Texas A & M University*

Christopher M. Schalk  
*Stephen F Austin State University, schalkc@sfasu.edu*

Follow this and additional works at: <https://scholarworks.sfasu.edu/forestry>

 Part of the [Ecology and Evolutionary Biology Commons](#), [Forest Sciences Commons](#), [Natural Resources Management and Policy Commons](#), and the [Zoology Commons](#)

Tell us how this article helped you.

---

### Repository Citation

Matich, Philip and Schalk, Christopher M., "Move it or lose it: interspecific variation in risk response of pond-breeding anurans" (2019). *Faculty Publications*. 476.  
<https://scholarworks.sfasu.edu/forestry/476>

This Article is brought to you for free and open access by the Forestry at SFA ScholarWorks. It has been accepted for inclusion in Faculty Publications by an authorized administrator of SFA ScholarWorks. For more information, please contact [cdsscholarworks@sfasu.edu](mailto:cdsscholarworks@sfasu.edu).

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

Philip Matich<sup>1,2</sup> and Christopher M. Schalk<sup>3</sup>

<sup>1</sup> Department of Marine Biology, Texas A&M University—Galveston, Galveston, TX, USA

<sup>2</sup> Texas Research Institute for Environmental Studies, Sam Houston State University, Huntsville, TX, USA

<sup>3</sup> Arthur Temple College of Forestry and Agriculture, Stephen F. Austin State University, Nacogdoches, TX, USA

## 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 sphenoccephalus*), 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.

**Subjects** Animal Behavior, Ecology, Zoology, Natural Resource Management, Environmental Impacts

**Keywords** Human impacts, Anthropogenic effects, Behavioral ecology, Edge habitat, Amphibian

## INTRODUCTION

Natural and anthropogenic disturbances continue to alter populations across terrestrial, freshwater, and marine ecosystems (*Abatzoglou & Williams, 2016; Hughes et al., 2017; Pecl et al., 2017*). Often as a first response to perturbation, changes in behavior

Submitted 20 November 2018

Accepted 13 April 2019

Published 7 June 2019

Corresponding author

Philip Matich, pmatich@tamug.edu

Academic editor

Louise Barrett

Additional Information and  
Declarations can be found on  
page 11

DOI 10.7717/peerj.6956

© Copyright

2019 Matich and Schalk

Distributed under

Creative Commons CC-BY 4.0

**OPEN ACCESS**

precede shifts in life history, fitness, and survival, which are of considerable interest for conservation in light of many imperiled species (Wong & Candolin, 2015). Habitat and dietary generalists are inherently more adept at responding to disturbance (Devictor, Julliard & Jiguet, 2008; Hamer & McDonnell, 2008; Clavel, Julliard & Devictor, 2011), however, species vary due to interspecific variability in morphology, physiology, and innate behavioral characteristics, regardless of being a specialist or generalist (McKinney, 2006; Battisti, Poeta & Fanelli, 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 (Bateman & Fleming, 2014; Wong & 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 (Chace & Walsh, 2006; Bateman & 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 (Ganzhorn & Abraham, 1991; Naughton-Treves, 1998). Not all species, however, have responded positively to anthropogenic impacts. Habitat alterations have been detrimental in many ecosystems, particularly for species that are less mobile and/or have stricter ecological and physiological requirements, like amphibians (Hamer & 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 & Wilbur, 1994; Gibbs, 1998; Houlihan 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 & Vredenburg, 2008; Grant et al., 2016; Lips, 2016). Approximately one third of amphibian species are threatened or endangered (IUCN; Collins & 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 & Krause, 2009; Stevens & 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 & 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 sphenoccephalus*), 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 AND METHODS

### Study site and species

Our study took place at Sam Houston State University's Center for Biological Field Studies (N30°45' W95°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 & 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, Morin & Lawler, 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 & 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

