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

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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.

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24 **Abstract**

25 Changes in behavior are often the proximate response of animals to human disturbance, with

26 variability in tolerance levels leading some species to exhibit striking shifts in life history,

27 fitness, and/or survival. Thus, elucidating the effects of disturbance on animal behavior, and

28 how this varies among taxonomically similar species with inherently different behaviors and life

29 histories is of value for management and conservation. We evaluated the risk response of three

30 anuran species - southern leopard frog (*Lithobates sphenocephalus*), Blanchard's cricket frog

31 (*Acris blanchardi*), and green tree frog (*Hyla cinerea*) – to determine how differences in

32 microhabitat use (arboreal vs ground-dwelling) and body size (small vs medium) may play a role

33 in response to a potential threat within a human-altered subtropical forest. Each species

34 responded to risk with both flight and freeze behaviors, however behaviors were species- and

35 context-specific. As distance to cover increased, southern leopard frogs increased freezing

36 behavior, green tree frogs decreased freezing behavior, and Blanchard's cricket frogs increased

37 flight response. The propensity of green tree frogs to use the canopy of vegetation as refugia,

38 and the small body size of Blanchard's cricket frogs likely led to greater flight response as

39 distance to cover increased, whereas innate reliance on camouflage among southern leopard

40 frogs may place them at greater risk to landscaping, agricultural, and transportation practices in

41 open terrain. As such, arboreal and small-bodied species may inherently be better suited in

42 human altered-landscapes compared to larger, ground-dwelling species. As land-use change

43 continues to modify habitats, understanding how species respond to changes in their environment

44 continues to be of importance, particularly in ecosystems where human-wildlife interactions are

45 expected to increase in frequency.

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

47 **Introduction**

48   Natural and anthropogenic disturbances continue to alter populations across terrestrial,

49 freshwater, and marine ecosystems (Abatzoglou and Williams 2016; Hughes et al. 2017; Pecl et

50 al. 2017). Often as a first response to perturbation, changes in behavior precede shifts in life

51 history, fitness, and survival, which are of considerable interest for conservation in light of many

52 imperiled species (Wong and Candolin 2015). Habitat and dietary generalists are inherently

53 more adept at responding to disturbance (Devictor et al. 2008; Hamer and McDonnell 2008;

54 Clavel et al. 2011), however species vary due to interspecific variability in morphology,

55 physiology, and innate behavioral characteristics, regardless of being a specialists or generalist

56 (McKinney 2006; Battisti et al. 2016; Legrand et al. 2017). As such, understanding how

57 perturbations lead to changes in behavior, and how this may vary across taxonomic groups is

58 important for developing a robust ecological paradigm for disturbance ecology (Caruso et al.

59 2016; Lany et al. 2017; Liu et al. 2017).

60   A variety of species have adjusted their behavior accordingly in response to a growing

61 human footprint (e.g. Bateman and Fleming 2014; Wong and Candolin 2015; Caruso et al.

62 2016). For example, many birds and mammals have progressively increased their capacity to use

63 human-altered habitats, and even thrive in some suburban and urban areas (e.g. Chace and Walsh

64 2006; Bateman and Fleming 2012; Meillère et al. 2015; Luscier 2018). Similarly, other species

65 have significantly increased in population sizes in response to increased food availability and

66 lower predation risk in agricultural areas and parks (e.g. Ganzhorn and Abraham 1991;

67 Naughton-Treves 1998). Not all species, however, have responded positively to anthropogenic

68 impacts. Habitat alterations have been particularly detrimental in many ecosystems, particularly

69 for species that are less mobile and/or have stricter ecological and physiological requirements,

70   like amphibians (Hamer and McDonnell 2008; Crump 2009; Hughes et al. 2017; Tilman et al.

71   2017). Compared to endotherms, amphibians have limited mobility due to physiological

72   constraints, which results in small home ranges (Wells 2007). Reduced mobility decreases the

73   ability of amphibians to leave altered or degraded habitats, and our understanding of the

74   proximate responses of amphibians (i.e. behavior) to land-use change is critical to inform

75   conservation strategies focused on the long-term persistence of amphibian populations

76   (Pechmann and Wilbur 1994; Gibbs 1998; Houlahan et al. 2000; Crump 2009).

