The Reproductive Behavior of the Bullfrog (*Rana catesbeiana*)

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The mating system of a population of bullfrogs, *Rana catesbeiana*, in New Jersey is resource defense polygyny. The sex ratio of the breeding population is skewed toward males. Males defend territories against conspecifics by stereotyped postures, vocalizations and physical combat. Females select mates and oviposit in the male's territory. This system presumably evolved in response to the prolonged breeding season, the temporally asynchronous arrival of females at the breeding pond, the skewed operational sex ratio and the ability of males to gain indirect access to females through defense of oviposition sites. This study is compared with previous reports of bullfrog social behavior. General characteristics of the mating system in different parts of the range are discussed. There are consistencies in social behavior within the species. However, there is a degree of behavioral plasticity previously unreported in anuran breeding behavior.

THERE has been increased interest in the ecology and evolution of mating systems (Emlen and Oring, 1977). Studies leading to the expansion and refinement of theory in this field almost exclusively concern social insects, birds and mammals. There are few studies of social behavior in amphibians. These animals, especially the anurans, show an immense variety of reproductive modes under a diversity of ecological conditions (Crump, 1974).

Aspects of the reproductive behavior of *Rana catesbeiana* have been reported by several authors. Wiewandt (1969) described the aggressive interactions and vocalizations of territorial males. Emlen (1968, 1976) first documented territoriality in *R. catesbeiana*. He described the mating system of a bullfrog population in Michigan as a lek, analogous to the lekking systems of some birds and mammals (Leuthold, 1966; Wiley, 1973). In the same pond in Michigan, Howard (1978) showed that male bullfrogs are territorial and defend areas which are utilized as oviposition sites.

The purpose of this study is to compare the mating systems of the bullfrog in different parts of its range. This provides the unique opportunity to evaluate the degree of intraspecific variation in social organization in an amphibian. I present the results of observations on the social behavior of the bullfrog in a breeding pond in New Jersey during 1976 and 1977. The mating system during 1976 is described in detail. These results are compared to other studies of bullfrog social behavior.
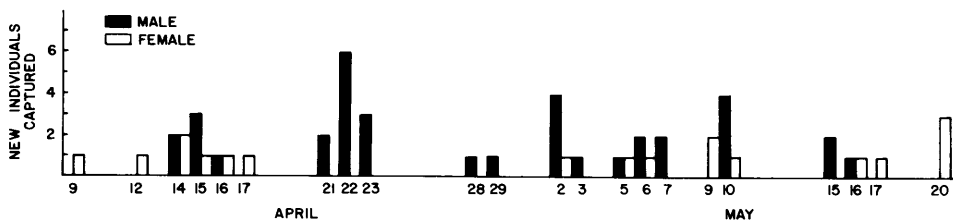
Fig. 1. The temporal distribution of newly captured males and females in Basking Pond.

STUDY AREA

This study was conducted at Basking Pond in the Great Swamp National Wildlife Refuge in Morris Co., New Jersey. This pond is permanent and artificial with an open canopy and no emergent vegetation. Logs, stumps and brush are present throughout the pond and protrude through the water's surface. Brush is concentrated ca 2 m from the center of the west shore. *Elodea* dominates the submerged vegetation and forms large mats covering the entire pond. Basking Pond is elliptical, ca 56 × 36 m and has an area of 0.17 ha. The perimeter of the pond was marked with wooden stakes at 2-m intervals. The interior of the pond was marked with small floats in areas where there were no natural landmarks. Air and water temperatures were monitored continually with seven-day Tempscribe® thermometers.

METHODS

Capture and marking of bullfrogs.—Bullfrogs were captured by hand at dusk and in early evening. All individuals were measured (snout-vent length, SVL), weighed, sexed and given a unique toe clip. Individuals >90 mm were banded to allow identification during behavioral observations. Frogs were marked with numbered, 5 × 5-cm, pieces of tape attached to a 25-cm length of elastic cord. The elastic cord was tied around the waist of the individual. While animals were partially submerged, the tape floated to the surface allowing identification of the individual. These bands were usually lost during overland movements. This technique also has been used successfully with *Rana palustris* (C. Keller, pers. comm.) and should prove effective for most pond breeding anurans.

