

In several species, females have been shown in laboratory discrimination tests to use vocalization parameters including call rate and duration, loudness, pulse rate, and dominant frequency to discriminate among potential males (e.g., Ryan, 1980; Klump and Gerhardt, 1987; Gerhardt, 1991). However, recent field studies indicate that females may only discriminate among male vocalizations in small choruses (Telford et al., 1989), within small subsets of males in large choruses (Morris, 1991), or may not discriminate at all (Sullivan and Hinshaw, 1992; Bertram, 1993).

A growing body of evidence suggests that a male frog's chorus tenure is an important determinant of his breeding success (Murphy, 1994a). Mating success has been positively correlated with male attendance in hylids (e.g., Godwin and Roble, 1983; Gerhardt et al., 1987; Murphy, 1994b), centrolenids (Jacobson, 1985), and neotropical frogs (Ryan, 1983) and has been suggested as the most important component to male lifetime mating success in common frogs (*Rana temporaria*; Elmberg, 1990). Although there seems to be strong selection for long chorus tenure in amphibian species, most males spend only a few evenings at breeding aggregations (Murphy, 1994a). Energy supplies limit chorus tenure in barking treefrogs (*Hyla gratioiosa*), with mortality and movement among choruses playing only a minor role (Murphy, 1994a).

Gray treefrogs (*Hyla versicolor*) breed in early summer throughout their range, with males chorusing in shallow water over a four- to seven-week season (Fellers, 1979a; Sullivan and Hinshaw, 1992; Bertram, 1993). Males of this genus use energetically expensive vocalizations (Taigen et al., 1985; Wells and Taigen, 1986) to compete with other males in the chorus and to attract females to the pond (Fellers, 1979a, 1979b). In two field studies on this species, the only parameter distinguishing frogs that mated from those that did not was the number of nights spent calling during the season; males that were successful in mating called on more nights during a season than males that did not (Sullivan and Hinshaw, 1992; Bertram, 1993).

Although the number of nights spent calling appears to be the most important component to male mating success in field populations of gray treefrogs, male frogs may also vary in the way they apportion their calling effort (Sullivan and Hinshaw, 1992; Bertram, 1993; Murphy, 1994a). For example, some males take nights off between chorusing evenings, whereas others do not, affecting the number of nights in a row that males attend the chorus. Finally, the day within the season that a male enters the chorus

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Male Mating Success and Variation
in Chorus Attendance within and among
Breeding Seasons in the Gray Treefrog
(*Hyla versicolor*)

SUSAN BERTRAM, MICHAEL BERRILL, AND
ERICA NOL

In most anurans, males use vocalizations to compete with other males at the chorus and to attract females to the chorus (e.g., Wells, 1977a; Howard, 1980; Forester and Czarnowsky, 1985).

is highly variable (Fellers, 1979a; Elmberg, 1990), and this variation may not necessarily be related to the number of nights that an individual eventually calls. Hence, although the number of nights that two mated frogs vocalize may be similar, their chorus attendance (pattern and seasonal onset) may differ.

We report here on how the pattern and apportionment of calling attendance within a season varied among all males and among those that eventually mated. Our results are based on an intensive study of a single gray treefrog population in southern Ontario where we identified individuals and matings on every night of the breeding chorus for each of three successive years.

Materials and methods.—Our study site was a small pond located on the property of Trent University, 6 km north of Peterborough, Ontario (44°22'N 78°17'W). The pond was permanent, measuring 80 m × 45 m in spring, and 20 m × 15 m at summer's end, with a maximum depth of 1 m. The pond was unusually accessible, with vegetation adequate for frog chorusing over most of its surface but not enough to hinder our access to frogs anywhere on the pond. The nearest other ponds with breeding gray treefrogs were located over 2 km away, and the daily and seasonal chorus onset and duration of these ponds were virtually identical to the study site (M. Berrill and S. Bertram, pers. obs.). Because of the distance between the ponds, between-pond migration seems unlikely but cannot be rejected.

Beginning the first week of May in 1991, 1992, and 1993, we arrived at the pond at dusk to listen for calling males. Once vocalizations began, we systematically circled the pond and located every calling male using both auditory and visual cues. We identified all vocalizing males by sketching their unique dorsal markings (Bertram, 1993), a technique that has been used for other species (Wells, 1977b; Tuckerman, 1982). Sketches were used instead of toe clipping or tattooing to avoid disruption of the frogs' breeding behavior. To confirm that dorsal markings remained unchanged over time, we sketched the dorsal pattern of a captive gray treefrog three times between May 1991 and May 1994 and found the pattern did not change. Because of the similarity of these sketches to a known individual, and the ease of using dorsal patterns to distinguish among frogs identified during both their daily chorus attendance and yearly chorus attendance, we were confident in our frog identification technique.