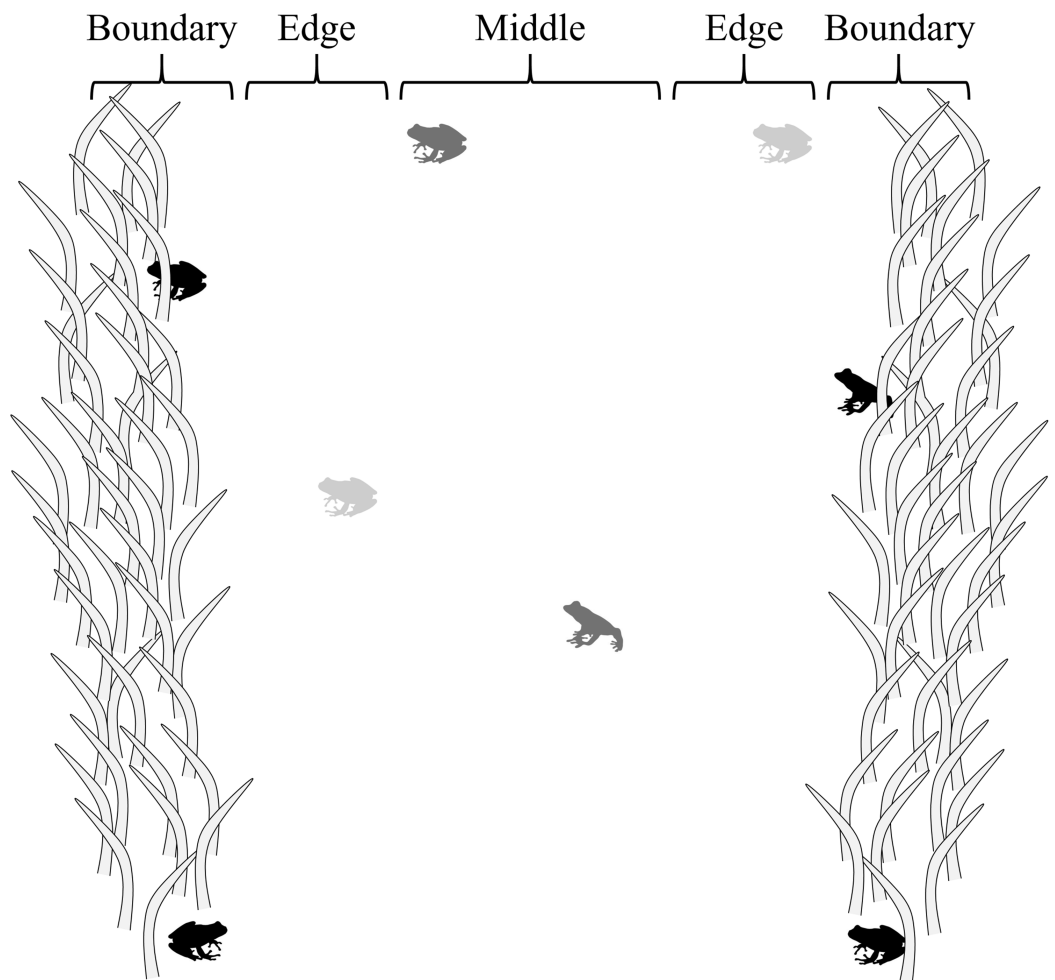
Four, *ca.* 1.5 m-wide belt transects (Amo, Lopez & Martin, 2006) 250, 500, 750, and 750 m long were walked at or after dusk, four times monthly from June to November 2017 to conduct visual surveys ( $n = 96$ ). Transects were paths and hatchery pond berms where vegetation had been cleared through mowing at the edges of forested habitat. The same belt transects were evaluated for each sampling event, in a randomly selected order, beginning  $<0.01$ – $3.78$  h after sunset, depending on selection order (mean =  $1.06$  h after sunset  $\pm 0.70$  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:

$$H_{ijkl} = \mu + s_j + x_k + m_l + (sx)_{jk} + (sm)_{jl} + (xm)_{kl} + \varepsilon_{ijkl} \quad (1)$$



**Figure 1** 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. [Full-size !\[\]\(1679558f37f6db0dd8360a2a7e913e90\_img.jpg\) DOI: 10.7717/peerj.6956/fig-1](https://doi.org/10.7717/peerj.6956/fig-1)

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 to November 2017, 639 southern leopard frogs, 247 Blanchard's cricket frogs, and 1,800 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](#)).

**Table 1** Sample sizes of study species observed during sampling period.

Species	Month	N
<i>L. sphenoccephalus</i>	June	54
	July	46
	August	36
	September	170
	October	163
	November	170
<i>A. blanchardi</i>	June	18
	July	13
	August	39
	September	45
	October	30
	November	102
<i>H. cinerea</i>	June	166
	July	777
	August	340
	September	268
	October	151
	November	98

**Note:**

Sampling period was from June to November 2017.

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%). A total of 66 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 1,702 were on transect boundaries (95%).

The generalized linear model ( $\chi^2 = 563.88$ ,  $df = 73$ ,  $p < 0.01$ ) indicated that species, transect section, and sampling month, as well as each two-way interaction were significant predictors of frog behavior (Table 2; Table S1). Evaluation against an intercept-only model indicated the significance of the model ( $\chi^2 = 2,029.99$ ,  $df = 33$ ,  $p < 0.01$ ). Green tree frogs exhibited greater stationary behavior than Blanchard's cricket frogs, which exhibited more mobile-then-stationary behavior ( $\chi^2 = 1,482.98$ ,  $p < 0.01$ ). 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 ( $\chi^2 = 1,325.34$ ,  $p < 0.01$ ). Blanchard's cricket frogs exhibited more mobile-then-stationary behavior than southern leopard frogs ( $\chi^2 = 30.04$ ,  $p < 0.01$ ).

