

## Seasonal Microhabitat Selection and Use of Syntopic Populations of *Lithobates okaloosae* and *Lithobates clamitans clamitans*

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**ABSTRACT.**—Quantifying and comparing habitat selection of related, syntopic species may help elucidate how species partition resources and compete. The Florida Bog Frog (*Lithobates okaloosae*) is endemic to northwestern Florida and is syntopic with the more widely distributed Bronze Frog (*Lithobates clamitans clamitans*). Our objective was to determine whether these closely related frogs selected different microhabitat characteristics at male calling sites, which in turn may influence successful reproduction or survival. From 2006 to 2008, we quantified microhabitat characteristics of male calling sites used by both species on Eglin Air Force Base, Florida. We created a suite of a priori models and used paired logistic regression to assess each species' habitat selection. Further, we compared habitat characteristics from each species' most highly supported model to directly compare habitat use. Model selection indicated that calling sites for *L. okaloosae* were best described by habitat features related to microhabitat cover (i.e., submergent vegetation, emergent vegetation, woody debris, frog-level canopy cover, distance to cover), whereas *L. c. clamitans* selected sites based on features that may be favorable for female oviposition or egg development (i.e., depth, water movement, depth × water movement interaction). Further, *L. c. clamitans* selected sites with 3.7 times less submergent vegetation and 1.6 times greater water depths than *L. okaloosae*. At this scale, these ranids select microhabitat differently; however, there is overlap among some selected variables. The habitat characteristics used by *L. okaloosae* may be associated with fire in the uplands and occasionally in the wetlands.

Understanding the role of competition in structuring communities is an important aspect of ecology. Directly interpreting competitive interactions between closely related species can be difficult, but it is assumed generally that coexistence of two species with similar ecological niches is the result of resource partitioning (Schoener, 1968). Resource partitioning between species can be influenced by multiple factors, including present and historical competitive interactions (Connell, 1980), predation, and physiological constraints (Toft, 1985). Generally, components of a species' niche are related to habitat, and knowledge of species-specific habitat relationships can also be considered an important component of conservation and management (Hobbs and Hanley, 1990; North and Reynolds, 1996). In particular, habitats where specific activities are carried out, such as feeding or breeding, can offer insight into a species' niche.

The Florida Bog Frog (*Lithobates okaloosae*), a northwestern Florida endemic, was discovered in 1982 (Moler, 1985). There is a paucity of information related to its habitat associations and life history. *Lithobates okaloosae* is the smallest member of the genus, and it has been found in relatively few locations in northwestern Florida (Gorman, 2009). The portion of Florida where *L. okaloosae* occurs includes a system of "steephead" ravines (i.e., perennial first-order streams that originate from springs [Means, 1975]) that are near the coastal plain of the Gulf of Mexico (Means, 2000). These types of drainages are thought to have become isolated by 2–5 m increases in sea level (Means, 2000). It has been hypothesized that the isolation of these drainages may have led to the differentiation of several new species (Means, 2000) and may have been a primary factor in the differentiation of *L. okaloosae* from the Bronze Frog (*Lithobates clamitans clamitans*). In contrast to *L. okaloosae*, *L. c. clamitans* is widely distributed and occurs throughout most of the southeastern United States. *Lithobates clamitans clamitans* is closely related to *L. okaloosae* (Austin et al., 2003) and is potentially its principal interspecific competitor (Moler, 1992).

Many members of the genus *Lithobates* have overlapping geographic ranges. For example, in northwestern Florida, Pig Frog (*Lithobates grylio*), Southern Leopard Frog (*Lithobates sphenoccephalus*), *L. c. clamitans*, and *L. okaloosae* all have overlapping ranges (Lannoo, 2005), and all of these species can occur at the same sites and be heard calling on the same night (TAG, unpubl. data). However, these ranids have

evolved different strategies for breeding and attracting mates, and it is believed that at some scale, whether temporal or spatial, resource partitioning occurs among these species. For example, *L. sphenoccephalus* generally breed from December to March, which only slightly overlaps the later breeding season of the other three ranids (Lannoo, 2005). However, aggressive interactions between *L. c. clamitans* and *L. sphenoccephalus* have been reported (Ritchie et al., 2008). *Lithobates grylio*, *L. c. clamitans*, and *L. okaloosae* are prolonged breeders and breed primarily from March to August (Lamb, 1984; Martof, 1953; Moler, 1992, respectively). *Lithobates grylio* call from deeper water (Lamb, 1984) and, therefore, do not appear to use the same microhabitats as these other species.

In contrast to these examples of occasional interactions, *L. c. clamitans* appears to be syntopic with *L. okaloosae* during their prolonged spring/summer breeding season (Gorman et al., 2009). In addition, hybrids between these two species have been reported (Moler, 1993; Bishop, 2005; Austin et al., 2011a). Based on nearest neighbor distances and dynamic interactions, *L. okaloosae* and *L. c. clamitans* did not appear to spatially exclude each other during the breeding season (Gorman et al., 2009). Instead, these two species had a clumped distribution at breeding sites, which suggested they may compete for resources that make up suitable calling sites.

