

# Move it or lose it: inter- and intraspecific variation in risk response of pond-breeding anurans

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As humans continue to incorporate themselves into the natural world, our actions increasingly lead to the expansion of human-altered ecosystems. While some species tolerate, or even thrive in such ecosystems, others respond more adversely. Thus, elucidating the interspecific variability of human impacts across 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 behavior and body size may play a role in response to a potential threat within a temperate forest. All three species responded to risk with both flight and freeze behaviors. Southern leopard frogs increased freezing behavior as distance to cover increased, green tree frogs decreased freezing behavior as distance to cover increased, and Blanchard's cricket frogs increased flight response as distance to cover increased. Both southern leopard frogs and Blanchard's cricket frogs decreased flight responses from summer to autumn, and small southern leopard frogs exhibited more frequent flight responses, and more variability in risk response than larger individuals. As such, arboreal and semi-aquatic anurans exhibited different responses to potential risks based on proximity to protective habitat, suggesting interspecific differences in exposure to natural and unnatural predators, and associated responses. As landscape management moves forward, considering how species respond to changes in their environment continues to be of importance, particularly in ecosystems where humans-species interactions are expected to increase in frequency.

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anurans**

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# Abstract

As humans continue to incorporate themselves into the natural world, our actions increasingly lead to the expansion of human-altered ecosystems. While some species tolerate, or even thrive in such ecosystems, others respond more adversely. Thus, elucidating the interspecific variability of human impacts across 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 behavior and body size may play a role in response to a potential threat within a temperate forest. All three species responded to risk with both flight and freeze behaviors. Southern leopard frogs increased freezing behavior as distance to cover increased, green tree frogs decreased freezing behavior as distance to cover increased, and Blanchard's cricket frogs increased flight response as distance to cover increased. Both southern leopard frogs and Blanchard's cricket frogs decreased flight responses from summer to autumn, and small southern leopard frogs exhibited more frequent flight responses, and more variability in risk response than larger individuals. As such, arboreal and semi-aquatic anurans exhibited different responses to potential risks based on proximity to protective habitat, suggesting interspecific differences in exposure to natural and unnatural predators, and associated responses. As landscape management moves forward, considering how species respond to changes in their environment continues to be of importance, particularly in ecosystems where humans-species interactions are expected to increase in frequency.

Keywords: Forest; fragmentation; frog; human impacts; risk

# Introduction

Natural and anthropogenic disturbances are globally altering populations and communities across terrestrial, freshwater, and marine ecosystems (Abatzoglou and Williams 2016; Hughes et al. 2017; Pecl et al. 2017). As such, understanding how perturbations lead to changes in behavior, life history, and fitness is essential for developing a robust ecological paradigm from which hypothesis testing can directly translate to more efficient management and conservation. However, context-specific responses still limit our predictive capabilities, necessitating continued research on the impacts of both chronic and acute disturbance, especially among imperiled species (Caruso et al. 2016; Lany et al. 2017; Liu et al. 2017).

Amphibians are among the most threatened taxonomic group worldwide, with fungal infections and habitat degradation serving as leading causes of species declines (Stuart et al. 2004; Grant et al. 2016). Indeed, approximately one third of amphibian species are threatened or endangered (IUCN; Stuart et al. 2004), highlighting the urgency of improving our understanding of their response to perturbations and other stressors, and appropriately managing habitat (Collins and Storfer 2003; Lips et al. 2016). Tropical and subtropical forests are noted for their biodiversity (Crump 2009; Hoorn et al. 2010; Basset et al. 2012), but amphibians in temperate forests comprise a substantial portion of biomass in their respective ecosystems (e.g. Burton and Likens 1976; Gibbons et al. 2006). Of particular importance, forests on the equatorial borders of temperate latitudes are likely to become more subtropical in environmental conditions and vegetative communities in response to warming temperatures, and may serve as refugia for many species, both temperate and tropical in origin (Stralberg et al. 2015; Morelli et al. 2016).

Habitat loss and fragmentation attributed to agriculture, urban development, logging, and other human actions in temperate forests continue to shape habitat use patterns, densities, and

reproductive capacities of many species, including amphibians (Cushman 2006; Semlitsch et al. 2009). Habitat- and landscape-scale shifts in resource availability, movement corridors, and exposure to risk (e.g. predators, suboptimal environmental conditions) challenge many species to keep pace with human resource needs and habitat alterations (Arroyo-Rodriguez et al. 2017; Lourenco et al. 2017; Tilman et al. 2017). As such, changes in population sizes, food web structure, and encounter rates of altered habitats such as roads, agricultural fields, and lawns continue to persist in many regions (Maerz, Blossey & Nuzzo 2005; Cheptou et al. 2017; Legrand et al. 2017). Here, we investigate the response of three anuran species - 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 order to improve our understanding of the effects of habitat alterations and the use of exposed areas in a temperate coniferous forest.

