

# Spatial Interactions between Two Species of Frogs: *Rana okaloosae* and *R. clamitans clamitans*

Thomas A. Gorman<sup>1</sup>, David C. Bishop<sup>1,2</sup>, and Carola A. Haas<sup>1</sup>

***Rana okaloosae* is endemic to northwestern Florida and is sympatric with *R. clamitans clamitans*, its closest relative and possibly its main interspecific competitor. We evaluated the movements, dynamic interactions, and nearest neighbor distances of male *R. okaloosae* and *R. c. clamitans* in Okaloosa County, Florida. Mean minimum daily distances moved and maximum daily distances moved were greater for *R. c. clamitans* than *R. okaloosae*. Dynamic interactions tended to be positive and suggested that there were positive associations between individuals of the two species. Further, nearest neighbor analyses suggested that calling males of both species were positioned in a clumped distribution on any single night. The intraspecific and interspecific interactions of these species were complex and suggested that these species may have selected similar calling locations and appeared not to exclude either conspecifics or heterospecifics.**

**A**N understanding of how organisms use space is essential to elucidate competitive relationships, social behavior (e.g., territoriality), habitat selection, and has implications for understanding population dynamics (Morris, 2003; Young and Shivik, 2005). Many researchers quantify home range overlap to assess spatial interactions; however, this does not take into account the possibility of temporal avoidance (Kernohan et al., 2001). Dynamic interactions between two individuals provide information on attraction and avoidance of animals that are in the same area at a single point in time (Powell, 2000).

*Rana okaloosae* is a rare North American ranid with an extremely limited distribution (Moler, 1985, 1993; Bishop, 2005). The entire known range of the species is restricted to a few drainages in Walton, Okaloosa, and Santa Rosa counties, Florida (Moler, 1993). Conversely, *R. clamitans clamitans* is a widely distributed species that occurs throughout most of the southeastern United States, and occurs at all known *R. okaloosae* sites. *Rana c. clamitans* is a close relative of *R. okaloosae*, is known to hybridize with it (Austin et al., 2003), and may be its principal interspecific competitor. Therefore, understanding the spatial interactions between these sympatric species may contribute to understanding patterns of distribution (Carpenter and MacMillen, 1976; Kernohan et al., 2001) and may be important to conservation efforts.

We monitored the movements and spatial interactions of these two sympatric ranids in northwestern Florida. Our null hypothesis was that individuals of each species would react the same to conspecifics or heterospecifics. This null hypothesis may likely be supported because hybridization has been documented (Bishop, 2005), and so heterospecifics may be viewed similarly to conspecifics. Alternatively, we hypothesized that we would observe greater avoidance between conspecifics than heterospecifics, because a conspecific may pose more of a threat to resources (e.g., space and females). We monitored the movements of *R. okaloosae* for two breeding seasons (2002, 2003) and the movements of *R. c. clamitans* for one breeding season (2003). We used the movement data of each species to assess intra- and interspecific interactions using dynamic interactions and we predicted there would be greater distances among conspecifics than heterospecifics. Additionally, we used nearest neighbor distance (NND) analyses to evaluate the distribu-

tional relationship of males of both species, and we predicted there would be uniform spacing of calling males.

## MATERIALS AND METHODS

**Study area.**—The study area was a 120-m section of headwater stream located on Eglin Air Force Base (Eglin) in Okaloosa County, Florida. The study area was located in a Longleaf Pine (*Pinus palustris*) and Turkey Oak (*Quercus laevis*) sandhill community. The stream varies between 7 and 22 m in width in the section we monitored. The upper 60 m of the creek is divided into two channels, separated by a strip of land approximately 5 m in width. Water levels ranged from <1 to 20 cm in depth across our study site and remained fairly stable during the study. Just outside the study area boundary the creek becomes progressively deeper downstream. Dominant canopy species along the creek are Sweetbay (*Magnolia virginiana*) and Black Titi (*Cliftonia monophylla*).