Observations.—Observations were conducted nightly, from the shore of the pond, from 9

April to 30 June 1976 and from 11 April to 19 June 1977. I began observations between 1900 and 2000 hr and continued until 2400 or 0200 hr depending on the level of activity in the pond. At dusk, unmarked individuals were captured and marked. During the night, the locations and postures of individuals as well as territorial encounters, matings and other pertinent information were recorded. Egg mass sites were plotted during daylight surveys. The distribution of egg masses was tested for randomness by comparing the observed number of egg masses per 5 × 5-m quadrat to the Poisson expectations (Chi-square test). The effect of location of call sites on egg mass distribution was also analyzed. The expected egg mass-calling site distance (E_i), given a random association, was calculated for each night: $E_i = \frac{1}{2}(\pi/\lambda)^{1/2}$; where the Poisson parameter, λ, denotes the mean number of individuals per circle of unit radius [$\lambda = (\pi)(\text{\# frogs/area of pond})$] (Pielou, 1969; 112). The null hypothesis of no effect was tested by comparing the expected and observed egg mass-calling site distances for each night (sign test).

RESULTS

The population.—The population at Basking Pond was dynamic with movements to and from the pond during the breeding season. Consequently, at no time were all the individuals in the pond marked. Fifty-five bullfrogs were captured and marked between 9 April and 20 May 1976. The mean SVL of males and females was significantly different ($\delta = 151.2$ mm, SE = 1.84, N = 37; $\female = 140.33$ mm, SE = 3.57, N = 18; Mann-Whitney U test, z = 2.52, P = .006). Fifty-one % of 37 males were recaptured once and 16% were recaptured at least three times; 56% of the 18 females were recaptured once and 22% were recaptured at least three times. These relatively low recapture
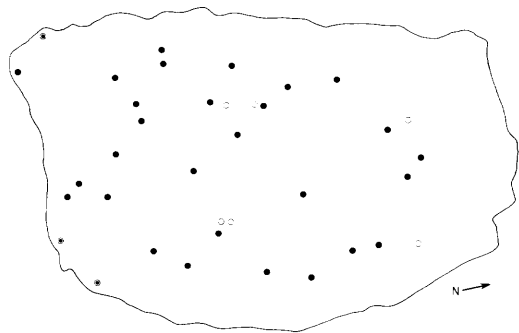
Fig. 2. Location of bullfrogs and egg masses deposited on 7 May 1976. Males = dots; females = dots in circles; egg masses = circles.

rates suggest that most individuals were not present in the pond throughout the study, but may have visited nearby areas.

Establishment of territories.—Early in the season, bullfrogs were found only within several meters of the shore in the "low" posture. These animals floated in the water with only their heads exposed. This posture was characteristic of females and nonterritorial males. Territorial males assumed the "high" posture. They floated on the water's surface with the lungs inflated and the bright yellow gular sac exposed. In 1976 calling began on 14 April with males producing both the "territorial" call and the "mating" call (see Capranica, 1968, for sonographical representation of these calls). On 14 April, a male was observed swimming around the perimeter of his calling site alternately giving both the "mating" and "territorial" call. This behavior did not appear to be directed towards a single individual and may function as a territorial advertisement display.