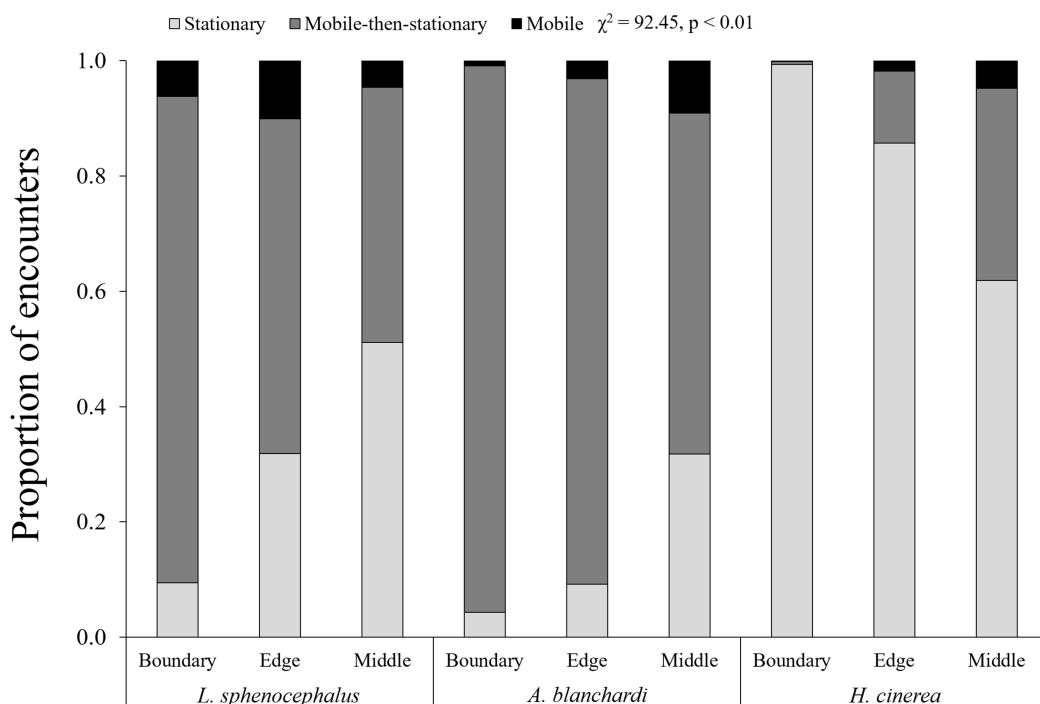
In general, frogs were more mobile at transect edges ( $\chi^2 = 6.13$ ,  $p = 0.01$ ) and middles ( $\chi^2 = 14.86$ ,  $p < 0.01$ ) than boundaries, however, this varied across species ( $\chi^2 = 92.45$ ,  $p < 0.01$ ). As distance from vegetation increased (i.e., boundary to edge to middle), southern leopard frogs increased stationary behavior ( $\chi^2 = 101.68$ ,  $p < 0.01$ ), switching from mobile and mobile-then-stationary behavior at transect boundaries,

**Table 2** Test statistics for the generalized linear model.

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

**Notes:**

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



**Figure 2** 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. sphenoccephalus*), Blanchard's cricket frogs (*A. blanchardi*), and green tree frogs (*H. cinerea*). [Full-size DOI: 10.7717/peerj.6956/fig-2](https://doi.org/10.7717/peerj.6956/fig-2)