**Capture.**—We located and captured *Rana okaloosae* and *R. c. clamitans* by thoroughly searching the site visually and aurally. Most searches were at night; however, some searching was conducted during the day. Although most captures were of calling males, we routinely located non-calling individuals throughout the season. Recapture rates of females were low for most individuals, so we excluded them from all analyses. When an individual was captured, we toe-clipped for identification and marked the location of each individual with a wire flag to identify the capture date and frog toe-clip code. Capture locations were georeferenced using an Asset Surveyor TDC2 GPS unit (Trimble Navigation Limited, Sunnyvale, CA) with sub-meter resolution. We captured *R. okaloosae* on 30 days between 27 May and 10 September in 2002, and we captured *R. okaloosae* and *R. c. clamitans* on 87 days between 27 March and 3 August in 2003.

**Movements.**—We calculated mean minimum daily distances moved (Harrison and Gilbert, 1985; Phillips et al., 1998; Shepard, 2004) and maximum daily distances moved for each individual that was captured  $\geq 5$  times within a season. Mean minimum daily distances were calculated between serial locations that were separated by one day, and the

<sup>1</sup> Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State University, 100 Cheatham Hall, Blacksburg, Virginia 24061; E-mail: (TAG) gormant@vt.edu. Send reprint requests to TAG.

<sup>2</sup> Present address: Low Country Institute, 40 Mobley Oaks Lane, Okatie, South Carolina 29902.

Submitted: 3 December 2007. Accepted: 2 September 2008. Associate Editor: J. W. Snodgrass.

© 2009 by the American Society of Ichthyologists and Herpetologists DOI: 10.1643/CE-07-258

maximum daily distance represents the largest single movement between successive locations separated by one day. We used a t-test to compare mean minimum daily distances and maximum daily distances between *R. okaloosae* and *R. c. clamitans* caught in 2003.

**Spatial interactions.**—Analysis of dynamic interactions between individuals maintains the serial correlation in location data, thereby explaining both the spatial and temporal aspects of one animal's influence on a second individual (Doncaster, 1990; Kernohan et al., 2001; Gorman et al., 2006). Using dynamic interactions, we assessed intraspecific interactions between individual *R. okaloosae* in 2002 and 2003 and *R. c. clamitans* in 2003. Additionally, we assessed interspecific interactions between individual *R. okaloosae* and *R. c. clamitans* in 2003. We calculated dynamic interactions between individuals during the summer breeding season. To determine a radius within which to consider individuals to be interacting, we used the mean maximum daily distance between individuals to allow for meaningful comparison. When analyzing intraspecific *R. okaloosae* interactions, we used a distance of 17 m; when analyzing intraspecific *R. c. clamitans* interactions, we used a distance of 25 m; and when comparing interspecific interactions between *R. okaloosae* and *R. c. clamitans*, we used the further distance of 25 m. We measured the observed distance between locations of frogs only if they were captured on the same night. Using these locations, we calculated the expected distance among all possible locations assuming random interaction between individuals (Kernohan et al., 2001; Gorman et al., 2006). We used a Wilcoxon signed-rank test (Zar, 1996) to test for differences between observed and expected distances within *R. okaloosae* and *R. c. clamitans* (i.e., analyses of conspecifics) and between *R. okaloosae* and *R. c. clamitans* (i.e., analysis of heterospecifics). Interactions were either positive (observed distance < expected), which suggested that the two individuals were attracted to each other, or negative (observed distance > expected), which suggested that the two individuals temporally avoided each other.

**Spatial distribution.**—To evaluate if calling sites of frogs were randomly distributed within the study site on a given night, we conducted nearest neighbor distances (NND) for 2003 data. For this analysis, we considered the study area to be the extent of the area used by individuals of both species. Nearest neighbor statistics indicate whether individuals in a designated area are randomly distributed, clumped, or evenly spaced (Clark and Evans, 1954). Specifically, we calculated an *R*-value, which is an index of the degree the observed spatial distribution departs from random. An *R*-value of 1.0 indicates a random distribution, an  $R < 1$  indicates a trend towards clumping, and an  $R > 1$  indicates a trend towards a uniform distribution. Nearest neighbor distances are used to calculate the standard deviate of the normal curve (*z*); if  $|z| \geq 1.96$ , there is a significant departure from randomness. We combined both species in the nearest neighbor analyses (i.e., we measured the spatial distribution of all calling males for each night). Nights for which we recorded a minimum of five calling individuals of each species (34 out of 87) were included in this analysis.