77   Amphibians are among the most threatened taxonomic groups worldwide, with fungal

78   infections and habitat degradation serving as leading causes of species declines (Stuart et al.

79   2004; Wake and Vredenburg 2008; Grant et al. 2016; Lips 2016). Approximately one third of

80   amphibian species are threatened or endangered (IUCN; Collins and Storfer 2003; Stuart et al.

81   2004), highlighting the urgency of improving our understanding of their behavioral responses to

82   perturbations, and their capacity to keep pace with human actions (Arroyo-Rodriguez et al. 2017;

83   Lourenco et al. 2017; Tilman et al. 2017). Of concern beyond habitat availability is the response

84   of amphibians to human-induced risk in altered habitats, because of the small body size and

85   primary antipredator response of many species – camouflage. Remaining stationary is an

86   effective antipredator response among many amphibians for natural predators that rely on visual

87   cues (Crowshaw 2005; Ioannou and Krause 2009; Stevens and Merilaita 2011; Dodd 2013;

88   Bulbert et al. 2017). However, remaining stationary may be detrimental in response to other

89   risks, such as humans walking or driving vehicles that could lead to non-consumptive mortality

90   (i.e. being stepped on or run over; *sensu* Andrews and Gibbons 2005; Beebee 2013; Heigl et al.

91   2017).

92   Here, we investigate the response of three anuran species with different body sizes, levels

93   of mobility, and microhabitat use patterns - southern leopard frog (*Lithobates sphenocephalus*),

94   Blanchard's cricket frog (*Acris blanchardi*), and green tree frog (*Hyla cinerea*) - to perceived

95   risk at altered edge habitats in a subtropical forest, in order to improve our understanding of the

96   effects of habitat alterations on amphibian response to perturbation. We predicted that in non-

97   vegetated edge habitats, the arboreal species (green tree frog) would exhibit a greater risk

98   response (i.e. flight) than the other species based on its propensity to be found in the canopy of

99   vegetation (Dodd 2013). We also predicted that Blanchard's cricket frogs would exhibit a

100   greater risk response than southern leopard frogs, because of their smaller body size (Dodd

101   2013).

102

103   **Materials & Methods**

104   *Study site and species*

105   Our study took place at Sam Houston State University's Center for Biological Field Studies

106   (N 30°45′ W 95°25′), which is bordered by the Sam Houston National Forest to the south and

107   east, and private ranching and timber holdings to the north and west. Within the Center for

108   Biological Field Studies, pine-hardwood forest, open prairie, old-field succession, and riparian

109   zones are the most abundant habitats (Dent and Lutterschmidt 2001), with amphibian monitoring

110   conducted around ephemeral and permanent ponds.

111   Amphibians within the study area are locally abundant across much of their range and use

112   a variety of altered and unaltered habitats (Pyburn 1958; Dodd et al. 2007; Dodd 2013), making

113   them good model organisms for arboreal species (green tree frog) and semi-aquatic species

114   (southern leopard frogs and Blanchard's cricket frogs) spanning a range of small (Blanchard's

115 cricket frog) to medium body sizes (southern leopard frog). While all three species breed in

116 lentic aquatic habitats, Blanchard's cricket frogs and green tree frogs breed in permanent aquatic

117 habitats, while southern leopard frogs breed in both temporary and permanent ponds. All three

118 species are primarily generalized invertivores that utilize a sit-and-wait foraging strategy (Dodd

119 2013). However, southern leopard frogs are also capable of consuming small vertebrates (e.g.,

120 fishes, other frogs; Dodd 2013). Southern leopard frogs call year-round in East Texas, while

121 calling activity is concentrated between April and August for both Blanchard's cricket frogs and

122 green tree frogs (Saenz et al. 2006).

123   When immobile, the coloration patterns of Blanchard's cricket frogs make them cryptic

124 on land, however, they are strong jumpers that can quickly change direction when approached

125 (Dodd 2013). Cricket frogs are also known to conceal themselves in vegetation. As such,

126 Blanchard's cricket frogs may respond to an approaching threat initially through crypsis, and

127 then seek vegetative cover. The match between green tree frogs and surrounding vegetation

128 coupled with their reduced diurnal movement serves as the primary anti-predator strategy for

129 green tree frogs when in the canopy of vegetation (Dodd 2013). However, when disturbed,

130 individuals are capable of leaping long distances to evade predators (John-Alder et al. 1988).