Our goal was to evaluate the microhabitat selection of male *L. okaloosae* and *L. c. clamitans* and to compare the amount of overlap in microhabitat use between them when males are selecting calling sites. We hypothesized that *L. okaloosae* would be a habitat obligate and select a narrower range of conditions compared to *L. c. clamitans* and that we would observe differences in microhabitat selected. Further, we predicted that the factors influencing site selection would include (1) variables describing cover for protection to calling males from predators, (2) variables describing good conditions for oviposition, or (3) variables that may encompass both increased cover and oviposition potential (Table 1). Therefore, we created a small suite of models that incorporated habitat variables known to be important for anuran reproduction and survival to fit within each of these three overarching predictions.

### MATERIALS AND METHODS

**Study Area.**—The study area is located on Eglin Air Force Base (Eglin) in Okaloosa and Santa Rosa counties in northwestern Florida (Fig. 1). Eglin occurs within the Gulf Coastal

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TABLE 1. A priori models developed to predict whether male frogs would (1) select calling sites that were suitable for female oviposition, (2) select sites that would provide cover from predators, or (3) select a combination of these characteristics. Models were grouped by prediction and in order of increasing complexity. This model set was used for the analyses of both *Lithobates okaloosae* and *Lithobates clamitans clamitans* microhabitat data from four sites on Eglin Air Force Base, Okaloosa and Santa Rosa counties, Florida, 2006–08.

Model name	Model variables
(1) Models associated with the potential for female oviposition	
Depth	Depth
Depth/water movement	Depth, water movement, depth $\times$ water movement
Thermoregulation	Water temperature, canopy, water temperature $\times$ canopy
Water	Depth, water movement, depth $\times$ water movement, water temperature, pH, water temperature $\times$ pH
Water/emergent	Depth, emergent, water movement, water temperature, pH, water temperature $\times$ pH
(2) Models associated with the potential of increased cover from predators	
Macrohabitat cover	Canopy, basal area, basal area $\times$ canopy
Microhabitat cover	Distance to cover, woody debris, emergent, submergent, frog-level canopy
(3) Models with components of both increased cover and oviposition potential	
Microhabitat cover/water	Depth, water movement, depth $\times$ water movement, emergent, submergent, distance to cover
Water/distance to cover	Depth, water movement, depth $\times$ water movement, water temperature, pH, water temperature $\times$ pH, distance to cover
Global	Depth, water movement, depth $\times$ water movement, water temperature, pH, water temperature $\times$ pH, emergent, submergent, woody debris, distance to cover, frog-level canopy, basal area, canopy cover, basal area $\times$ canopy

Plain physiographic province and the overall topography has little relief, but there are steep ravines associated with headwater streams (i.e., steepheads), where slopes can be  $\geq 30\%$  (Means, 1975; Eglin Air Force Base, 2002). The vegetation associated with these steepheads and other wetlands used by *L. okaloosae* is dominated by black titi (*Cliftonia monophylla*), sweetbay magnolia (*Magnolia virginiana*), Atlantic white cedar (*Chamaecyparis thyoides*), swamp titi (*Cyrilla raceformia*), and blackgum (*Nyssa sylvatica*) (Gorman, 2009). The upland habitat of the study area is a longleaf pine (*Pinus palustris*) and turkey oak (*Quercus laevis*) sandhill community that encompasses the majority of Eglin. We selected four sites where both *Lithobates okaloosae* and *L. c. clamitans* occurred; no sites are known where *L. okaloosae* occurs without *L. c. clamitans*. The study sites were

located on three separate streams (two sites were located on one stream and were separated by approximately 1.3 km straight line distance) that occurred within the known geographic range of *L. okaloosae*. Two study sites were located at steepheads (i.e., Live Oak Tributary and East Bay), and two sites were located adjacent to the main stream channel (i.e., Live Oak Creek and Weaver Creek).

**Capture.**—We captured and marked *L. okaloosae* and *L. c. clamitans* at night when the frogs were most active from May to August 2006–08. During each sampling event, we extensively searched each site to capture calling males of both species. We marked individuals of both species uniquely using visible implant alphanumeric (VIA) tags (Northwest Marine Technologies Inc., Olympia, WA). Tags were implanted into the hind