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%,

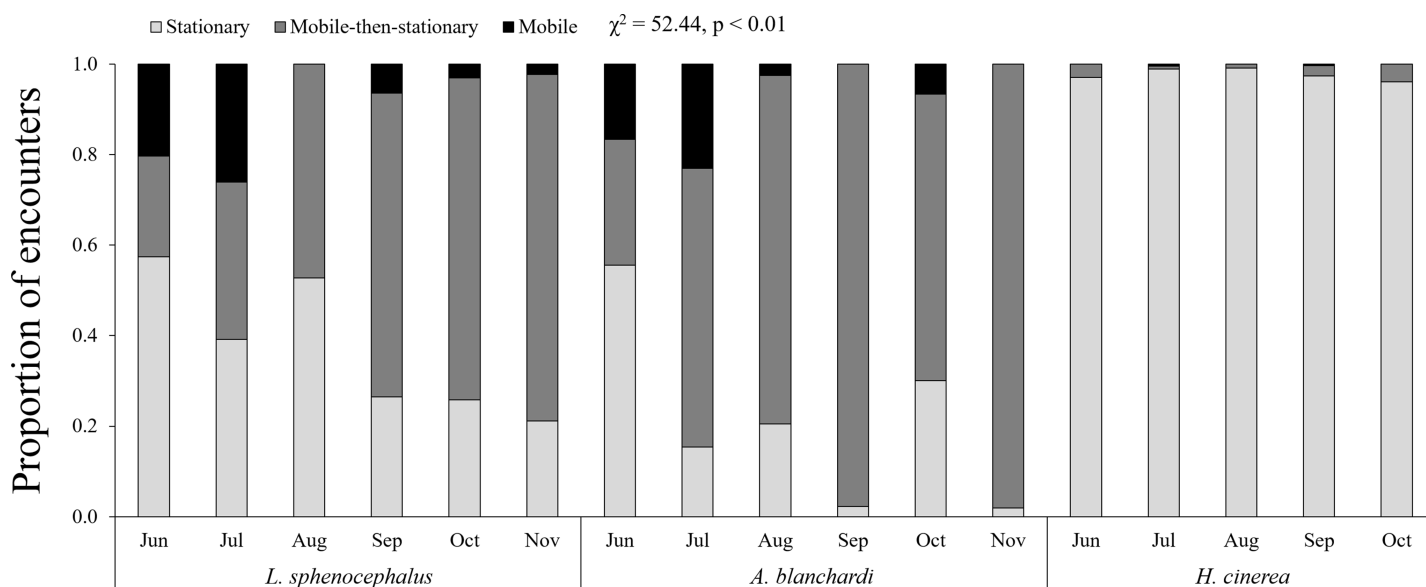


**Table 3** Post hoc results for Chi squared test of location-specific differences in risk behavior.

	Boundary	Edge	Middle
<i>L. sphenoccephalus</i>	M & MS > S	MS & S > M	S & MS > M
<i>A. blanchardi</i>	MS > S > M	MS > M & S	M & MS > S
<i>H. cinerea</i>	S > MS > M	S > M & MS	ND

**Notes:**

M, indicates mobile behavior; MS, indicates mobile-then-stationary behavior; S, indicates stationary behavior, and ND, indicates no difference between behaviors.



**Figure 3** 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. sphenoccephalus*), Blanchard's cricket frogs (*A. blanchardi*), and green tree frogs (*H. cinerea*).

Full-size DOI: 10.7717/peerj.6956/fig-3

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, Poeta & Fanelli, 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 & Anderson, 1978). However, the efficacy of risk responses may differ based on

**Table 4** Post hoc results for Chi squared test of month-specific differences in risk behavior.

	June	July	August	September	October	November
<i>L. sphenoccephalus</i>	–MS	–MS, +M	–MS, –M	ND	+MS	+MS
<i>A. blanchardi</i>	–MS	+M	ND	+MS	+MS	+MS
<i>H. cinerea</i>	ND	–MS	ND	ND	+MS	+MS

**Notes:**

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.

characteristics of habitat (open or covered) and risk (visual, olfactory, heat sensing, non-consumptive, natural vs unnatural; [Gregory, 1979](#); [Wells, 2007](#); [Bulbert, Page & Bernal, 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 & 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 & 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 & Anderson, 1978](#)). Species-specific differences in risk responses may also be innate—some amphibians actively evade predators ([Tollrian & Harvell, 1999](#)), some species engage or scare predators ([Altig, 1974](#)), and many remain motionless and use camouflage to blend in to their environments to avoid detection ([Marchisin & Anderson, 1978](#); [Stevens & 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 & Schalk, 2016](#)). Camouflage is a primary antipredator response of many frogs ([Marchisin & 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 & 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 & 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 (*Fedriani, Fuller & Sauvajot, 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-Villalba, Quevedo & Edelaar, 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 & Frissell, 2000; Kirk, Lindsay & Brook, 2011; Carvalho et al., 2017*). For many species, humans present unnatural conditions and perturbations that heighten risk (*Cushman, 2006; Wong & 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 & Kiesecker, 2005; Hamer & McDonnell, 2008; Scheffers & Paszkowski, 2012*). Identifying species at greater risk and greater adaptability is of importance moving forward in urban and disturbance ecology, as well as conservation, in which identifying general behavioral patterns may be of great value (*Lima & Dill, 1990; Wong & Candolin, 2015; Battisti, Poeta & Fanelli, 2016*). Our data suggest that arboreal and small-bodied species may be more able to adjust to human impacts than larger-bodied, ground-dwelling species, however, more refined study designs are needed to test this hypothesis.

### **Caveats**

In light of the observed behavioral patterns and the extensive use of stationary/freeze responses by all three study species, observations may have been biased based on the researcher's ability to detect immobile frogs near or in vegetation (boundary and edge habitats). Yet, substantially more individuals were detected along the boundaries of transect ( $n = 2,062$ ) compared to transect edges ( $n = 300$ ) and middles ( $n = 325$ ). Thus, detection bias was an unlikely factor in shaping the observed trends, and was uniform across all sampling events, because the same observer collected all sampling data.

Seasonal variability in environmental conditions and reproduction often shape animal behavior in subtropical latitudes (*Matich et al., 2017*), and frogs exhibited monthly differences in behavior. Yet, temporal trends in behavior were limited among the study species. Frogs became more mobile from Summer to Autumn, which could be due to decreased vegetation on transects as air temperature decreased, reducing the effectiveness of camouflage, and/or differences in ground and air temperatures, food availability, or breeding cycles (*Saenz et 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.

## ACKNOWLEDGEMENTS

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.

