

Spatial Relationships of Male Green Frogs (*Rana clamitans*) throughout the Activity Season

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ABSTRACT.—The spatial relationships exhibited by individuals in a population may indicate their social organization. In territorial species interactions between individuals should lead to maximal spacing in a uniform pattern. Using nearest neighbor distances (NND), I tested for territoriality in the green frog (*Rana clamitans*) by determining if males were uniformly dispersed within breeding choruses. Observed dispersion patterns were not consistent with territoriality. Males were randomly dispersed on all seven nights during the breeding period, four of five nights during the nonbreeding period and uniformly dispersed on one night during the nonbreeding period. Dispersion did not differ between periods although density was higher and NND was smaller during the breeding period. There was also no correlation between male size and NND. The disparity of my results might be explained by differences in male density and resource distribution and its effect on habitat quality since these factors influence behavior and spacing. Alternatively, uniform spacing may not be a reliable characteristic of territoriality.

INTRODUCTION

The social organization of a population depends largely upon the spatial and temporal structure of resources (Wiens, 1976). Territoriality may occur when required resources are limited and economically defendable (Brown, 1964). In many species, males benefit reproductively by defending or excluding conspecific males from an area containing limited resources required by females (Brown, 1964; Wells, 1977a). Males advertise their position through calling and/or visual displays and may engage in physical contests to defend an exclusive area. Social interactions between territorial individuals should lead to maximal spacing and result in a uniform dispersion throughout the area of suitable habitat (Davies, 1978).

Much research on territoriality has focused on anurans because they form large breeding choruses where there is intense male-male competition for mates (*see* Wells, 1977a). Males advertise by calling and may exhibit aggression towards conspecific males. Male bullfrogs (*Rana catesbeiana*) frequently engage in physical contests presumably in defense of oviposition sites that result in lower rates of embryo mortality (Howard, 1978a, b). Larger males usually hold a competitive advantage, possess the best territories and have the highest reproductive success (Howard, 1978a). Aggression may also be used to maintain an individual distance or personal space with no specific resources (Wells, 1977a). Whitney and Krebs (1975) reported that male *Hyla regilla* exhibited aggression in the maintenance of an individual distance, which consequently resulted in a uniform dispersion. Although *H. regilla* were aggressive and uniformly spaced, they were not considered territorial because there were no resources involved and no site tenacity (Wells, 1977a; Mathis *et al.*, 1995). Few studies have examined the pattern of intermale spacing in territorial anurans (but *see* Arak, 1983; Backwell and Passmore, 1990; Dyson and Passmore, 1992) with most reporting only the distance between males (Martof, 1953; Emlen, 1968;

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Wells, 1977b; Boatright-Horowitz *et al.*, 2000). It remains unknown for most species whether uniform dispersion occurs or if it is an accurate characteristic of territoriality.

The green frog (*Rana clamitans*) has a prolonged breeding season and is considered territorial (Wells, 1977a, b), making it ideal for testing hypotheses concerning the relationship between territoriality and intermale spacing. Males have been observed in physical encounters, are often found calling from the same site on successive nights and appear to be uniformly spaced (Martof, 1953; Brode, 1959; Schroeder, 1968; Wells, 1977b, 1978). My objectives were to test if male *R. clamitans* are uniformly dispersed within breeding choruses and compare dispersion, density and distance to nearest neighbor between breeding and nonbreeding periods.

STUDY AREA AND METHODS

My study area was a ca. 180 × 80 m emergent wetland located 3 km east of the Illinois River near the junction of Illinois Highway 26 and the Atchison, Topeka, and Sante Fe Railroad, Marshall County, Illinois (40°55'N, 89°25'W; 146 m). Emergent vegetation was most concentrated in the northern and southern ends and consisted predominately of arrowhead (*Sagittaria latifolia*), willow (*Salix* sp.), bulrushes (*Scirpus* spp.), common cattail (*Typha latifolia*), narrowleaf cattail (*Typha angustifolia*), bur reed (*Sparganium eurycarpum*), sedges (*Carex* spp.), reedgrass (*Phragmites* sp.), arrow arum (*Peltandra virginica*) and water plantain (*Alisma subcordatum*). Duckweed (*Lemma* sp.) covered much of the water surface. Water depth varied from 20–80 cm depending on location, precipitation and time of year, but areas used by *Rana clamitans* were typically 20–50 cm.