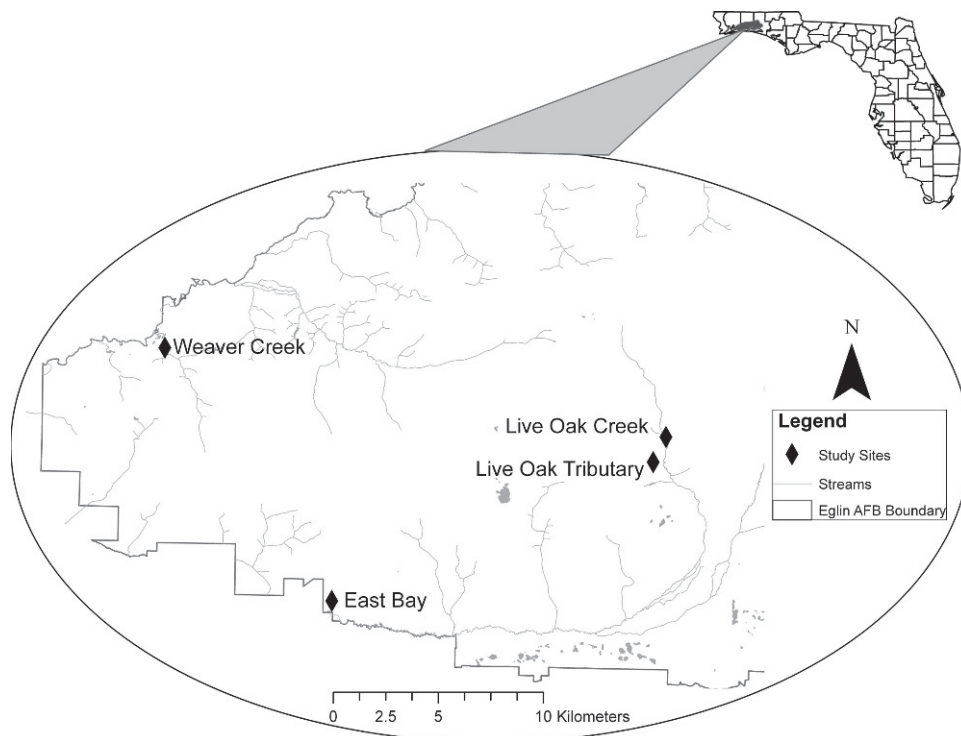


FIG. 1. Location of four study sites (diamonds) where we captured and marked *Rana okaloosae* and *Rana clamitans clamitans* and sampled used and random habitat characteristics, Eglin Air Force Base, Florida, 2006–08.

limb of the frog. A blood lancet was used to make a small incision in the skin, and then a tag implanter was used to insert the tag between the skin and the adductor muscles (Buchan et al., 2005). Visible implant alphanumeric tags have been used successfully in other members of the family Ranidae and are used extensively in *Pseudacris regilla*, a hylid as small as *L. okaloosae* (Buchan et al., 2005).

**Morphology.**—We determined the sex of each individual primarily by its calling status and secondarily for *L. okaloosae* by examining the presence or absence of vocal air sacs (Bishop, 2005) and for *L. c. clamitans* by assessing the size of its tympanum (Martof, 1956). We voided the bladder and weighed each animal to the nearest 0.2 g using a 20 g Pesola scale or to the nearest 0.5 g using a 60 g Pesola scale and measured the snout-vent length to the nearest 0.1 mm using dial calipers. We compared body weight and snout-vent length between syntopic species using independent samples *t*-tests.

**Microhabitat Selection.**—Capture locations were marked and georeferenced with a Trimble Asset Surveyor TDC2 GPS unit (Trimble Navigation Limited, Sunnyvale, CA) with submeter resolution. Microhabitat variables were measured at the first location where each individual was captured and at a paired random location (Compton et al., 2002). Paired locations were chosen by randomly selecting a distance between 1 and 5 m (the range of distance that encompasses the mean minimum daily distance moved for both species [Gorman et al., 2009]) from the initial location of the frog at a random azimuth. Paired locations were restricted to the wetland area. Therefore, we did not compare a used location at one study site with a random location at another.

We measured habitat variables that may affect the quality of oviposition sites (i.e., water depth, pH, water temperature, water movement) (Crump, 1991; Watson et al., 2003; Bishop, 2005) and variables that may reflect escape cover for calling males (i.e., distance to cover, basal area, and percentage of canopy cover at frog-level [i.e., a measure of ground-level horizontal cover]) (Watson et al., 2003; Bishop, 2005; Smith et al., 2005), and variables that may be important for both oviposition and escape (i.e., percentage of canopy cover at 1.5 m, percent cover of submergent vegetation, percent cover of emergent vegetation [i.e., a measure of ground-level vertical cover], and percent cover of woody debris) (Crump, 1991; Watson et al., 2003; Bishop, 2005; Smith et al., 2005). We measured water depth using a metric ruler. We measured pH and water temperature using an Extech ExStik II meter that records these parameters simultaneously. Water movement (i.e., flow of water) was recorded as a binary variable (i.e., movement or no movement). Distance to cover was measured to the closest discernible point where cover was available that would conceal above and  $\geq 3$  sides of an individual (e.g., undercut bank or hummock). We measured basal area using a Jim-Gem Cruz-All (English basal area factor of 5) at both the used and random locations and recorded the number of trees that contributed to the basal area. We measured the percent of canopy cover using a convex spherical densiometer at the level of the frog and at 1.5 m above the ground. We visually estimated the percentage of emergent (e.g., *Sphagnum* spp. and *Carex* spp.) and submergent vegetation (e.g., algal mats and submergent *Carex* spp.) and the percentage of woody debris within a  $0.5 \times 0.2$  m rectangular plot at the used and random locations using the Daubenmire (1959) cover class scale.