## 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 vegetated by loblolly pine (*Pinus taeda*), and a mix of hardwoods (e.g. *Acer negundo*, *Liquidamber styraciflua*, *Populus deltoids*, *Quercus nigra*) and grasses (e.g. *Andropogon glomeratus*). The herpetological community in the study

area was dominated by southern leopard frog, cricket frog, green tree frog, bronze frog (*Lithobates clamitans*), American bullfrog (*Lithobates catesbeianus*), gray tree frog (*Hyla versicolor*), Gulf coast toad (*Incilius nebulifer*), eastern narrow mouth toad (*Gastrophryne carolinensis*), ground skink (*Scincella lateralis*), copperhead (*Agkistrodon contortrix*), cottonmouth (*Agkistrodon piscivorus*), and western ribbon snake (*Thamnophis proximus*) (Wasko unpublished data).

Amphibians within the study area are locally abundant across much of their range (Pyburn 1958; Dodd et al. 2007; Dodd 2013), making them good model organisms for arboreal frogs (green tree frog) and semi-aquatic species (southern leopard frogs and cricket frogs), and spanning a range of small (Blanchard's cricket frog) to medium body sizes (southern leopard frog). While all three species breed in lentic 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 (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 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 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, but path and berm edges retained vegetation to replicate anthropogenically created habitat edges. 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  $\pm$  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. 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). Remaining stationary is an effective antipredator response among some frogs for some natural predators that rely on visual cues (Crowshaw 2005; Ioannou and Krause 2009; 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). The size of leopard frogs was also measured or estimated to the nearest 10 mm snout vent length (SVL) size-class. 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. 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. Logistic regression was



also used to evaluate the effect of leopard frog size class on risk response. 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 1702 were on transect boundaries (95%).

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, to mobile-then-stationary and stationary behavior at transect edges, to stationary and mobile-then-stationary behavior in the middle of transects (Fig. 1, Table 2). 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. 1, Table 2).

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. 2, Table 3). 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. 2). 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 3).

Southern leopard frog size-classes ranged from 20-29 mm SVL to 80-89 mm SVL, with most individuals (60%) 50-69 mm SVL (Fig. S1). Behavioral difference in size-classes were significant ( $\chi^2 = 71.26$ ,  $p < 0.01$ ), but limited. Smaller frogs (20-49 mm SVL) were more mobile than larger individuals, while moderately sized individuals (40-69 mm SVL) exhibited more mobile-then-stationary behavior (Fig. 3). Trends across transect areas were also limited (Fig. 3) - stationary behavior decreased as frog size increased at transect boundaries ( $\chi^2 = 42.88$ ,  $p < 0.01$ ), and stationary behavior was greater among the smallest frogs (20-29 mm SVL) and largest frogs (70-89 mm SVL) compared to other individuals at boundaries ( $\chi^2 = 40.54$ ,  $p < 0.01$ ). Behavior was similar among size-classes in the middle of transects ( $\chi^2 = 27.45$ ,  $p < 0.01$ ).

## Discussion

Deforestation and other habitat-altering impacts are of conservation concern, because of the ecological implications of altering vegetative communities and protective cover for mobile

and immobile species (Becker et al. 2007). As mobile species, frogs are able to avoid predators and other risks through both flight and camouflage (Marchisin and Anderson 1978). However, risk responses may differ in effectiveness based on 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 study showed that green tree frogs decreased stationary behavior as the distance to vegetative cover increased, while southern leopard frogs increased stationary behavior as the distance to vegetative cover increased, suggesting an innate response of leopard frogs to freeze in response to risk in open terrain. Results suggest that ground dwelling frogs with similar behavior to that of leopard frogs may be at greater risk of human-induced injury or mortality than tree dwelling species due to differences in inherent risk responses, particularly in the event of increased deforestation and fragmentation (Beebee 2013; Sosa and Schalk 2016).