Methods.—With the aid of a headlamp, I made behavioral observations and hand-captures of *Rana clamitans* on thirty nights between 1 May and 7 September 1999. I individually marked frogs by toe-clipping, but did not clip the thumbs of males because of their potential role in amplexus and fighting. My activities did not appear to affect frog behavior and I observed no adverse reaction to toe-clipping. For each frog I measured snout-vent length (SVL) to the nearest 1 mm using a hand ruler and noted whether males were calling. Frogs were sexed by comparing relative sizes of the eye and tympanum (Conant and Collins, 1991) or by other external characteristics such as venter coloration. I constructed a grid system consisting of numbered wooden stakes at 4 m intervals. Upon capturing a frog, I marked the site with flagging tape labeled with the date and the individual's ID number. On a subsequent day, I measured the distance (to the nearest 0.1 m) and bearing to the site from the nearest stake using a measuring tape and compass. I converted these measurements to X-Y coordinates then obtained distances to neighbors by calculating distances between points. I classified the breeding period as the period between the days the first and last egg masses were deposited as determined by routine visual encounter surveys.

Data analysis.—To test for uniform dispersion I examined spatial relationships of males using Nearest Neighbor Distances (NND; Clark and Evans, 1954) corrected for edge effects and correlations (Donnelly, 1978). For calculations I used the area occupied by the chorus on the given night, not the entire area of the site. I calculated the index of dispersion, R (the ratio of observed to expected mean NND if the population was randomly dispersed), which indicates the dispersion is clumped when $R = 0$, random when $R = 1$ and uniform as R approaches 2.1491. I tested the significance of the departure from random by comparing c (the standard variate of the normal curve) against the critical value of the normal curve at $\alpha = 0.05$ (± 1.96). Dispersion is uniform if $c > 1.96$, clumped if $c < -1.96$ and random if $-1.96 < c < 1.96$. To test if male dispersion differed between periods, I compared mean R values using Donnelly's (1978) correction

of the ANOVA method of Clark and Evans (1954). To ensure independence of mean R values for the breeding and nonbreeding periods, I used the mean NND for each individual based on data from several nights over the time period and the mean density of those nights.

I calculated the Pearson Correlation Coefficient to test if male size (SVL) was correlated with NND during the breeding period and used linear regression to analyze the relationship between density and NND over the entire season. I then used t -tests (two-tailed) to test for differences in density and NND between periods. Data were analyzed using Microsoft Excel and SAS version 8.01 (SAS Institute, Inc., Cary, NC). Results were considered significant at $\alpha = 0.05$.

RESULTS

Sufficient data were available for analysis of spatial relationships on 12 nights (7 breeding, 5 nonbreeding). Noncalling males were not used in the analysis during the breeding period because of the satellite mating behavior displayed by some noncalling males. During the breeding period (18 May to 27 July), the dispersion of males in the chorus was random on all seven nights (Table 1) and SVL was not significantly correlated with NND ($r = 0.11$, $n = 61$, $P = 0.39$). During the nonbreeding period, male dispersion was random on four of five nights and uniform on one night (Table 1).

Mean R values for the breeding ($R_B = 1.27$) and nonbreeding periods ($R_{NB} = 1.26$) did not differ ($F_{1,81} = 0.002$, $P > 0.90$). There was a negative relationship between mean NND and density over the entire activity season ($y = -0.52x + 6.50$, $r^2 = 0.51$, $F_{1,10} = 10.56$, $P = 0.01$; Fig. 1) with little overlap between periods. During the breeding period, mean density was higher (breeding mean ($\pm SE$) = 5.5 ± 0.6 males/100 m², nonbreeding mean ($\pm SE$) = 3.6 ± 0.4 males/100 m²; $t_{10} = 2.43$, $P = 0.04$) and mean NND was smaller than in the nonbreeding period (breeding mean ($\pm SE$) = 3.4 ± 0.2 m, nonbreeding mean ($\pm SE$) = 4.9 ± 0.5 m; $t_{10} = -3.01$, $P = 0.01$).

DISCUSSION

Male *Rana clamitans* maintained a mean NND of 3.4 m during the breeding period with 0.6 m being the shortest distance observed between two calling males. Martof (1953) noted that male *Rana clamitans* in Michigan were spaced at rather uniform distances of 2–3 m and as close as 0.3 m. Wells (1977b) stated that male *R. clamitans* in New York were spaced 1–1.5 m in heavily vegetated areas and 4–6 m in more open areas. However, neither of these studies tested whether the dispersion pattern was nonrandom. Male *R. clamitans* are thought to defend premium areas within the chorus which females use for oviposition (Wells, 1977b). Interactions between individuals defending these resources should result in uniform spacing throughout the area of suitable habitat (Davies, 1978), but males at my site were not uniformly dispersed during the breeding period.