We used a paired logistic regression approach to estimate habitat selection of *L. okaloosae* and *L. c. clamitans* at the microhabitat scale (Hosmer and Lemeshow, 1989; Compton et al., 2002). This logistic regression technique uses the difference between the used site and a paired random site to create a vector of the differences for all the independent variables and the dependent variable. The logistic procedure is then performed on these vectors so that models do not include an

TABLE 2. Number of individuals and the percentage of individuals of *Lithobates okaloosae* and *Lithobates clamitans clamitans* captured at four study sites on Eglin Air Force Base, Okaloosa and Santa Rosa counties, Florida, 2006–08.

Site	<i>L. okaloosae</i>	<i>L. c. clamitans</i>	<i>L. okaloosae</i> (%)	<i>L. c. clamitans</i> (%)
Weaver	18	19	18.2	33.9
East Bay	23	8	23.2	14.3
Live Oak Trib.	44	21	44.4	37.5
Live Oak	14	8	14.1	14.3
Total	99	56	100.0	100.0

intercept term. Also, this approach facilitates comparison of used locations with a paired location at the same place and time and under the same habitat availability and weather conditions (Compton et al., 2002; Moore and Gillingham, 2006) making this approach more appropriate for species with limited mobility. This approach has been used successfully for other pond- or stream-dwelling herpetofauna (e.g., Compton et al., 2002; Harden et al., 2009). We used an information-theoretic approach and Akaike's Information Criteria (AIC) corrected for small sample sizes (AIC<sub>c</sub>) to examine the relative strength of a priori hypotheses. We considered the model with the lowest AIC<sub>c</sub> to be the model with the best balance between statistical parsimony and goodness of fit for the empirical data (Burnham and Anderson, 2002). Further, we considered models with  $\Delta AIC_c$  values  $\leq 2.0$  as equally supported by the data (Burnham and Anderson, 2002) and models that were  $>2.0$  and  $<4.0$  to have some support.

**Microhabitat Overlap.**—We compared the most highly supported models for *L. okaloosae* and *L. c. clamitans* to evaluate the similarity between the habitat selection of calling sites between the two species. Further, we compared the means of the habitat variables present in the most highly supported *L. okaloosae* and *L. c. clamitans* models of habitat selection with a Hotelling's  $T^2$ . If a difference between the two species was detected with the omnibus Hotelling's  $T^2$  then we continued with a series of univariate *t*-tests. For all analyses, we used SAS 9.2 (SAS Institute Inc., Cary, NC) and set  $\alpha = 0.05$ .

## RESULTS

We captured 99 male *L. okaloosae* and 56 male *L. c. clamitans* at four study sites on Eglin from 2006 to 2008 (Table 2). *Lithobates okaloosae* had a mean mass of 6.3 g (SE = 0.2, range = 1.9–13.8) and mean snout-vent length of 39.7 mm (SE = 0.4, range = 26.6–49.8). *Lithobates clamitans clamitans* had a mean mass of 22.9 g (SE = 1.0, range = 10.2–48.4) and mean snout-vent

TABLE 3. Paired logistic regression modeling results of microhabitat selection of male *Lithobates okaloosae* ( $N = 99$ ) at four sites on Eglin Air Force Base, Okaloosa and Santa Rosa counties, Florida, 2006–08 ( $k$  = number of parameters, AIC<sub>c</sub> = second-order Akaike's Information Criteria [i.e., for small sample sizes],  $\Delta AIC_c$  = the change in AIC<sub>c</sub>, and  $w_i$  = the relative amount of support for the model). Variables included in each model are listed in Table 1.

Model	$k$	AIC <sub>c</sub>	$\Delta AIC_c$	$w_i$
Microhabitat cover	5	110.56	0.00	0.85
Microhabitat cover/water	6	114.11	3.55	0.14
Global	14	125.65	15.08	0.00
Water/emergent	8	131.20	20.64	0.00
Water/distance to cover	6	131.50	20.93	0.00
Depth/water movement	3	133.20	22.63	0.00
Macrohabitat cover	3	133.36	22.80	0.00
Water	6	137.72	27.15	0.00
Depth	1	138.13	27.57	0.00
Thermoregulation	3	139.41	28.85	0.00

TABLE 4. Parameter coefficients, odds ratios, and 95% confidence intervals for the most highly supported model of microhabitat selection of male *Lithobates okaloosae* at four sites on Eglin Air Force Base, Okaloosa and Santa Rosa counties, Florida, 2006–08.

Parameter	Coefficient	Estimate	Odds ratio	
			95% Confidence limit	
			Low	High
Distance to cover	-0.043	0.958	0.929	0.988
Woody debris	0.025	1.025	1.002	1.048
Emergent vegetation	0.017	1.017	0.999	1.034
Submergent vegetation	0.052	1.053	1.022	1.086
Frog-level canopy	-0.003	0.997	0.971	1.024

length of 59.1 mm (SE = 1.0, range = 36.8–80.0). *Lithobates clamitans clamitans* were 3.6 times larger than *L. okaloosae* in mass ( $t = -16.59$ ,  $P < 0.001$ ) and had 1.5 times larger snout-vent lengths ( $t = -19.04$ ,  $P < 0.001$ ; Fig. 1).