## RESULTS

We captured and toe-clipped 44 different male *R. okaloosae* over the two breeding seasons (2002 and 2003) and 45 male

**Table 1.** Mean Neighbor Distances for *Rana okaloosae* (ROK) and *R. c. clamitans* (RCL) at One Site in Okaloosa County, FL. On each observation night ( $n = 34$ ), the distance to the nearest calling conspecific and heterospecific individual measured for each calling male.

	Mean	SD	Range	95% CI
Calling males present ( <i>n</i> ):				
<i>R. okaloosae</i>	7.3	1.5	5–10	6.8–7.8
<i>R. c. clamitans</i>	9.6	3.2	5–16	8.5–10.7
All frogs	16.9	3.5	11–24	15.7–18.2
Distances (m):				
ROK to ROK	9.2	3.6	4.4–18.3	7.9–10.4
ROK to RCL	6.5	2.2	2.3–12.1	5.7–7.3
RCL to RCL	7.8	2.7	3.2–16.2	6.8–8.7
RCL to ROK	7.7	3.4	3.8–19.1	6.5–8.9

*R. c. clamitans* in 2003. We estimated mean minimum daily distance moved, maximum daily distances moved, and dynamic interactions for 41 *R. okaloosae* males and 26 *R. c. clamitans* males with  $\geq 5$  locations. For the nearest neighbor analysis, we used only animals that we captured on selected nights.

The mean minimum daily distance moved for *R. okaloosae* (mean = 1.8 m,  $n = 16$ ) was less than that for *R. c. clamitans* (mean = 3.3 m,  $n = 18$ ;  $t = -2.449$ ,  $P = 0.020$ ) in 2003. However, no difference was detected in the maximum daily distance moved between *R. okaloosae* (mean = 8.9 m,  $n = 16$ ) and *R. c. clamitans* (14.8 m,  $n = 18$ ;  $t = -1.488$ ,  $P = 0.147$ ).

In 2002, 63% of the dynamic interactions between *R. okaloosae* were positive (i.e., observed distance < expected distance); however, this difference was marginally significant ( $z = -1.932$ ,  $P = 0.053$ ,  $n = 43$  interactions). In 2003, only 56% of the interactions among *R. okaloosae* were positive, and this difference was not significant ( $z = -1.010$ ,  $P = 0.313$ ,  $n = 32$  interactions). Similarly, in 2003 55% of the dynamic interactions among *R. c. clamitans* were positive, but not statistically different than expected ( $z = -0.832$ ,  $P = 0.405$ ,  $n = 88$  interactions). Finally, in 2003 55% of the dynamic interactions between *R. c. clamitans* and *R. okaloosae* were positive and differed significantly from random expectations ( $z = -2.288$ ,  $P = 0.022$ ,  $n = 146$  interactions).

On the 34 nights for which nearest neighbor distances were calculated between calling males in 2003, we captured an average of 16.9 individuals, of which 57% were *R. c. clamitans* and 43% were *R. okaloosae*. Calling males of both species combined were not distributed randomly within the study site on any of the nights, rather they were clumped (mean  $R = 9.9 \times 10^{-6}$ ,  $R$  range:  $4.9 \times 10^{-6}$ – $1.5 \times 10^{-5}$ , mean  $|z| = 7.82$ ,  $|z|$  range: 6.35–9.37;  $P < 0.001$ ; Table 1).

## DISCUSSION

Intraspecific competition is often assumed to be greater than interspecific competition, because of similarities in resource requirements and competition for mates. Generally, this results in higher levels of aggression between conspecifics than heterospecifics (Gerhardt and Schwartz, 1995). Further, populations that exhibit territoriality or competitive exclusion would distribute themselves uniformly (Shepard, 2004),

and dynamic interactions would be negative (Powell, 2000). Our data indicate that the populations of *R. okaloosae* and *R. c. clamitans* both had fewer negative intraspecific interactions than positive. Further, we saw significantly greater positive interspecific interactions on our study site, and the animals were spaced in a clumped distribution, suggesting that if competitive exclusion occurs it may be weak.