131 Southern leopard frogs utilize multiple anti-predator strategies, and can remain motionless and

132 lower their body in a crouching position, or conceal themselves in vegetation (Marchisin and

133 Anderson 1978). The dorsal color and spot patterning enable individuals to match background

134 vegetation (Dodd 2013). Similar to Blanchard's cricket frogs, leopard frogs likely respond first

135 through crypsis, and then seek vegetative cover. Southern leopard frogs also emit a warning

136 scream that functions to startle approaching predators, enabling individuals to escape.

137

138   *Data collection*

139   Four, *ca.* 1.5 m-wide belt transects (Amo et al. 2006) 250 m, 500 m, 750 m, and 750 m

140   long were walked at or after dusk, four times monthly from June-November 2017 to conduct

141   visual surveys (n = 96). Transects were paths and hatchery pond berms where vegetation had

142   been cleared through mowing at the edges of forested habitat. The same belt transects were

143   evaluated for each sampling event, in a randomly selected order, beginning <0.01 to 3.78 hours

144   after sunset, depending on selection order (mean = 1.06 hrs after sunset ± 0.70 SD). Transects

145   were divided into three sections - middle, edge, and boundary - to evaluate how the risk response

146   of frogs to a potential threat (presence of a human) was influenced by proximity to

147   cover/vegetation (Fig. 1). Middle sections were located within the interiors of belt transects, *ca.*

148   25 cm from cover with limited vegetation (i.e. low cut grass); edge sections were adjacent to

149   middle section *ca.* 0-25 cm from cover with limited vegetation (i.e. low cut grass); and boundary

150   sections were adjacent to edge sections at the boundary of transects, *ca.* 25 cm into vegetation

151   (grasses, forbes, trees).

152   The same researcher walked slowly on each transect (<1 m/s) to detect anurans, and then

153   moved more slowly (<0.5 m/s) upon encounters to simulate a threat, but effectively identify

154   anurans (Cooper 2009). Once detected, study taxa were visually identified to species, location

155   on transect was recorded (middle, edge, or boundary), and risk response was recorded -

156   stationary (S; i.e. a freeze response), mobile (M - moving upon encounter; i.e. a flight response),

157   or mobile-then-stationary (MS - mobile, then stationary after initial movement; i.e. a flight-then-

158   freeze response). Research was conducted under Sam Houston State University IACUC #17-02-

159   13-1034-3-01.

160

161 *Data analysis*

162   Data were organized by individual animal encounter. A generalized linear model using

163 logistic regression was used to investigate the effects of species and transect section (middle,

164 edge, boundary) on frog risk response. Due to the seasonal variability in environmental

165 conditions within the subtropical study location, and habitat use patterns of the study species

166 (Dodd 2013), monthly variability in frog behavior was considered as a predictor variable in

167 addition to species and transect section. Friedman's test was used to investigate the potential

168 effects of sampling across different months, with significant results ($\chi^2 = 35.56$, p < 0.01).

169 Therefore, sampling month was included as a factor in the model. Significant differences were

170 not found across transects ($\chi^2 = 1.06$, p = 0.90), thus data were pooled. All main effects (species,

171 section, month) and two-way interactions were included in the model:

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

173 Where s is species, x is transect section, m is month, i is the number of sampling events, j is the

174 number of species, k is the number of sections, and l is the number of months. Significance

175 thresholds were corrected for multiple post-hoc comparisons. All analyses were conducted in

176 IBM SPSS 22.

177

178 **Results**

179   From June-November 2017, 639 southern leopard frogs, 247 Blanchard's cricket frogs,

180 and 1800 green tree frogs were encountered during 24 nights of sampling across four belt

181 transects (n = 96 total; Table 1). Leopard frogs and cricket frogs were more abundant in

182 September-November, while green tree frogs were more abundant in July-September (Table 1).

183   Among southern leopard frogs, 217 encounters were in the middle of transects (34%),

184   179 were on transect edges (28%), and 243 were on transect boundaries (38%). Sixty-six

185   Blanchard's cricket frogs were encountered in the middle of transects (27%), 65 were on transect

186   edges (26%), and 116 were on transect boundaries (47%). Among green tree frogs, 42

187   encounters were in the middle of transects (2%), 56 were on transect edges (3%), and 1702 were

188   on transect boundaries (95%).