Innate responses to predators vary taxonomically, with some species actively evading predators (e.g. Tollrian and Harvell 1999), some species engaging or scaring predators (e.g. Altig 1974), and others remaining motionless and using camouflage to blend in order to their environments and avoid detection (e.g. Marchisin and Anderson 1978). All three study species exhibited stationary behavior (98%, 30%, and 13%, respectively for green tree frogs, southern leopard frogs, and Blanchard's cricket frogs), suggesting camouflage is an important anti-predator tactic. However, behavior was species- and context-specific – green tree frogs were highly stationary at boundaries, but decreased stationary behavior as distance to cover increased, whereas southern leopard frogs increased their stationary behavior as distance to cover increased. Blanchard's cricket frogs, another ground-dwelling species, increased mobility as distance to cover increased, which could be attributed to inherent size differences between southern leopard

frogs, and smaller-bodied Blanchard's cricket frogs. Movement may serve as an indicator to visual predators (Ioannou and Krause 2009), and therefore ground dwelling frogs that spend most of their time on the ground (or in the water) 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). However, body size appeared to play a role in risk response of ground dwelling frogs during our study. Of concern, stationary behavior during risk encounters with motor vehicles at patch edges is likely an inappropriate response.

Temporal trends in behavior were limited among the study species, but frogs became more mobile from Summer to Autumn. Increased activity levels in Autumn could be due to decreased vegetation on transects, reducing the effectiveness of camouflage, and/or differences in ground and air temperatures, food availability, or breeding cycles (Wells 2007; Saenz et al. 2006). Seasonal variability in predation risk could also lead to seasonal patterns in activity levels and behavior of frogs (Lode 2000; Sperry et al. 2008). More controlled experiments will enable these hypotheses to be tested.

Size-specific responses of southern leopard frogs were also limited. Smaller leopard frogs exhibited greater mobility, as well as more variability in risk response among individuals. Anurans exhibit ontogenetic shifts in diet and foraging sites (Christian 1982, Schalk and Fitzgerald 2015), as well decreased vulnerability to predators with an increasing body size (Werner, Wellborn & McPeck 1995). As such, defense tactics (e.g. flight or camouflage) may develop during this time period before reaching 50 mm SVL (Wells 2007; Gall and Mathis 2011; Crane and Ferrari 2017). Alternatively, camouflage may be an ineffective response to risk among smaller-bodied individuals because of predator gape widths and search images, particularly in open terrain at patch edges or in deforested habitats.

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 ( $n = 2062$ ) compared to transect edges ( $n = 300$ ) and middles ( $n = 325$ ). Thus, detection bias was an unlikely factor in shaping the observed trends.

## Conclusions

Habitat loss and degradation continue 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 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 and habitat use among frogs affects antipredator behavior, and with growing perturbation to many forested regions, these context-specific behaviors are of important consideration for future conservation and management.

## 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.

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**Table 1**(on next page)

Sample sizes of study species observed during sampling period.

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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

## Table 2 (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 2: 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
<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



# **Table 3**(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 3: 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.

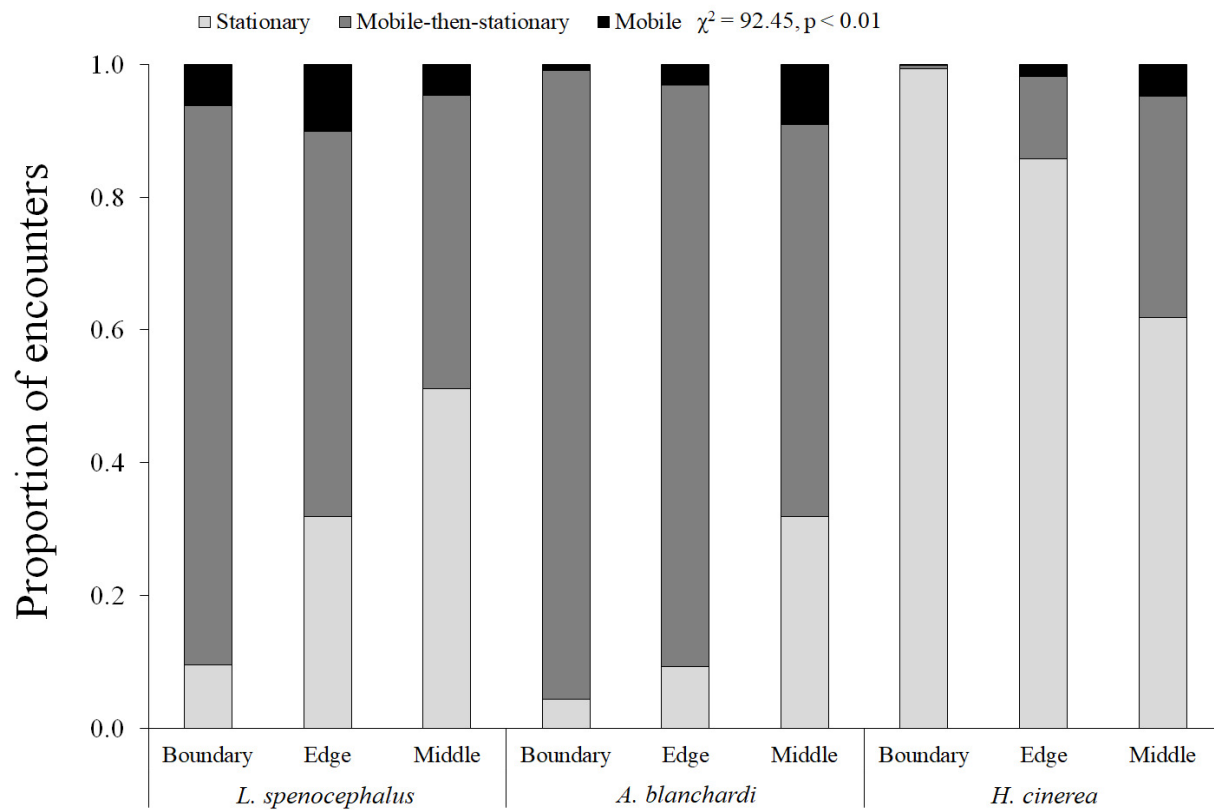
	Jun	Jul	Aug	Sep	Oct	Nov
<i>L. sphenoccephalus</i>	-MS	-MS, +M	-MS, -M	ND	+MS	+MS
<i>A. blanchardi</i>	-MS	+M	ND	+MS	+MS	+MS
<i>H. cinerea</i>	ND	-MS	ND	ND	+MS	+MS