Littlejohn (1977) and Wells (1977) documented that males of species with prolonged breeding seasons often space themselves out to minimize competition, and some research has suggested that males may use the calls of neighbors to determine minimum spacing distances (Dyson and Passmore, 1992; Halliday and Tejedo, 1995). On our study site, calling males were not distributed randomly on any observation night or over the entire study period, which is similar to the findings of other studies that have documented nonrandom spacing of frogs (Whitney and Krebs, 1975; Given, 1988; Wilczynski and Brenowitz, 1988).

If conspecifics were more territorial, then we would expect to see greater distances between calling conspecifics than between heterospecifics. Conversely, males may prefer to call in conspecific aggregations (Martof, 1953a; Given, 1988), possibly because of similar habitat preferences or an increased chance of attracting mates. Spacing may also be related to the distribution of preferred calling sites or the density of frogs (Shepard, 2002). These two species are believed to be recently diverged and hybridization has occurred (Austin et al., 2003), so these two species may select for similar resources which may explain the greater number of positive associations between heterospecifics. While neither species displayed significantly greater positive than negative interactions, the trends for conspecific interactions of both species were positive.

Both *R. okaloosae* and *R. c. clamitans* showed relatively little movement during the breeding season (less than 10 or 15 m per day, respectively) and called at or near the same site on multiple nights. *Rana okaloosae* do have the capability to move relatively large distances, even through normally unused habitats. For example, we found one male (42.0 mm SVL) in an isolated wetland 130 m from the main study site where it was marked initially. Separating the two sites was dry sandhill habitat dominated by saw palmetto (*Serenoa repens*), longleaf pine, and turkey oak. Three days of rain occurred between the previous capture date at the main site and the date it was found in the isolated wetland. Others have reported long-distance movements in ranids during rain events (Martof, 1953b; Dole, 1965).

Other ranids typically are absent from sites containing *R. okaloosae* and *R. c. clamitans*; *Acris gryllus* and *A. crepitans* generally are the only other anurans consistently present. Adults of the two ranids may compete for oviposition and calling sites and food resources, and perhaps even for mates, because apparent hybrids between the two species do occur (Austin et al., 2003; Bishop, 2005), but our data do not support exclusive use of space. Breeding sites of rare species, such as *R. okaloosae*, may be essential for conservation and the interactions with other species may inform future conservation strategies. Conservation of amphibian breeding habitats by minimizing negative disturbances may increase survival of a species because it will protect all the life stages of the species. For conservation of *R. okaloosae*, a focus should be placed on identifying high quality breeding sites, which may reduce the likelihood of hybridization events with *R. c. clamitans*.

## ACKNOWLEDGMENTS

This research was financially supported by the Natural Resources Branch (Jackson Guard) of Eglin Air Force Base and administered through USGS Biological Resources Division. We thank K. Gault and B. Hagedorn for logistical support, L. Phillips, Jr. and P. Gault for field assistance, S. Klopfer for GIS support, T. Michaels and A. Priestly for assistance with data entry, and J. Homyack for helpful comments on an early draft of this manuscript. This research was conducted under Florida Fish and Wildlife Conservation Commission Permit WV01232 and Virginia Tech Institutional Animal Care and Use Committee Protocol 02-084-F&W.