189   The generalized linear model (χ^2 = 563.88, df = 73, p < 0.01) indicated that species,

190   transect section, and sampling month, as well as each two-way interaction were significant

191   predictors of frog behavior (Table 2, 1S). Evaluation against an intercept-only model indicated

192   the significance of the model (χ^2 = 2029.99, df = 33, p < 0.01). Green tree frogs exhibited

193   greater stationary behavior than Blanchard's cricket frogs, which exhibited more mobile-then-

194   stationary behavior (χ^2 = 1482.98, p < 0.01). Green tree frogs also exhibited greater stationary

195   behavior than southern leopard frogs compared to mobile (χ^2 = 282.21, p < 0.01) and mobile-

196   then-stationary behavior (χ^2 = 1325.34, p < 0.01). Blanchard's cricket frogs exhibited more

197   mobile-then-stationary behavior than southern leopard frogs (χ^2 = 30.04, p < 0.01).

198   In general, frogs were more mobile at transect edges (χ^2 = 6.13, p = 0.01) and middles (χ^2

199   = 14.86, p < 0.01) than boundaries, however this varied across species (χ^2 = 92.45, p < 0.01). As

200   distance from vegetation increased (i.e. boundary to edge to middle), southern leopard frogs

201   increased stationary behavior (χ^2 = 101.68, p < 0.01), switching from mobile and mobile-then-

202   stationary behavior at transect boundaries, to mobile-then-stationary and stationary behavior at

203   transect edges, to stationary and mobile-then-stationary behavior in the middle of transects (Fig.

204   2, Table 3). In contrast, Blanchard's cricket frogs exhibited increased mobility from transect

205   boundary to middle ($\chi^2 = 40.05$, p < 0.01), while green tree frogs decreased stationary behavior

206   from transect boundary to middle ($\chi^2 = 353.79$, p < 0.01; Fig. 2, Table 3).

207   Temporally, green tree frogs and Blanchard's cricket frogs exhibited limited seasonal

208   trends in behavior, while southern leopard frogs exhibited a decrease in stationary behavior from

209   June to November (Fig. 3, Table 4). Southern leopard frogs and Blanchard's cricket frogs were

210   more mobile in June (17% and 20%, respectively) and July (23% and 26%, respectively)

211   compared to the rest of the sampling period (1% and 4%, respectively; Fig. 3). All three species

212   exhibited less mobile-then-stationary behavior than expected at the beginning of the sampling

213   period (June and July), and more mobile-then-stationary behavior than expected at the end of the

214   sampling period (October and November; Table 4).

215

216   **Discussion**

217   As human impacts continue to alter ecosystems, understanding animal behavior and

218   species abilities to adjust to changing landscapes is of importance for wildlife and habitat

219   management to ensure the maintenance of ecological communities (Becker et al. 2007; Battisti et

220   al. 2016; Legrand et al. 2017; Pecl et al. 2017). Our study shows that the risk response of frogs

221   in an altered forest ecosystem is both species- and context-specific, with some species (i.e.

222   southern leopard frogs) at potentially greater risk to human actions in open terrain than others

223   (i.e. green tree frog). As mobile species, frogs are able to avoid predators and other risks through

224   both flight and camouflage (Marchisin and Anderson 1978). However, the efficacy of risk

225   responses may differ based on characteristics of habitat (open or covered) and risk (visual,

226   olfactory, heat sensing, non-consumptive, natural vs unnatural; Gregory 1979; Wells 2007;

227   Bulbert et al. 2015). Our results suggest that morphology, including the ability to use trees and

228   other vegetation as refuge, and body size can potentially lead to important differences in the

229   response of animals to risk factors.