Our modeling suggested that male *L. okaloosae* select a suite of habitat characteristics describing high levels of microhabitat cover that are consistent with reducing predation risk (Table 3). The most highly supported of the 10 a priori models included distance to cover, percent cover of woody debris, percent cover of emergent vegetation, percent cover of submergent vegetation, and frog-level canopy (Table 3). *Lithobates okaloosae* used sites that had a distance to cover that was 2.3 times less than random locations. Odds ratios of coefficients predicted a 4.2% decrease in the chance of a site being used with every 1 cm in increase from cover, a 2.5% increase in use of a site for every 1% increase in woody debris, a 5.3% increase in use for every 1% increase in submergent vegetation, and a 1.7% increase in use of a site for every 1% increase in emergent vegetation (only marginally significant) (Table 4). Frog-level canopy was not significantly different between random and used sites (Table 5). When considering mean values for used versus random sites, percent cover at used sites was 1.4 times greater for woody debris, 1.5 times greater for emergent vegetation, and 1.6 times greater for submergent vegetation. Frog-level canopy was similar between used and paired random sites (Table 5). The second most supported model was  $>2.0 \Delta AIC_c$  from the most highly supported model. This model included depth, water movement, the interaction of depth and water movement, emergent vegetation, submergent vegetation, and distance to cover (Table 3).

For *L. c. clamitans*, modeling suggested that males select sites with still, shallow water that were likely more attractive for female oviposition (Table 6). The most highly supported model of the 10 a priori models included water movement, water depth, and the interaction of these two characteristics (Table 6).

The odds ratio of the coefficient for the interaction of water depth and water movement predicted a 2.5% increase in use of a site when there is a decrease in water movement and a decrease in depth. Individually, water depth and water movement were not significant (Table 7). The mean values of sites used by *L. c. clamitans* were 1.5 times less likely to have water movement than random sites and had 1.1 times less water depth than random (Table 5). The second most supported model was slightly  $> 2.0 \Delta AIC_c$  from the most highly supported model. This model included depth, water movement, the interaction of depth and water movement, emergent vegetation, submergent vegetation, and distance to cover (Table 6).

We detected differences between the microhabitat characteristics used by *L. okaloosae* and *L. c. clamitans* (Wilks  $\lambda = 0.845$ ,  $df = 147$ ,  $T^2 = 124.22$ ,  $P < 0.001$ ) based on the variables that were the best predictors of *L. okaloosae* and *L. c. clamitans* calling sites (Tables 3, 6). Subsequent univariate tests of habitat characteristics determined that *L. okaloosae* selected calling sites with 3.7 times more submergent vegetation ( $df = 153$ ,  $t = -3.24$ ,  $P = 0.002$ ) and 1.6 times less water depth ( $df = 153$ ,  $t = 3.43$ ,  $P < 0.001$ ) than *L. c. clamitans* (Table 5). We did not detect a difference between distance from cover ( $df = 153$ ,  $t = -1.77$ ,  $P = 0.078$ ), percent of woody debris ( $df = 153$ ,  $t = -1.65$ ,  $P = 0.101$ ), water movement ( $df = 153$ ,  $t = 1.25$ ,  $P = 0.213$ ), frog-level canopy cover ( $df = 153$ ,  $t = 1.44$ ,  $P = 0.152$ ), or percent of emergent vegetation ( $df = 153$ ,  $t = -1.17$ ,  $P = 0.242$ ) between the two species (Table 5).

#### DISCUSSION

Our results suggest that male *L. okaloosae* and *L. c. clamitans* are selecting different microhabitat characteristics when choosing a calling site. *Lithobates okaloosae* selected for a suite of habitat characteristics associated with increased cover. Further, *L. okaloosae* selected for features within a site at a higher frequency than they were available, which may indicate they are an obligate user of those microhabitats. In contrast, *L. c. clamitans* did not select for specific vegetative features, which suggests they are less dependent on vegetative cover. In addition to the modeling of habitat selection, direct comparison of the variables that were selected by each species suggests that *L. okaloosae* and *L. c. clamitans* did not select for the same microhabitat characteristics. However, there was overlap in the habitat characteristics used by these two syntopic species.

At broader spatial scales, our surveys indicate vast overlap in sites that are used by these two species (Gorman, 2009), but at fine spatial scales, there was separation in habitat characteristics selected. Therefore, these results are an example of the importance of choosing scale appropriately (Wiens, 1989), because at the microhabitat scale, we observed a difference in

TABLE 5. Mean habitat characteristics and standard errors (SE) at used calling sites of male *Lithobates okaloosae* (LO) ( $N = 99$ ) and male *Lithobates clamitans clamitans* (LC) ( $N = 56$ ) and respective paired random sites at four study sites on Eglin Air Force Base, Okaloosa and Santa Rosa counties, Florida, 2006–08.