## 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.
- Bishop, D. C. 2005. Ecology and distribution of the Florida bog frog and flatwoods salamander on Eglin Air Force Base. Unpubl. Ph.D. diss., Virginia Polytechnic Institute and State University, Blacksburg, Virginia.
- Carpenter, F. L., and R. E. MacMillen. 1976. Threshold model of feeding territoriality and test with a Hawaiian honeycreeper. *Science* 104:639–642.
- Clark, P. J., and F. C. Evans. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology* 35:445–453.
- Dole, J. W. 1965. Summer movements of adult leopard frogs, *Rana pipiens* Schreber, in northern Michigan. *Ecology* 46:236–255.
- Doncaster, C. P. 1990. Non-parametric estimates of interaction from radio-tracking data. *Journal of Theoretical Biology* 143:431–443.
- Dyson, M. L., and N. I. Passmore. 1992. Inter-male spacing and aggression in African painted reed frogs, *Hyperolius marmoratus*. *Ethology* 91:237–247.
- Gerhardt, H. C., and J. J. Schwartz. 1995. Interspecific interactions in anuran courtship, p. 603–632. *In: Amphibian Biology, Volume 2: Social Behavior*. H. Heatwole and B. K. Sullivan (eds.). Surrey Beatty and Sons, Chipping Norton, NSW, Australia.
- Given, M. F. 1988. Territoriality and aggressive interactions of male carpenter frogs, *Rana virgatipes*. *Copeia* 1988:411–421.
- Gorman, T. A., J. D. Erb, B. R. McMillan, and D. J. Martin. 2006. Space use and sociality of river otters (*Lontra canadensis*) in Minnesota. *Journal of Mammalogy* 87:740–747.
- Halliday, T., and M. Tejedo. 1995. Intrasexual selection and alternative mating behavior, p. 419–468. *In: Amphibian Biology, Vol. 2: Social Behavior*. H. Heatwole and B. K. Sullivan (eds.). Surrey Beatty and Sons, Chipping Norton, NSW, Australia.
- Harrison, D. J., and J. R. Gilbert. 1985. Denning ecology and movements of coyotes in Maine during pup rearing. *Journal of Mammalogy* 66:712–719.
- Kernohan, B. J., R. A. Gitzen, and J. J. Millspaugh. 2001. Analysis of animal space use and movements, p. 125–166. *In: Radio Tracking and Animal Populations*. J. J. Mill-

- spaugh and J. M. Marzluff (eds.). Academic Press, San Diego, California.
- Littlejohn, M. J.** 1977. Long-range acoustic communication in anurans: an integrated and evolutionary approach, p. 263–294. *In: The Reproductive Biology of Amphibians*. D. H. Taylor and S. I. Guttman (eds.). Plenum Press, New York.
- Martof, B.** 1953a. Territoriality in the green frog, *Rana clamitans*. *Ecology* 34:165–174.
- Martof, B.** 1953b. Home range and movements of the green frog, *Rana clamitans*. *Ecology* 34:529–543.
- Moler, P. E.** 1985. A new species of frog (Ranidae: *Rana*) from northwestern Florida. *Copeia* 1985:379–383.
- Moler, P. E.** 1993. *Rana okaloosae* Moler Florida bog frog. *Catalogue of American Amphibians and Reptiles* 561:1–3.
- Morris, D. W.** 2003. Toward an ecological synthesis: a case for habitat selection. *Oecologia* 136:1–13.
- Phillips, D. M., D. J. Harrison, and D. C. Payer.** 1998. Seasonal changes in home-range area and fidelity of martens. *Journal of Mammalogy* 79:180–190.
- Powell, R. A.** 2000. Animal home ranges and territories and home range estimators, p. 65–110. *In: Research Techniques in Animal Ecology*. L. Boitani and T. K. Fuller (eds.). Columbia University Press, New York.
- Shepard, D. B.** 2002. Spatial relationships of male green frogs (*Rana clamitans*) throughout the activity season. *American Midland Naturalist* 148:394–400.
- Shepard, D. B.** 2004. Seasonal differences in aggression and site tenacity in male green frogs, (*Rana clamitans*). *Copeia* 2004:159–164.
- Wells, K. D.** 1977. The social behavior of anuran amphibians. *Animal Behaviour* 25:666–693.
- Whitney, C. L., and J. R. Krebs.** 1975. Spacing and calling in Pacific tree frogs, *Hyla regilla*. *Canadian Journal of Zoology* 53:1519–1527.
- Wilczynski, W., and E. A. Brenowitz.** 1988. Acoustic cues mediate inter-male spacing in a neotropical frog. *Animal Behavior* 36:1054–1063.
- Young, J. K., and J. A. Shivik.** 2005. What carnivore biologists can learn from bugs, birds, and beavers: a review of spatial theories. *Canadian Journal of Zoology* 84:1703–1711.
- Zar, J. H.** 1996. *Biostatistical Analysis*. Third edition. Prentice Hall, Englewood Cliffs, New Jersey.