230   As predicted, arboreal green tree frogs decreased stationary behavior as the distance to

231   vegetative cover increased, likely due to their propensity to use the canopy of vegetation for

232   refuge (Dodd 2013). Similarly, Blanchard's cricket frogs, a ground-dwelling species, increased

233   mobility as distance to cover increased, which could be attributed to the inherent risk faced by

234   this species based on its small body size (Werner and Gilliam 1984). Supportive of our second

235   hypothesis, southern leopard frogs exhibited the greatest likelihood to freeze in more open terrain

236   (i.e. middle sections of transects), with increased stationary behavior as distance to cover

237   increased. Movement may serve as an indicator to visual predators (Ioannou and Krause 2009),

238   and therefore some ground dwelling frogs may remain stationary, and even flatten themselves

239   against the substrate to avoid detection by predators, such as snakes, birds, and mammals

240   (Marchisin and Anderson 1978). Species-specific differences in risk responses may also be

241   innate - some amphibians actively evade predators (e.g. Tollrian and Harvell 1999), some species

242   engage or scare predators (e.g. Altig 1974), and many remain motionless and use camouflage to

243   blend in to their environments to avoid detection (e.g. Marchisin and Anderson 1978; Stevens

244   and Merilaita 2011).

245   Yet, species with greater tendencies to remain stationary in open but risky habitats may

246   face greater challenges adjusting to human-altered landscapes, with larger-bodied, ground

247   dwelling animals (e.g., leopard frogs) potentially at greater risk of human-induced injury or

248   mortality in unvegetated habitats compared to tree dwelling species (Beebee 2013; Sosa and

249   Schalk 2016). Camouflage is a primary antipredator response of many frogs (Marchisin and

250   Anderson 1978), and all three study species exhibited stationary behavior (98%, 30%, and 13%,

251   respectively for green tree frogs, southern leopard frogs, and Blanchard's cricket frogs), overall

252   with more frequent freeze responses in more vegetated transect sections (boundary, edge). In

253   terrestrial habitats, species at risk may be more vigilant as terrain becomes less protected by

254   vegetation or landscape features, and flee into more covered habitat when risk exceeds a

255   threshold in open habitats (Edut and Eilam 2003; Stankowich 2008). Green tree frogs and

256   Blanchard's cricket frogs followed this model, while southern leopard frogs did not, exhibiting

257   an inverse relationship between distance to cover and flight (Takada et al. 2018).

258   Across human-altered ecosystems, some innate behaviors remain beneficial, and the

259   plasticity of other behaviors make them more advantageous in disturbed ecosystems (Chace and

260   Walsh 2006; McKinney 2006; McCleery 2009). For example, the scavenging nature of some

261   predators increases their foraging efficiency in urban and suburban environments where

262   discarded human food is nutritionally beneficial and widely available, reducing energetic costs

263   (e.g. Fedriani et al. 2001; Merkle et al. 2013). Similarly, human structures can be readily

264   incorporated and utilized by species that rely on camouflage for protection (Merilaita 2003;

265   Banos-Villaba et al. 2018). However, camouflage in ecosystems used by humans is likely most

266   effective for species that blend-in with elevated structure, both natural and man-made. Indeed,

267   camouflage and freeze responses among ground-dwelling species likely provide little protection

268   from agricultural, landscaping, and transportation practices, each presenting lethal risk

269   (Trombulak and Frissell 2000; Kirk et al. 2001; Carvalho et al. 2017). For many species,

270   humans present unnatural conditions and perturbations that heighten risk (Cushman 2006; Wong

271   and Candolin 2015; Li et al. 2017). Yet while camouflage may be the primary risk response of

272   many frogs, this behavior is apparently not ubiquitous among all species, enabling some taxa to

273   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

296   in activity levels and behavior of frogs (Lode 2000; Sperry et al. 2008), however more controlled

297   experiments are needed to test these hypotheses.

298

299   *Conclusions*

300   Habitat degradation continues to pose important conservation concerns across all

301   ecosystems, including forests harvested for timber and converted to agricultural and ranch lands

302   (Arroyo-Rodriguez et al. 2017; Lourenco et al. 2017; Tilman et al. 2017). Amphibians rely on

303   tropical, subtropical, and temperate forests for habitat and food resources, and in strongholds

304   where diseases have not infected populations, habitat management and conservation is of great

305   importance (Stuart et al. 2004; Grant et al. 2016). Our results suggest that differences in distance

306   to cover, habitat use patterns, and body size may affect frog behavior, with a greater propensity

307   for flight responses to risk by arboreal frogs in open terrain (green tree frogs), and a greater

308   propensity for freeze responses to risk by larger, ground-dwelling frogs (southern leopard frogs).

309   With growing perturbations to many forested regions, these context-specific behaviors are of

310   important consideration for future conservation and management in human-altered systems.

311

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318

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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 .