Habitat variables	LO used	LO random	LC used	LC random
	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)
Depth (cm)	3.1 (0.3)	3.5 (0.3)	4.8 (0.5)	5.2 (0.7)
pH	5.19 (0.03)	5.19 (0.03)	5.32 (0.02)	5.32 (0.02)
Water temperature (°C)	25.4 (0.2)	25.5 (0.2)	24.8 (0.3)	25.0 (0.3)
Water movement (%)	15.2 (3.6)	30.3 (4.6)	23.2 (5.7)	35.7 (6.5)
Distance to cover (cm)	10.1 (1.4)	23.5 (3.6)	6.3 (1.4)	12.9 (2.8)
Basal area (m <sup>2</sup> /ha)	9.9 (0.6)	10.4 (0.6)	9.1 (0.7)	9.1 (0.7)
Frog-level canopy (%)	73.7 (1.9)	72.0 (2.3)	78.3 (2.5)	72.0 (3.5)
Canopy cover (%)	62.0 (2.2)	60.4 (2.4)	66.8 (3.3)	62.7 (3.9)
Emergent (%)	32.2 (2.8)	22.1 (2.8)	26.7 (3.8)	21.0 (3.7)
Submergent (%)	18.0 (2.9)	11.3 (2.0)	4.8 (1.6)	4.6 (1.3)
Woody debris (%)	19.1 (2.0)	13.8 (1.6)	13.3 (3.1)	12.0 (1.8)

TABLE 6. Paired logistic regression modeling results of microhabitat selection of male *Lithobates clamitans clamitans* ( $N = 56$ ) at four sites on Eglin Air Force Base, Florida, 2006–08 ( $k$  = number of parameters,  $AIC_c$  = second-order Akaike's Information Criteria [i.e., for small sample sizes],  $\Delta AIC_c$  = the change in  $AIC_c$ , and  $w_i$  = the relative amount of support for the model). Variables included in each model are listed in Table 1.

Model	k	$AIC_c$	$\Delta AIC_c$	$w_i$
Depth/water movement	3	74.82	0.00	0.54
Microhabitat cover/water	6	76.91	2.09	0.19
Water/distance to cover	8	79.19	4.38	0.06
Thermoregulation	3	79.33	4.52	0.06
Depth	1	79.46	4.64	0.05
Microhabitat cover	5	79.87	5.05	0.04
Water	6	80.42	5.60	0.03
Macrohabitat cover	3	81.83	7.01	0.02
Water/emergent	6	86.42	11.60	0.00
Global	14	96.81	21.99	0.00

selection, whereas at broader spatial scales, these differences are less apparent. It is possible that we might have found stronger differences in resource use if we had not limited our studies of *L. c. clamitans* to sites where *L. okaloosae* also occurs. Sites where *L. okaloosae* do not occur may reflect past competition for resources. Thus, it is possible that the limited geographic range of *L. okaloosae* can be explained by competitive exclusion by *L. c. clamitans* from sites that would be marginal for *L. okaloosae* (e.g., deeper water and lower amounts of cover). However, it is equally possible that *L. okaloosae* are so specialized in exploiting a specific habitat type that they may view adjacent deeper water habitats as barriers to dispersal and will not attempt to exploit these habitats, as has been hypothesized for other species that occur in similar habitat types (e.g., Means, 1975). Further, recent genetic evidence suggests that *L. okaloosae* have limited dispersal (Austin et al., 2011b). This seems likely because steephead habitat is a rare habitat type that does not occur much beyond a few counties in the northwestern panhandle of Florida (Florida Fish and Wildlife Conservation Commission, 2005). Thus, specialization in exploiting this habitat type would leave *L. okaloosae* with little ability to expand its geographic range.

The large differences in weight and snout-vent length between *L. okaloosae* and *L. c. clamitans* may be good predictors that these two species are not directly competing for resources. Differences in size could suggest that these two species partition other resources beyond calling sites, such as prey items. Further, there are other clear morphological differences between these two species. For example, *L. okaloosae* has reduced webbing and long toes (Moler, 1985), which is likely an adaptation that resulted from the species' exclusive use of shallow water habitats. Although shallow water was not present in the most highly supported model for *L. okaloosae*, this only suggests that within a site where *L. okaloosae* breed there are no differences between water depths at used and random sites (i.e., both occurred in shallow water). Further, there do appear to be differences in habitat selection within a site between *L. okaloosae* and *L. c. clamitans*. Water depth was one habitat characteristic where differences were detectable, but there were other characteristics with overlap, and the two species do occasionally interbreed (Moler, 1993; Bishop, 2005; Austin et al., 2011a). Therefore, it is possible that following the divergence between the two species, *L. c. clamitans* recolonized areas where they had been excluded during the period of higher sea levels and subsequently came in contact with *L. okaloosae*. *Lithobates clamitans clamitans* are known to be capable of moving large distances (Lamoureux and Madison, 1999) and may be more capable of dispersing to new habitats than are *L. okaloosae*. It has been hypothesized that hybridization occurs

TABLE 7. Parameter coefficients, odds ratios, and 95% confidence intervals for the most highly supported model of microhabitat selection of male *Lithobates clamitans clamitans* at four sites on Eglin Air Force Base, Okaloosa and Santa Rosa counties, Florida, 2006–08.