Chorusing began on 22 April, although it was limited in duration and frequency. A large number of males entered the pond on 2 May after heavy rains and an increase in mean air temperature (7 C to 19 C). This resulted in the ratio of receptive males to receptive females in the pond, or the operational sex ratio (OSR; Emlen, 1976) being skewed toward males (Fig. 1). This skewed OSR (e.g. 28 males to 3 females on 7 May, Fig. 2) was apparent for the duration of the breeding season. Territorial encounters and chorusing increased after the 2 May migration. During the next three weeks males were distributed throughout the pond, but most females remained near the shore. On 7
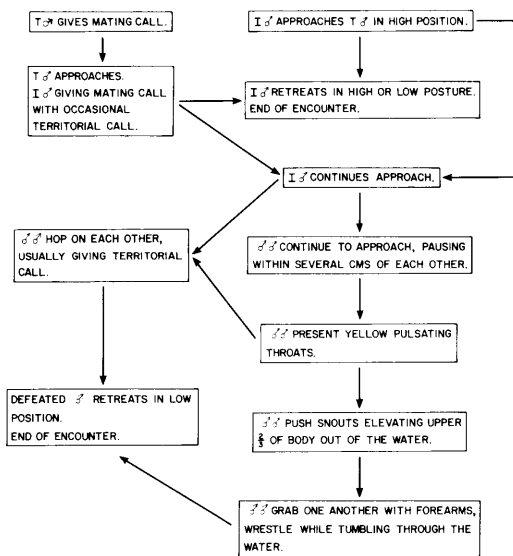

Fig. 3. Flow chart of a "typical" territorial encounter. (T = territorial male, I = intruder male.)

May, when the male density was at its peak, the mean distance between territorial males was 4.1 m (Fig. 2). All territorial males defended their territories from conspecifics in the high posture. These aggressive encounters were described by Emlen (1968) with the exception of the presentation of the gular sac. In this behavior males approached within several cms of each other, halted, and tilted their heads back exposing the brilliantly colored gular sac. The gular sac is sexually dichromatic in bullfrogs. The yellow sac is characteristic of males and presumably plays some role in territorial encounters or mate attraction, although the evidence for these functions is circumstantial.

Not all male-male encounters ended in physical contact since encounters could be terminated any time prior to physical combat (Fig. 3). Individuals in the low posture (i.e. females and nonterritorial males) did not elicit an aggressive response from territorial males.

Large numbers of territorial encounters continued until 10 May. Intense chorusing was noted until 20 May. After the latter date there was no chorusing from Basking Pond, but limited chorusing commenced in an adjacent marsh. Some marked frogs were later found in this marsh. Only one chorus occurred in Basking Pond after 20 May. On 16 June, six males were observed in chorus and successful matings occurred on 16 and 17 June.
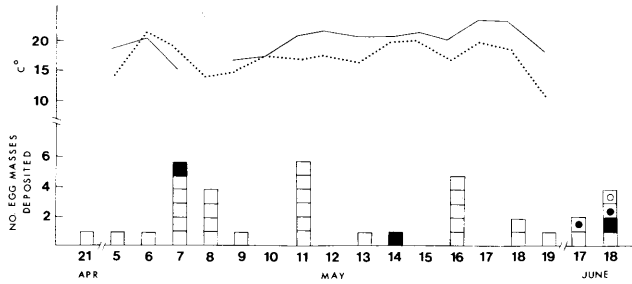
Fig. 4. Mean air (solid line) and water (dotted line) temperatures during the study period and number and size of egg masses deposited in Basking Pond as a function of time. (hollow square < 10,000 eggs per mass; solid block = >10,000 < 15,000; dot in hollow square = > 15,000 < 20,000; circle in hollow square = > 20,000 eggs per mass.)

The oviposition site.—Bullfrog egg masses float on the water's surface and are particularly well adapted for a warm water environment (Moore, 1940; Ryan, 1978). Egg masses were easily located during daylight. Area of the irregular shaped mass was estimated by measuring the "radius" of the mass and calculating the area of a circle. The number of eggs in a 10 × 10-cm area was used to estimate total number of eggs per mass. Egg masses averaged 3,208 cm² (SE = 336.4, N = 36) with a mean 7,360 eggs per mass (SE = 741.7, N = 36). Thirty-six egg masses were deposited in Basking Pond on 14 nights from 21 April to 18 June. Eleven nights of mating activity were between 5 and 19 May (Fig. 4). Egg masses were deposited throughout the pond in areas which varied in depth from 0.5 to 1.5 m. The number of egg masses per 5 × 5-m quadrat did not depart significantly from the Poisson expectations (χ^2 = 9.21, P > .10); thus egg masses appear to be randomly distributed with respect to each other.