We were able to approach a calling frog to within 50 cm. The first time a male appeared in the chorus, his dorsal pattern was sketched and added to the pattern album of all previously identified individuals; on subsequent sightings, each individual's identification was confirmed through the dorsal pattern sketches in the album. Both the sketcher and her assistant were able to identify individuals using this technique. The procedure allowed rapid identification of both returning males and individuals new to the chorus. During the 1992 and 1993 field seasons, the former years' sketches were used to identify individuals that had been present in the chorus in previous years.

In 1991, mating pairs were located and identified during searches of the pond for chorusing individuals. In 1992 and 1993, we tied a strip of fluorescent flagging tape to every site where a male vocalized. As the evening progressed, we returned to every individual's marked site to relocate the individual. If he was no longer vocalizing, we searched the area to determine whether the male was in amplexus or had left the chorus. At the end of every evening's chorus we remained at the pond until we had either located all mating males or were certain that they had left the chorus. Since amplexus lasted for several hours, we are confident we witnessed most of the matings.

Because the breeding season started on different calendar dates in different years, we assigned day 1 of each season to the first evening of the calendar year that males called at the study pond. "Start night" was the first evening within the season that an individual was found vocalizing in the pond (e.g., start night = 5 indicates that the individual first vocalized on the fifth evening frogs were present and calling in the chorus). "Stop night" was the last evening we saw the animal vocalizing. "Number of nights" was the total number of evenings an individual was found vocalizing in the pond throughout the entire season. Evenings that had no frogs chorusing (e.g., nights that were too cold for vocalizing) were left out of the analysis. "Bout length" represented the number of evenings in a row a frog was found vocalizing. When a frog was not in attendance at the chorus for one or more evenings, provided the evenings he was missing were ones in which frogs chorused, he was said to be taking a break. "Break length" represented the number of evenings in a row a frog was not in attendance at the chorus.

We tested the data for normality in all analyses using the Shapiro-Wilk statistic (SAS/STATTM User's Guide, 6.05 ver., SAS Insti-

TABLE 1. ANNUAL VARIATION (MEANS, SE, RANGE) IN CALLING EFFORT BY MALES AT THE STUDY POND FROM 1991 TO 1993. Start night = first suitable night males join the chorus. No. of nights = total number of suitable nights spent calling. Bout length = number of consecutive nights calling. No. of breaks = number of times absent from the chorus for one or more nights. Break length = average number of nights in a row absent from the chorus. Stop night = last night in the chorus.

	1991	1992	1993	F	P
Start date	10/5	10/5	5/5		
Stop date	8/6	7/6	26/6		
No. of suitable nights	24	13	37		
No. of males	77	30	64		
No. of matings	10	4	19		
Start night	8.3 (5.76) (1-28)	10.7 (9.25) (1-29)	19.5 (14.91) (1-48)	20.0	0.0001
No. of nights	6.9 (4.70) (1-18)	4.2 (2.61) (1-10)	7.0 (5.28) (1-20)	4.21	0.016
Bout length	2.3 (1.47) (1-8.5)	2.5 (1.25) (1-6)	2.3 (1.69) (1-11)	0.86	ns
No. of breaks	2 (1.54) (0-6)	0.8 (1.00) (0-3)	2.3 (2.19) (0-8)	7.61	0.0007
Break length	1.7 (1.41) (0-5.5)	1.1 (1.54) (0-6)	2.46 (2.57) (0-13)	5.69	0.004
Stop night	19.9 (5.94) (2-30)	23.0 (9.10) (3-29)	38.3 (13.50) (4-54)	63.5	0.0001

tute, Cary, NC, 1988, unpubl.) before applying parametric statistical tests. For individuals that were found in more than one season, we ranked the raw data and analyzed the effect of year and the added variance components of individuals using two-way analysis of variance (ANOVAs; Conover, 1980). We used $P < 0.05$ to indicate statistically significant differences and provided exact probabilities when $P < 0.1$; otherwise we indicated that results were not significant (ns).

Results.—Although the treefrogs initiated their breeding season at a similar time in each of the three years, the breeding season length, the number of evenings suitable for chorus attendance, and the number of males found vocalizing each year varied (Table 1). We found 77 males and observed 10 matings in 1991, 30 males and four matings in 1992, and 64 males and 19 matings in 1993.

On each night with chorusing, males started vocalizing at dusk. Calling individuals moved from the trees to the floating mats of vegetation on the pond or into the bushes surrounding the pond. Although early in the evening some males moved a few meters from their initial site of vocalization, most remained at the same calling site throughout the evening (2100–0300 h). Females that entered the chorus initiated contact with a male, and the breeding pair then re-

mained in amplexus in the same general area for several hours.