Parameter	Coefficient	Estimate	Odds ratio	
			Low	High
Depth	0.108	1.114	0.943	1.354
Water movement	-0.507	0.951	0.860	1.045
Depth $\times$ water movement	0.253	1.026	1.006	1.057

more frequently when one species in the interaction is a recent invader of the habitat or when one species in the interaction is rare (Randler, 2002; Riley et al., 2003). Currently, research is being directed toward understanding the conservation genetics of these two species and how hybridization is impacting populations of *L. okaloosae* (Austin et al., 2011a).

*Lithobates okaloosae* is a rare species of conservation concern that occurs primarily in a region where the suitable habitat type used by the species is also uncommon (Means, 1975). Therefore, conservation of *L. okaloosae* should focus on maintaining breeding habitats of high quality that can support all life stages of the species. High-quality breeding habitats should have an abundance of cover (e.g., woody debris and emergent and submergent vegetation), which should provide the best attributes for survival and female oviposition sites (i.e., emergent vegetation and coarse woody debris are often used as attachment sites for egg masses; Bishop, 2005). Further, patches of suitable habitat may need to be in close proximity, because populations appear to be displaying metapopulation dynamics (Gorman, 2009) and *L. okaloosae* may have limited dispersal capabilities. Habitat characteristics used by *L. okaloosae* may be a result of fire in both the uplands and occasionally in the wetlands (Enge, 2005). For example, submergent vegetation (e.g., algal mats) may increase following upland fires, because of higher nutrient concentrations in runoff (Minshall et al., 2001). Also, fire may play a role in increasing other forms of cover and may increase hydroperiod by decreasing the amount of woody vegetation and, thus, evapotranspiration in the surrounding area (Provencher et al., 2001, 2003). In addition to high quality breeding habitat, many anurans also require high-quality terrestrial habitat that surrounds breeding sites (Semlitsch, 2002). Terrestrial habitat can be important as refugia, for feeding, or to facilitate movement among breeding sites (Semlitsch, 2002). However, habitat use by *L. okaloosae* during the nonbreeding season and the importance of upland habitats for overwintering is not well studied and warrants investigation.

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#### LITERATURE CITED

- AUSTIN, J. D., S. C. LOUGHEED, P. E. MOLER, AND P. T. BOAG. 2003. Phylogenetics, zoogeography, and the role of dispersal and vicariance in the evolution of the *Rana catesbeiana* (Anura: Ranidae) species group. *Biological Journal of the Linnean Society* 80:601–624.