It is possible that males in my population of *Rana clamitans* were not territorial. This might be attributable to differences in density between my site and other sites since the density of competing males influences behavior (Brown, 1964; Wells, 1977a). For example, male *Bufo cognatus* display different mating behaviors in high vs. low chorus densities (Brown and Pierce, 1967). Density can also affect the pattern of male spacing as demonstrated by *Hyla* (= *Pseudacris*) *crucifer* and *Hyperolius marmoratus*, which were uniformly dispersed at low densities, but randomly dispersed at high densities (Fellers, 1979; Dyson and Passmore, 1992). Previous work on territoriality in *R. clamitans* by Wells (1977b, 1978) was carried out in an enclosed 21 × 21 m man-made pond containing 25 transplanted males. If all areas of his pond were used equally, the density would have been 5.7 males/

TABLE 1.—Spatial relationship analysis of male *Rana clamitans* using nearest neighbor distances (NND) for nights during the breeding (B) and nonbreeding (NB) periods. r_A = observed mean NND, r_E = expected mean NND, R = index of dispersion (r_A/r_E) and c = standard variate of the normal curve. Dispersion is uniform if $c > 1.96$, clumped if $c < -1.96$, and random if $-1.96 < c < 1.96$

Period	Date	n	Density (males/100 m ²)	r_A	r_E	R	SE of r_E	c	Dispersion
B	05/20/99	13	4.3	3.96	3.03	1.31	0.51	1.30	Random
B	05/29/99	7	4.0	3.52	3.42	1.03	0.78	0.11	Random
B	06/14/99	9	6.3	3.54	2.57	1.37	0.52	1.33	Random
B	06/15/99	11	4.6	3.60	2.84	1.26	0.51	1.05	Random
B	06/18/99	15	5.5	2.18	2.59	0.84	0.40	-0.65	Random
B	06/21/99	8	8.3	3.02	2.12	1.42	0.45	1.33	Random
B	07/27/99	6	5.4	4.02	2.79	1.44	0.68	1.49	Random
NB	08/06/99	12	4.7	3.42	2.81	1.21	0.49	0.87	Random
NB	08/11/99	10	3.5	4.98	3.45	1.44	0.66	1.88	Random
NB	08/26/99	6	2.3	6.60	4.44	1.49	1.09	2.07	Uniform
NB	08/30/99	5	4.5	4.89	3.25	1.50	0.87	1.76	Random
NB	09/02/99	7	3.1	4.77	3.89	1.23	0.89	0.93	Random

100 m² (Wells, 1977b, 1978), which is similar to the mean density of 5.5 males/100 m² observed during the breeding period in my natural population. However, because large areas in the middle of Wells' pond were not used, the actual male density was several times higher. The higher density was likely associated with a decrease in NND, which has been shown to result in more frequent male-male aggressive encounters (Backwell and Passmore, 1990; Dyson and Passmore, 1992). Wells (1978) reported 105 wrestling bouts over three years in contrast to only two wrestling bouts observed in this study (Shepard, 2000) and no wrestling bouts observed by Martof (1953).

The higher density, particularly in corners and along edges, observed by Wells (1977b, 1978) may be due to the distribution of resources in and shape of his artificial pond. In ponds *Rana clamitans* are primarily found in a narrow band along the perimeter (Wells, 1977b; Bee *et al.*, 1999; D. Shepard, pers. obs.) because ponds are relatively heterogeneous with large open areas in the center and vegetation concentrated in corners and along edges. In contrast emergent wetlands are rather homogeneous with vegetation more evenly distributed providing a wider area of suitable habitat. Relatively permanent sources of water are required by *R. clamitans* because of its long breeding season and because tadpoles often overwinter (Wright and Wright, 1949; Smith, 1961). Man-made impoundments, such as ponds, do not represent natural habitat and, although *R. clamitans* are capable of living and reproducing in these artificial environments, individuals may exhibit abnormal behaviors due to the different physical parameters. Further, environmental factors can affect ponds and wetlands differently and result in different behavioral responses by breeding anurans (Shepard and Kuhns, 2000).