## ADDITIONAL INFORMATION AND DECLARATIONS

### Funding

The open access publishing fees for this article have been covered by the Texas A&M University Open Access to Knowledge Fund (OAKFund), supported by the University Libraries and the Office of the Vice President for Research, as well as the Office of Research and Sponsored Programs at Stephen F. Austin State University. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

### Grant Disclosures

The following grant information was disclosed by the authors:  
Texas A&M University Open Access to Knowledge Fund (OAKFund).  
University Libraries and the Office of the Vice President for Research.  
Office of Research and Sponsored Programs at Stephen F. Austin State University.

### Competing Interests

The authors declare that they have no competing interests.

## Author Contributions

- Philip Matich conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft.
- Christopher M. Schalk authored or reviewed drafts of the paper, approved the final draft.

## Animal Ethics

The following information was supplied relating to ethical approvals (i.e., approving body and any reference numbers):

Research was conducted under Sam Houston State University IACUC #17-02-13-1034-3-01.

## Data Availability

The following information was supplied regarding data availability:

The raw data in the [Supplemental Files](#) includes the sampling month, location on transect, study species, and associated risk behavior of frogs.

## Supplemental Information

Supplemental information for this article can be found online at <http://dx.doi.org/10.7717/peerj.6956#supplemental-information>.

## REFERENCES

- Abatzoglou JT, Williams AP. 2016.** Impact of anthropogenic climate change on wildfire across western US forests. *Proceedings of the National Academy of Sciences of the United States of America* **113**(42):11770–11775 DOI [10.1073/pnas.1607171113](https://doi.org/10.1073/pnas.1607171113).
- Altig R. 1974.** Defense behavior in *Rana areolata* and *Hyla avivoca*. *Quarterly journal of the Florida Academy of Sciences* **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. *Biological Conservation* **131**(3):402–409 DOI [10.1016/j.biocon.2006.02.015](https://doi.org/10.1016/j.biocon.2006.02.015).
- Andrews KM, Gibbons JW. 2005.** How do highways influence snake movement? Behavioral responses to roads and vehicles. *Copeia* **2005**(4):772–782 DOI [10.1643/0045-8511\(2005\)005\[0772:hdhism\]2.0.co;2](https://doi.org/10.1643/0045-8511(2005)005[0772:hdhism]2.0.co;2).
- Arroyo-Rodriguez V, Melo FPL, Martinez-Ramos M, Bongers F, Chazdon RL, Meave JA, Norden N, Santos BA, Leal IR, Tabarelli M. 2017.** Multiple successional pathways in human-modified tropical landscapes: new insights from forest succession, forest fragmentation and landscape ecology research. *Biological Reviews* **92**(1):326–340 DOI [10.1111/brv.12231](https://doi.org/10.1111/brv.12231).
- Banos-Villalba A, Quevedo DP, Edelaar P. 2018.** Positioning behavior according to individual color variation improves camouflage in novel habitats. *Behavioral Ecology* **29**(2):404–410 DOI [10.1093/beheco/arx181](https://doi.org/10.1093/beheco/arx181).
- Bateman PW, Fleming PA. 2012.** Big city life: carnivores in urban environments. *Journal of Zoology* **287**(1):1–23 DOI [10.1111/j.1469-7998.2011.00887.x](https://doi.org/10.1111/j.1469-7998.2011.00887.x).
- Bateman PW, Fleming PA. 2014.** Does human pedestrian behaviour influence risk assessment in a successful mammal urban adapter? *Journal of Zoology* **294**(2):93–98 DOI [10.1111/jzo.12156](https://doi.org/10.1111/jzo.12156).