1 Table 1: Sample sizes of study species observed during sampling period from June – November
2 2017.
3

Species	Month	N
L. sphenocephalus	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

4
5

Table 2 (on next page)

Test statistics for the generalized linear model .

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*.

1 Table 2: Test statistics for the generalized linear model investigating the effects of species,
2 location on transection (i.e. section), and sampling month on the risk response of *A. blanchardi*,
3 *H. cinerea*, and *L. sphenocephalus*.
4

Factor	χ^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

5

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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.

1   Table 3: Post hoc results for chi squared test of location-specific differences in risk behavior. M
2   indicates mobile behavior, MS indicates mobile-then-stationary behavior, S indicates stationary
3   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

4

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.

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

	Jun	Jul	Aug	Sep	Oct	Nov
L. sphenocephalus	-MS	-MS, +M	-MS, -M	ND	+MS	+MS
A. blanchardi	-MS	+M	ND	+MS	+MS	+MS
H. cinerea	ND	-MS	ND	ND	+MS	+MS

6

Figure 1(on next page)

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.
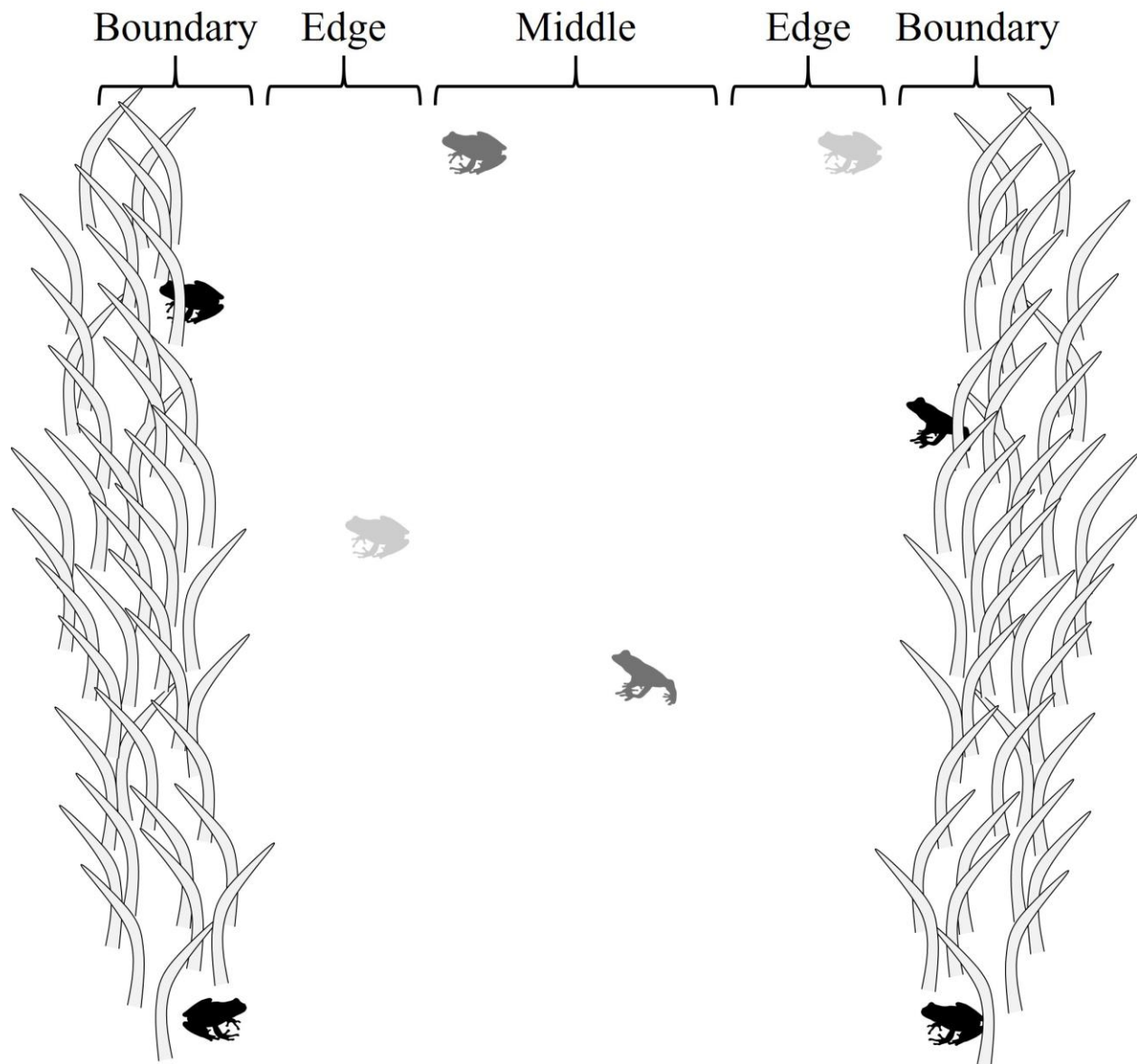
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Figure 1: Transect sections used to evaluate how the risk response of frogs was influenced by proximity to cover. Middle sections were located *ca.* 25 cm from cover; edge sections were *ca.* 0-25 cm from cover; and boundary sections were adjacent 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.