Female behavior was similar to that described by Emlen (1976). Females swam through the chorus and initiated amplexus by making physical contact with a calling male. Female choice seems to be an important determinant in mate selection. Amplexed pairs would flee at the slightest disturbance. Only three matings which resulted in oviposition were observed.

The results of this study strongly suggest that oviposition took place in the male's territory, implying that males defended oviposition sites. During 1976, portions of at least 10 amplexes were observed; all involved territorial males. Three amplexes which resulted in oviposition were witnessed. In each of these cases eggs were deposited in the male's territory. Daylight survey of egg masses revealed that most egg masses were deposited near a male's calling site on the previous night; 69% were deposited within 1 m of a calling site and 87% were within 2 m (Fig. 5). The expected egg mass-calling site distance ($\bar{x}_e$ = 5.68 m) was significantly greater than the observed egg mass-calling site distance ($\bar{x}_o$ = 1.96 m, z = 2.41, P = .008, sign test). Therefore, the distribution of egg masses is not random with respect to the location of calling sites.

DISCUSSION

The adaptive significance of resource defense polygyny.—This study shows that the bullfrog mating system is characterized by: a prolonged breeding season, continual presence of males at the pond, temporally asynchronous arrival of females at the breeding site, a male-biased OSR, intense male-male competition for mates, male territoriality, and female choice.

The temporal distribution of receptive females is an important determinant of male-male competition (Trivers, 1972; Emlen, 1976;
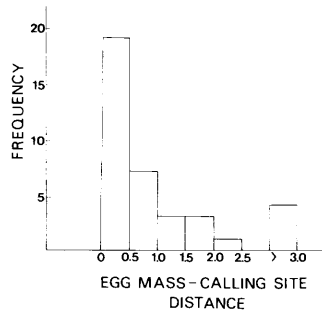

Fig. 5. Distance of egg masses from nearest calling site.

TABLE 1.   VARIATION IN BULLFROG MATING SYSTEMS.

	Emlen	Howard	Ryan
Study site	Crane Pond, Mich.	Crane Pond, Mich.	Basking Pond, N.J.
Oviposition site	Outside chorus area	In male's territory	In male's territory
Distribution of male size classes within chorus	Larger males in center of chorus	Apparently random	Apparently random
Chorus location	Edge of shore or mats of vegetation	Edge of shore or mats of vegetation	Throughout pond
Chorus duration	3–5 days	3–7 days	3 wk

Emlen and Oring, 1977; Wells, 1977). The asynchronous arrival of receptive females at the pond favors males that attract females from stationary calling sites (Wells, 1977). This contrasts with the scramble competition of some explosive breeders (e.g. *Scaphiopus holbrooki*, Pearson, 1955) where a male actively searches for and initiates amplexus with a female. When female availability is synchronous and of short duration, rapid acquisition of mates is crucial for male reproductive success. Therefore, in explosive breeders, selection will favor males that actively search for females. This would be an inefficient strategy for a prolonged breeding anuran where the possibility of encountering a female is reduced due to the skewed OSR. Wells (1977) provided a detailed discussion on the effect of the temporal distribution of receptive females on anuran mating systems.

Male bullfrogs defend territories from conspecifics in the high posture. These territories function as display areas and oviposition sites. The defense of an oviposition site is an important determinant in the evolution of the bullfrog mating strategy. Howard (1978) showed significant variation in the quality of the males' territories judged by percent egg mortality prior to hatching. Orians (1969) suggested that in cases where male parental care is of little consequence, female choice should be based on both male phenotype and territory quality. Therefore, one would predict that a male bullfrog would increase his ability to attract a mate by defending a high quality territory to be used as an oviposition site. Emlen and Oring (1977) proposed the term "resource defense polyg-

yny" to describe a mating system where males indirectly gain access to females through defense of a critical resource. I believe this term accurately describes the bullfrog mating system in this study. This mating system presumably has evolved in response to the prolonged breeding season, the continual presence of males at the breeding site, the temporally asynchronous distribution of receptive females and the consequentially skewed OSR, and the ability of males to indirectly gain access to females through defense of oviposition sites (also see Emlen, 1976; Wells, 1977; Howard, 1978).