# **Figure 1**(on next page)

Behavior of study species across transect sections

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, Blanchard's cricket frogs, and green tree frogs.

Figure 1: 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, Blanchard's cricket frogs, and green tree frogs.

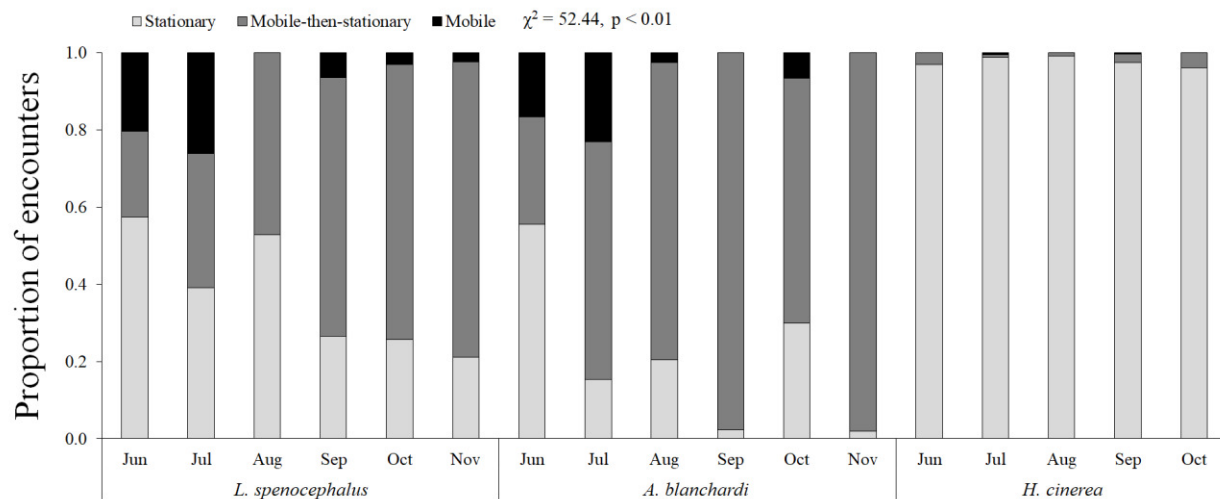


## Figure 2 (on next page)

Monthly patterns in behavior

Monthly patterns in behavior [stationary (S; light gray), mobile-then-stationary (MS; dark gray), and mobile (M; black)] among southern leopard frogs, Blanchard's cricket frogs, and green tree frogs.

Figure 2: Monthly patterns in behavior [stationary (S; light gray), mobile-then-stationary (MS; dark gray), and mobile (M; black)] among southern leopard frogs, Blanchard's cricket frogs, and green tree frogs.



# **Figure 3**(on next page)

Southern leopard frog behavior across size-classes

Proportion of encounters among southern leopard frogs in transect sections that remained stationary (S; light gray), mobile-then-stationary (MS; dark gray), and mobile (M; black) across size-classes.

Figure 3: Proportion of encounters among southern leopard frogs in transect sections that remained stationary (S; light gray), mobile-then-stationary (MS; dark gray), and mobile (M; black) across size-classes.