- Battisti C, Poeta G, Fanelli G. 2016.** *An introduction to disturbance ecology. A road map for wildlife management and conservation.* Vol. 178. Singapore: Springer.
- Becker CG, Fonseca CR, Haddad CFB, Batista RF, Prado PI. 2007.** Habitat split and the global decline of amphibians. *Science* **318**(5857):1775–1777 DOI [10.1126/science.1149374](https://doi.org/10.1126/science.1149374).
- Beebee TJC. 2013.** Effect of road mortality and mitigation measures of amphibian populations. *Conservation Biology* **27**(4):657–668 DOI [10.1111/cobi.12063](https://doi.org/10.1111/cobi.12063).
- Bulbert MW, Page RA, Bernal XE. 2015.** Danger comes from all fronts: predator-dependent escape tactics of Túngara frogs. *PLOS ONE* **10**(4):e0120546 DOI [10.1371/journal.pone.0120546](https://doi.org/10.1371/journal.pone.0120546).
- Bulbert MW, White TE, Saporito RA, Kraus F. 2017.** Ontogenetic colour change in *Oreophryne ezra* (Anura: Microhylidae) reflects an unusual shift from conspicuousness to crypsis but not in toxicity. *Biological Journal of the Linnean Society* **123**(1):12–20 DOI [10.1093/biolinnean/blx124](https://doi.org/10.1093/biolinnean/blx124).
- Caruso N, Lucherini M, Fortin D, Casanave EB. 2016.** Species-specific responses of carnivores to human-induced landscape changes in central Argentina. *PLOS ONE* **11**(3):e0150488 DOI [10.1371/journal.pone.0150488](https://doi.org/10.1371/journal.pone.0150488).
- Carvalho F, Santos SM, 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*. Singapore: Springer, 23–42.
- Chace JF, Walsh JJ. 2006.** Urban effects on native avifauna: a review. *Landscape and Urban Planning* **74**(1):46–69 DOI [10.1016/j.landurbplan.2004.08.007](https://doi.org/10.1016/j.landurbplan.2004.08.007).
- Clavel J, Julliard R, Devictor V. 2011.** Worldwide decline of specialist species: toward a global functional homogenization? *Frontiers in Ecology and the Environment* **9**(4):222–228 DOI [10.1890/080216](https://doi.org/10.1890/080216).
- Collins JP, Storfer A. 2003.** Global amphibian declines: sorting the hypotheses. *Diversity Distributions* **9**(2):89–98 DOI [10.1046/j.1472-4642.2003.00012.x](https://doi.org/10.1046/j.1472-4642.2003.00012.x).
- Cooper WE Jr. 2009.** Fleeing and hiding under simultaneous risks and costs. *Behavioral Ecology* **20**(3):665–671 DOI [10.1093/beheco/arp049](https://doi.org/10.1093/beheco/arp049).
- Crowshaw DA. 2005.** Cryptic behavior is independent of dorsal color polymorphism in juvenile northern leopard frogs (*Rana pipiens*). *Journal of Herpetology* **39**(1):125–129 DOI [10.1670/0022-1511\(2005\)039\[0125:cbiiod\]2.0.co;2](https://doi.org/10.1670/0022-1511(2005)039[0125:cbiiod]2.0.co;2).
- Crump ML. 2009.** Amphibian diversity and life history. In: Dodd CK Jr, ed. *Amphibian Ecology and Conservation. A Handbook of Techniques*. Oxford: Oxford University Press, 3–20.
- Cushman SA. 2006.** Effects of habitat loss and fragmentation on amphibians: a review and prospectus. *Biological Conservation* **128**(2):231–240 DOI [10.1016/j.biocon.2005.09.031](https://doi.org/10.1016/j.biocon.2005.09.031).
- Dent L, Lutterschmidt WI. 2001.** The ichthyofauna of Harmon and Wynne Creeks sampled within the center for biological field studies, Walker County, Texas. *Texas Journal of Science* **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**(4):507–514 DOI [10.1111/j.0030-1299.2008.16215.x](https://doi.org/10.1111/j.0030-1299.2008.16215.x).
- Dodd CK. 2013.** *Frogs of the United States and Canada, 2-vol. set (Vol. 1&2)*. Baltimore: JHU Press.
- Dodd CK Jr, Barichivich WJ, Johnson SA, Staiger JS. 2007.** Changes in a northwestern Florida gulf coast herpetofaunal community over a 28-y period. *American Midland Naturalist* **158**(1):29–48 DOI [10.1674/0003-0031\(2007\)158\[29:cianfg\]2.0.co;2](https://doi.org/10.1674/0003-0031(2007)158[29:cianfg]2.0.co;2).

- 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 JM, Fuller TK, Sauvajot RM. 2001.** Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California. *Ecography* 24(3):325–331 DOI 10.1111/j.1600-0587.2001.tb00205.x.
- Ganzhorn JU, Abraham J-P. 1991.** Possible role of plantations for lemur conservation in Madagascar: food for folivorous species. *Folia Primatologica* 56(3):171–176 DOI 10.1159/000156544.
- Gibbs JP. 1998.** Genetic structure of redback salamander *Plethodon cinereus* populations in continuous and fragmented forests. *Biological Conservation* 86(1):77–81 DOI 10.1016/s0006-3207(97)00173-0.
- Grant EHC, Miller DA, Schmidt BR, Adams MJ, Amburgey SM, Chambert T, Cruickshank SS, Fisher RN, Green DM, Hossack BR, Johnson PT, Joseph MB, Rittenhouse TA, Ryan ME, Waddle JH, Walls SC, Bailey LL, Fellers GM, Gorman TA, Ray AM, Pilliod DS, Price SJ, Saenz D, Sadinski W, Muths E. 2016.** Quantitative evidence for the effects of multiple drivers on continental-scale amphibian declines. *Scientific Reports* 6(1):25625 DOI 10.1038/srep25625.
- Gregory PT. 1979.** Avoidance behavior of the red-legged frog (*Rana aurora*). *Herpetologica* 35:175–184.
- Hamer AJ, McDonnell MJ. 2008.** Amphibian ecology and conservation in the urbanizing world: a review. *Biological Conservation* 141(10):2432–2449 DOI 10.1016/j.biocon.2008.07.020.
- Heigl F, Horvath K, Laaha G, Zaller JG. 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(1):24 DOI 10.1186/s12898-017-0134-z.
- Houlahan JE, Findlay CS, Schmidt BR, Meyer AH, Kuzmin SL. 2000.** Quantitative evidence for global amphibian population declines. *Nature* 404(6779):752–755 DOI 10.1038/35008052.
- Hughes TP, Barnes ML, Bellwood DR, Cinner JE, Cumming GS, Jackson JBC, Kleypas J, Van De Leemput IA, Lough JM, Morrison TH, Palumbi SR, Van Nes EH, Scheffer M. 2017.** Coral reefs in the Anthropocene. *Nature* 546(7656):82–90 DOI 10.1038/nature22901.
- Ioannou CC, Krause J. 2009.** Interactions between background matching and motion during visual detection can explain why cryptic animals keep still. *Biology Letters* 5(2):191–193 DOI 10.1098/rsbl.2008.0758.
- John-Alder HB, Morin PJ, Lawler S. 1988.** Thermal physiology, phenology, and distribution of tree frogs. *American Naturalist* 132(4):506–520 DOI 10.1086/284868.
- Kirk DA, Lindsay KE, Brook RW. 2011.** Risk of agricultural practices and habitat change to farmland birds. *Avian Conservation and Ecology* 6(1):5 DOI 10.5751/ace-00446-060105.
- Lany NK, Zarnetske PL, Gouhier TC, Menge BA. 2017.** Incorporating context dependency of species interactions in species distribution models. *Integrative and Comparative Biology* 57(1):159–167 DOI 10.1093/icb/ix057.
- Legrand D, Cote J, Fronhofer EA, Holt RD, Ronce O, Schtickzelle N, Travis JMJ, Clobert J. 2017.** Eco-evolutionary dynamics in fragmented landscapes. *Ecography* 40(1):9–25 DOI 10.1111/ecog.02537.
- 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. *Scientific Reports* 7(1):16614 DOI 10.1038/s41598-017-16907-z.
- Lima SL, Dill LM. 1990.** Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68(4):619–640 DOI 10.1139/z90-092.