Variation in bullfrog mating systems.—The bullfrog is the only species of anuran for which there are now comparative data on mating systems. These studies (Emlen, 1968, 1976; Howard, 1978; this study) reveal major consistencies in the mating system. Similarities are reflected in: the length of the breeding season, the OSR, the form of male-male competition, and the existence of female choice. However, there is a degree of behavioral plasticity within the species previously unreported in anuran breeding behavior (Table 1).

The mating system at Basking Pond is an example of resource defense polygyny. Howard (1978) showed that male bullfrogs at Crane Pond also defend territories which are utilized as oviposition sites. Emlen (1976), who also conducted his study at Crane Pond, described the mating system as a lek. He suggested that the sole function of the territory was to attract females and that oviposition took place outside the chorus area, off the male's territory. Al-

though the number of observations of oviposition sites are small, Emlen did show that larger males occupied central territories in the chorus and that smaller males were in the periphery or isolated from the chorus. A similar spatial organization is characteristic of the leks of some birds and mammals (Leuthold, 1966; Wiley, 1973). This spatial distribution of male size classes did not occur in the other two studies.

According to Emlen and Oring (1977), lekking behavior has evolved due to the inability of males to monopolize females or the resources they require. One would predict that with a drastic increase in density, sites may not be economically defendable (Brown, 1964) and a shift from territoriality to a dominance hierarchy would occur. This phenomenon has been reported in several lekking species of ungulates (e.g. Uganda kob, Leuthold, 1966). It has been suggested that a shift from lekking behavior to resource defense in bullfrogs may be influenced by population density (Emlen, pers. comm.). The influence of population density on social organization in the bullfrog is not clear and is being investigated (Emlen, pers. comm.).

In Basking Pond males were distributed throughout the pond and participated in intense chorusing from 2 May until 20 May 1976. Choruses at Crane Pond were mobile and centered near the shore or along vegetative mats. Emlen (1976) reported that the average longevity of a chorus was from three to five nights and observed the formation of eight choruses during his five weeks of observation. Howard (1978) noted chorus durations similar to those reported by Emlen. Both authors reported that choruses were mobile and Howard (1978) suggested that water temperature and submerged vegetation affect chorus movement. Although the chorus at Basking Pond was not mobile, the distribution of egg masses within the chorus was random. This would not be expected if the spatial distribution of males and territorial parameters were stable. I suggest that males and/or females were tracking environmental parameters within the chorus, thus resulting in the random distribution of oviposition sites.

Predation pressures seemed to be considerably different between Basking and Crane ponds. Both Emlen and Howard noted predation of calling males by the snapping turtle, *Chelydra serpentina*. Larger males in the deeper water especially were prone to predation. The only nocturnal predator in Basking Pond was the water snake, *Natrix sipedon*, which seemed to restrict its foraging to within several meters of the shore. Howard (1978) reported predation on eggs by the leech, *Macrobdella decora*. No significant egg predation was noted at Basking Pond. I suggest that some of the variation in chorus structure between Basking and Crane Ponds might be a result of differences in habitat structure (especially submerged vegetation), climate and predation pressure.

It seems likely that studies of anuran social behavior will reveal a diversity of mating systems. Studies of bullfrog social behavior indicate that there are general characteristics of a species' breeding system which are consistent in different parts of its range. However, there is a certain amount of behavioral plasticity within the species reflected by differences in social behavior between populations. Some causes of the variance in social behavior are suggested but remain purely speculative. Not only are more studies of anuran social behavior needed but such studies should consider the diversity as well as the consistencies of behavior within a species. Only with such studies can we hope to generate a more inclusive and general theory of vertebrate social behavior.

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