- AUSTIN, J. D., T. A. GORMAN, D. BISHOP, AND P. MOLER. 2011a. Genetic evidence of contemporary hybridization in one of North America's rarest anurans, the Florida Bog Frog. *Animal Conservation*. doi: 10.1111/j.1469-1795.2011.00461.x.
- AUSTIN, J. D., T. A. GORMAN, AND D. C. BISHOP. 2011b. Assessing fine-scale genetic structure and relatedness in the micro-endemic Florida Bog Frog. *Conservation Genetics* 12:833–838.
- BISHOP, D. C. 2005. Ecology and Distribution of the Florida Bog Frog and Flatwoods Salamander on Eglin Air Force Base. Unpubl. PhD diss., Virginia Polytechnic Institute and State University, Blacksburg.
- BUCHAN, A., L. SUN, AND R. S. WAGNER. 2005. Using alpha numeric fluorescent tags for individual identification of amphibians. *Herpetological Review* 36:43–44.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model Selection and Inference: A Practical Information-Theoretic Approach. 2nd ed. Springer-Verlag, New York.
- COMPTON, B. W., J. M. RHYMER, AND M. McCULLOUGH. 2002. Habitat selection by Wood Turtles (*Clemmys insculpta*): an application of paired logistic regression. *Ecology* 83:833–843.
- CONNELL, J. H. 1980. Diversity and coevolution of competitors, or the ghost of competition past. *Oikos* 35:131–138.
- CRUMP, M. L. 1991. Choice of oviposition site and egg load assessment by a treefrog. *Herpetologica* 47:308–315.
- DAUBENMIRE, R. F. 1959. A canopy-coverage method of vegetational analysis. *Northwest Science* 33:43–64.
- EGLIN AIR FORCE BASE. 2002. Integrated Natural Resource Management Plan 2002–2006. Air Armament Center Eglin Air Force Base, FL.
- ENGE, K. M. 2005. Herpetofaunal drift-fence surveys of steephead ravines in the Florida Panhandle. *Southeastern Naturalist* 4:657–678.
- FLORIDA FISH AND WILDLIFE CONSERVATION COMMISSION. 2005. Florida's Wildlife Legacy Initiative. Florida's Comprehensive Wildlife Conservation Strategy, Tallahassee.
- GORMAN, T. A. 2009. Ecology of Two Rare Amphibians of the Gulf Coastal Plain. Unpubl. PhD diss., Virginia Polytechnic Institute and State University, Blacksburg.
- GORMAN, T. A., D. C. BISHOP, AND C. A. HAAS. 2009. Spatial interactions between two species of frogs: *Rana okaloosae* and *R. clamitans*. *Copeia* 2009:138–141.
- HARDEN, L. A., S. J. PRICE, AND M. E. DORCAS. 2009. Terrestrial activity and habitat selection of Eastern Mud Turtles (*Kinosternon subrubrum*) in a fragmented landscape: implications for habitat management of golf courses and other suburban environments. *Copeia* 2009:78–84.
- HOBBS, N. T., AND T. A. HANLEY. 1990. Habitat evaluation: do use/availability reflect carrying capacity? *Journal of Wildlife Management* 54:515–522.
- HOSMER, D. W., AND S. LEMESHOW. 1989. Applied Logistic Regression. Wiley, New York.
- LAMB, T. 1984. The influence of sex and breeding condition on microhabitat selection and diet in the Pig Frog, *Rana grylio*. *American Midland Naturalist* 111:311–318.
- LAMOUREUX, V. S., AND D. M. MADISON. 1999. Overwintering habitats of radio-implanted Green Frogs, *Rana clamitans*. *Journal of Herpetology* 33:430–435.
- LANNOO, M. J. (ED.). 2005. Amphibian Declines: The Conservation Status of United States Species. University of California Press, Berkeley.
- MARTOF, B. 1953. Home range and movements of the Green Frog, *Rana clamitans*. *Ecology* 34:529–543.
- . 1956. Growth and development of the Green Frog, *Rana clamitans*, under natural conditions. *American Midland Naturalist* 55:101–117.
- MEANS, D. B. 1975. Competitive exclusion along a habitat gradient between two species of salamanders (*Desmognathus*) in western Florida. *Journal of Biogeography* 2:253–263.
- . 2000. Southeastern U.S. coastal plain habitats of the Plethodontidae: the importance of relief, ravines, and seepage. In R. C. Bruce, R. G. Jaeger, and L. D. Houck (eds.), *The Biology of Plethodontid Salamanders*, pp. 287–302. Kluwer Academic/Plenum Publishers, New York.
- MINSHALL, G. W., J. T. BROCK, D. A. ANDREWS, AND C. T. ROBINSON. 2001. Water quality, substratum and biotic responses of five central Idaho (USA) streams during the first year following the Mortar Creek fire. *International Journal of Wildland Fire* 10:185–199.
- MOLER, P. E. 1985. A new species of frog (Ranidae: *Rana*) from northwestern Florida. *Copeia* 1985:379–383.
- . 1992. Florida Bog Frog, *Rana okaloosae* Moler. In P. E. Moler (ed.), *Rare and Endangered Biota of Florida*. Vol. 3: Amphibians and Reptiles, pp. 30–33. University Press of Florida, Gainesville.
- . 1993. *Rana okaloosae* Moler Florida Bog Frog. *Catalogue of American Amphibians and Reptiles* 561:1–3.
- MOORE, J. A., AND J. C. GILLINGHAM. 2006. Spatial ecology and multi-scale habitat selection by a threatened rattlesnake: the Eastern Massasauga (*Sistrurus catenatus catenatus*). *Copeia* 2006:742–751.
- NORTH, M. P., AND J. H. REYNOLDS. 1996. Microhabitat analysis using radiotelemetry locations and polytomous logistic regression. *Journal of Wildlife Management* 60:639–653.
- PROVENCHER, L., B. J. HERRING, D. R. GORDON, H. L. RODGERS, G. W. TANNER, J. L. HARDESTY, L. A. BRENNAN, AND A. R. LITT. 2001. Longleaf pine and oak responses to hardwood reduction techniques in fire-suppressed sandhills in northwest Florida. *Forest Ecology and Management* 148:63–77.
- PROVENCHER, L., A. R. LITT, AND D. R. GORDON. 2003. Predictors of species richness in northwest Florida longleaf pine sandhills. *Conservation Biology* 17:1660–1671.
- RANDLER, C. 2002. Avian hybridization, mixed pairing and female choice. *Animal Behavior* 63:103–119.
- RILEY, S. P. D., H. B. SHAFFER, S. R. VOSS, AND B. M. FITZPATRICK. 2003. Hybridization between a rare, native Tiger Salamander (*Ambystoma californiense*) and its introduced congener. *Ecological Applications* 13:1263–1275.
- RITCHIE, S. C., B. K. RINCON, AND T. A. GORMAN. 2008. Ranid aggression and interspecies amplexus. *Herpetological Review* 39:80.
- SCHOENER, T. W. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* 49:704–726.
- SEMLITSCH, R. D. 2002. Critical elements for biologically based recovery plans of aquatic-breeding amphibians. *Conservation Biology* 16:619–629.
- SMITH, G. R., A. TODD, J. E. RETTIG, AND F. NELSON. 2005. Microhabitat selection by Northern Cricket Frogs (*Acris crepitans*) along a west-central Missouri creek: field and experimental observations. *Journal of Herpetology* 37:383–385.
- TOFT, C. A. 1985. Resource partitioning in amphibians and reptiles. *Copeia* 1985:1–21.
- WATSON, J. W., K. R. McALLISTER, AND D. J. PIERCE. 2003. Home ranges, movements, and habitat selection of Oregon Spotted Frogs (*Rana pretiosa*). *Journal of Herpetology* 37:292–300.
- WIENS, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385–397.

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