- Lips KR. 2016. Overview of chytrid emergence and impacts on amphibians. *Philosophical Transactions of the Royal Society B: Biological Sciences* 371(1709):20150465 DOI 10.1098/rstb.2015.0465.
- Liu XP, Liang X, Li X, Xu XC, Ou JP, Chen YM, Li SY, Wang SJ, Pei FS. 2017. A future land use simulation model (FLUS) for simulating multiple land use scenarios by coupling human and natural effects. *Landscape Urban Planning* 168:94–116 DOI 10.1016/j.landurbplan.2017.09.019.
- Lode T. 2000. Functional response and area-restricted search in a predator: seasonal exploitation of anurans by the European polecat, *Mustela putorius*. *Austral Ecology* 25(3):223–231 DOI 10.1046/j.1442-9993.2000.01024.x.
- Lourenco A, Alvarex D, Wang IJ, Velo-Anton G. 2017. Trapped within the city: integrating demography, time since isolation and population-specific traits to assess the genetic effects of urbanization. *Molecular Ecology* 26(6):1498–1514 DOI 10.1111/mec.14019.
- Luscier JD. 2018. Effects of urbanization on great-tailed grackle habitat use and nest success in Sherman Texas. *Urban Naturalist* 15:1–14.
- Marchisin A, Anderson JD. 1978. Strategies employed by frogs and toads (Amphibia, Anura) to avoid predation by snakes (Reptilia, Serpentes). *Journal of Herpetology* 12(2):151–155 DOI 10.2307/1563401.
- Matich P, Ault JS, Boucek RE, Bryan DR, Gastrich KR, Harvey CL, Heithaus MR, Kiszka JJ, Paz V, Rehage JS, Rosenblatt AE. 2017. Ecological niche partitioning within a large predator guild in a nutrient-limited estuary. *Limnology and Oceanography* 62(3):934–953 DOI 10.1002/lno.10477.
- McCleery RA. 2009. Changes in fox squirrel anti-predator behaviors across the urban–rural gradient. *Landscape Ecology* 24(4):483–493 DOI 10.1007/s10980-009-9323-2.
- McKinney ML. 2006. Urbanization as a major cause of biotic homogenization. *Biological Conservation* 127(3):247–260 DOI 10.1016/j.biocon.2005.09.005.
- Meillère A, Brischoux F, Parenteau C, Angelier F. 2015. Influence of urbanization on body size, condition, and physiology in an urban exploiter: a multi-component approach. *PLOS ONE* 10(8):e0135685 DOI 10.1371/journal.pone.0135685.
- Merilaita S. 2003. Visual background complexity facilitates the evolution of camouflage. *Evolution* 57(6):1248–1254 DOI 10.1111/j.0014-3820.2003.tb00333.x.
- Merkle JA, Robinson HS, Krausman PR, Alaback P. 2013. Food availability and foraging near human developments by black bears. *Journal of Mammalogy* 94(2):378–385 DOI 10.1644/12-mamm-a-002.1.
- Naughton-Treves L. 1998. Predicting patterns of crop damage by wildlife around Kibale National Park, Uganda. *Conservation Biology* 12(1):156–168 DOI 10.1046/j.1523-1739.1998.96346.x.
- Pechmann JHK, Wilbur HM. 1994. Putting declining amphibian populations in perspective—natural fluctuations and human impacts. *Herpetologica* 50(1):65–84.
- Pecl GT, Araujo MB, Bell JD, Blanchard J, Bonebrake TC, Chen IC, Clark TD, Colwell RK, Danielsen F, Evengård B, Falconi L, Ferrier S, Frusher S, Garcia RA, Griffis RB, Hobday AJ, Janion-Scheepers C, Jarzyna MA, Jennings S, Lenoir J, Linnertved HI, Martin VY, McCormack PC, McDonald J, Mitchell NJ, Mustonen T, Pandolfi JM, Pettorelli N, Popova E, Robinson SA, Scheffers BR, Shaw JD, Sorte CJ, Strugnell JM, Sunday JM, Tuanmu MN, Vergés A, Villanueva C, Wernberg T, Wapstra E, Williams SE. 2017. Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. *Science* 355(6332):eaai9214 DOI 10.1126/science.aai9214.