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. sphenocephalus), 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*).
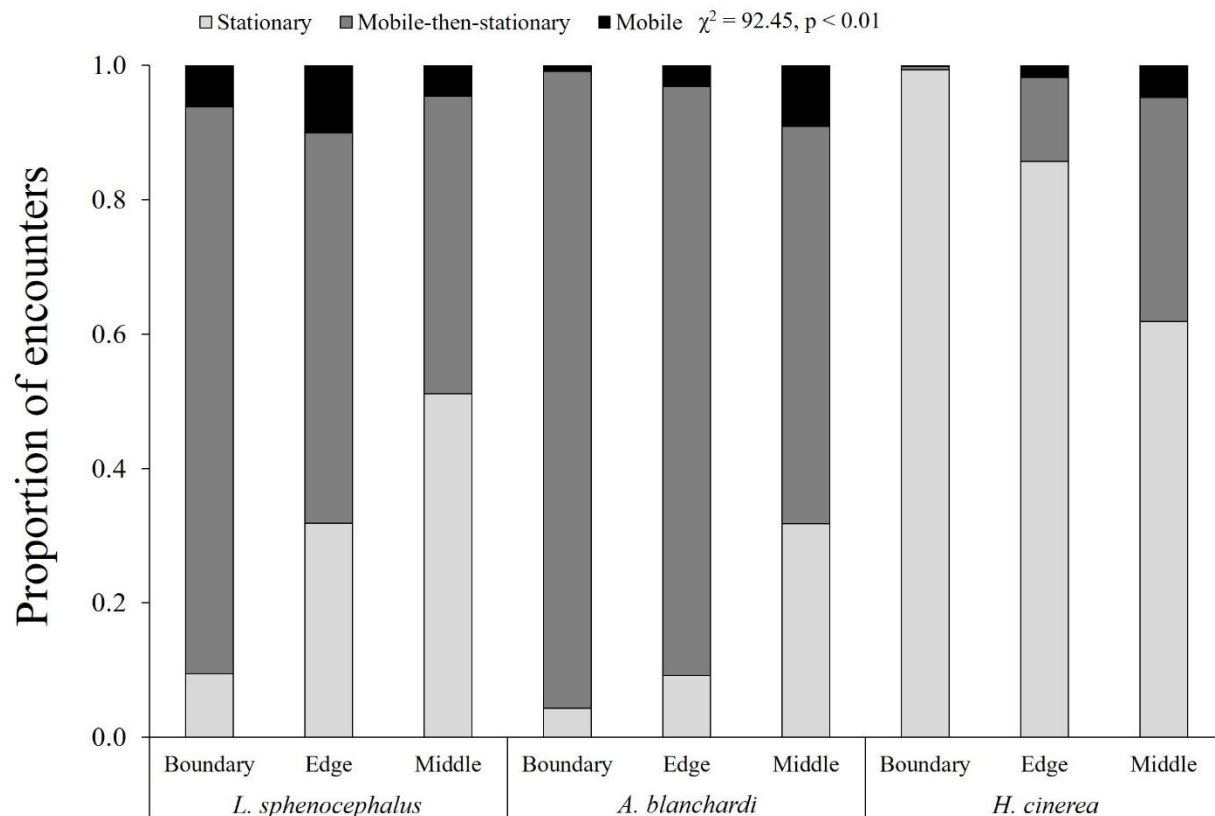
Figure 3(on next page)

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*).