The most evident difference in spatial relationships between periods was higher density and smaller NND during the breeding period, which as stated above, probably increases the likelihood of physical encounters. Despite differences in density and NND between the breeding and nonbreeding periods, dispersion did not differ. If male *R. clamitans* are territorial only during the breeding period (Wells, 1977b, 1978), then the dispersion of males should change from a uniform to a random pattern between periods because the interactions that maintain spacing should be present only during breeding. Physical aggression has not been observed outside the breeding period although males may con-

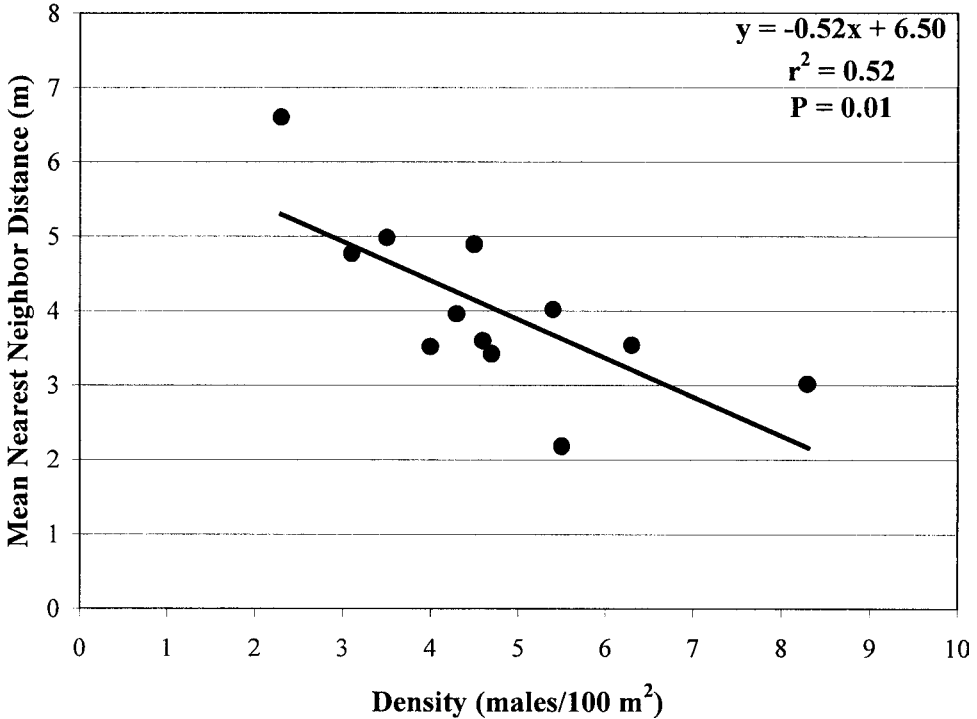


FIG. 1.—Relationship between density and mean nearest neighbor distance throughout the activity season (each point represents a single night)

tinue vocalizing (Wells, 1978; D. Shepard, pers. obs.). A territory may be maintained through advertisement, but the purpose of maintaining a territory in the nonbreeding period is uncertain and it is not known why males were uniformly dispersed on a night in the nonbreeding period. The prediction of uniform dispersion of territorial individuals assumes that resources are evenly distributed; however, resources are typically spatially and temporally heterogeneous (Wiens, 1976). Thus, uniform spacing may not be an accurate characteristic of territoriality.

Because larger males should have a competitive advantage, they might be expected to maintain larger territories. However, there was no significant correlation between male size and NND during the breeding period. If male *Rana clamitans* defend premium oviposition sites (Wells, 1977b, 1978), then there may be no advantage in defending an area larger than is necessary for oviposition. Therefore, territory quality should be independent of size with larger males controlling the best and not necessarily the largest territories. Although I did not examine territory quality, Wells (1977b) found that large male *Rana clamitans* possessed the highest quality territories.

Forms of social organization may have characteristic patterns of individual spacing under some conditions. Because social behavior depends largely on population density and the spatio-temporal distribution of resources (Brown, 1964; Wiens, 1976), spacing patterns may not be consistent features. Additional work is needed examining the effects of density, the spatio-temporal distribution of resources and the interaction between these

factors on social behavior and organization in anurans. Studies on the same species often report different behaviors and result in disparate conclusions pertaining to the social organization (e.g., Emlen, 1976 and Howard, 1978a). If researchers report information such as density, it may provide insight into the relationship between these factors and social behavior and help explain inconsistencies between studies.

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