- Pyburn WF. 1958.** Size and movements of a local population of cricket frogs (*Acris crepitans*). *Texas Journal of Science* **10**:325–342.
- Rubbo MJ, Kiesecker JM. 2005.** Amphibian breeding distribution in an urbanized landscape. *Conservation Biology* **19**(2):504–511 DOI [10.1111/j.1523-1739.2005.00101.x](https://doi.org/10.1111/j.1523-1739.2005.00101.x).
- Saenz D, Fitzgerald LA, Baum KA, Conner RN. 2006.** Abiotic correlates of anuran calling phenology: the importance of rain, temperature, and season. *Herpetological Monographs* **20**(1):64–82.
- Scheffers BR, Paszkowski CA. 2012.** The effects of urbanization on North American amphibian species: identifying new directions for urban conservation. *Urban Ecosystems* **15**(1):133–147 DOI [10.1007/s11252-011-0199-y](https://doi.org/10.1007/s11252-011-0199-y).
- Sosa R, Schalk CM. 2016.** Seasonal activity and species habitat guilds influence road–kill patterns of Neotropical snakes. *Tropical Conservation Science* **9**(4):1–12.
- Sperry JH, Peak RG, Cimprich DA, Weatherhead PJ. 2008.** Snake activity affects seasonal variation in nest predation risk for birds. *Journal of Avian Biology* **39**(4):379–383 DOI [10.1111/j.0908-8857.2008.04451.x](https://doi.org/10.1111/j.0908-8857.2008.04451.x).
- Stankowich T. 2008.** Ungulate flight responses to human disturbance: a review and meta-analysis. *Biological Conservation* **141**(9):2159–2173 DOI [10.1016/j.biocon.2008.06.026](https://doi.org/10.1016/j.biocon.2008.06.026).
- Stevens M, Merilaita S. 2011.** *Animal camouflage: mechanisms and function*. Vol. 357. Cambridge: Cambridge University Press.
- Stuart SN, Chanson JS, Cox NA, Young BE, Rodrigues AS, Fischman DL, Waller RW. 2004.** Status and trends of amphibian declines and extinctions worldwide. *Science* **306**(5702):1783–1786 DOI [10.1126/science.1103538](https://doi.org/10.1126/science.1103538).
- Takada H, Nakamura K, Takatsuki S, Minami M. 2018.** Freezing behavior of the Japanese serow (*Capricornis crispus*) in relation to habitat and group size. *Mammal Research* **63**(1):107–112 DOI [10.1007/s13364-017-0338-9](https://doi.org/10.1007/s13364-017-0338-9).
- Tilman D, Clark M, Williams DR, Kimmel K, Polasky S, Packer C. 2017.** Future threats to biodiversity and pathways to their prevention. *Nature* **546**(7656):73–81 DOI [10.1038/nature22900](https://doi.org/10.1038/nature22900).
- Tollrian R, Harvell CD. eds. 1999.** *The ecology and evolution of inducible defenses*. Princeton: Princeton University Press.
- Trombulak SC, Frissell CA. 2000.** Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* **14**(1):18–30 DOI [10.1046/j.1523-1739.2000.99084.x](https://doi.org/10.1046/j.1523-1739.2000.99084.x).
- Wake DB, Vredenburg VT. 2008.** Are we in the midst of the sixth mass extinction? A view from the world of amphibians. *Proceedings of the National Academy of Sciences of the United States of America* **105**(Supplement 1):11466–11473 DOI [10.1073/pnas.0801921105](https://doi.org/10.1073/pnas.0801921105).
- Wells KD. 2007.** *The ecology and behavior of amphibians*. Chicago: The University of Chicago Press.
- Werner EE, Gilliam JF. 1984.** The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics* **15**(1):393–425 DOI [10.1146/annurev.es.15.110184.002141](https://doi.org/10.1146/annurev.es.15.110184.002141).
- Wong BBM, Candolin U. 2015.** Behavioral responses to changing environments. *Behavioral Ecology* **26**:665–673 DOI [10.1093/beheco/aru183](https://doi.org/10.1093/beheco/aru183).