In all three years, at least one male joined the chorus for the first time (start night) on each night of the season; and beginning with the second (1991), third (1992), or fourth (1993) night of the season, at least one individual called for his last night (stop night) on each night of the season (Table 1). The number of evenings males spent participating in the chorus (number of nights) also varied highly among males within a season and among years.

Bout length and break length varied within and among both individual frogs and years. Some frogs appeared at the chorus and vocalized for only one night, whereas others vocalized for several days before taking a break or stopping for the season. There was no significant difference in bout length among years; on average bouts lasted for just over two days. However, number of breaks and break length varied among individuals within a season and among years.

The operational and seasonal sex ratios were extremely male biased and the number of matings low, but females were available for mating throughout the breeding seasons (Fig. 1). The distribution of calling males was not significantly different than the distribution of matings over the three breeding seasons ($G = 0.22$, df

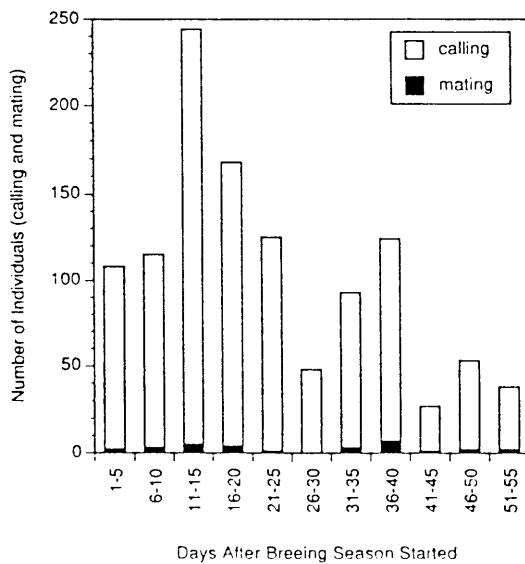


Fig. 1. Distribution of number of males calling (white bars) and mating (black bars) at the pond over the three breeding seasons. Dates were collapsed to five-day intervals.

= 1). Dates and years were collapsed to the first 15 days and the last 22 days of the season for analysis; males attending for more than one breeding season were randomly omitted from all but one of the years they attended. Males were as equally likely to mate if they joined the chorus (start night) late in the season than they were if they joined the chorus early in the season ($G = 0.95$, $df = 1$, ns).

Most males did not mate; only 24 of the 171 males (14%) in attendance during the three years mated. In 1991, eight males mated once and one male mated twice. In 1992, only four males

mated, each only once. In 1993, eight males mated once, one mated twice, one mated three times, and one mated six times. The proportion of males that mated was not significantly different among years ($G = 0.88$, $df = 2$, ns). None of the returning males that had mated in the previous year(s) were found to mate again. Because of the possibility of redundant information in our measures of calling effort, we ran a stepwise logistic regression (Sokal and Rohlf, 1995) to determine which chorus attendance variable contributed most to distinguishing mated and unmated males. The only variable to enter the logistic regression at a significance level was the number of nights that a male called. This was also the only variable that distinguished males using a univariate analysis (Table 2).

Once a frog mated, the probability of his mating again was not significantly different than his original chances of attracting a mate (original probability 0.14, probability of mating again 0.18; Binomial test: $B^* = 0.57$; Hollander and Wolfe, 1973). Using the logistic regression, none of the calling effort measures significantly distinguished males that mated only once ($n = 20$) from the four males that mated more than once, although bout length of males that mated more than once was significantly longer than bout length of males that mated only once [males mating more than once, mean (SE): 4.5(0.99)d; males mating once, 2.6(0.26)d; $t = 2.63$, $P = 0.015$].

Of the 24 males that mated, 13 did so on their first or second evening of chorus attendance; the others mated after being at the chorus for 3–13 suitable nights. Males likely mated on the first or second night simply because they made up a larger proportion of the total number of

TABLE 2. A COMPARISON OF CALLING EFFORT OF FROGS THAT MATED AND THOSE THAT DID NOT MATE DURING THE STUDY PERIOD (1991–1993). See Table 1 for definitions.

	Unmated ($n = 147$)	Mated ($n = 24$)	t	P
Start night	13.6 (1.01) (1–48)	9.3 (1.82) 1–35	1.68	0.095
No. of nights	5.9 (0.37) (1–18)	9.5 (1.10) (2–20)	3.64	0.0004
Bout length	2.3 (0.12) (1–11)	2.9 (0.30) (1.33–6.33)	1.96	0.051
No. of breaks	1.8 (0.14) (0–8)	2.7 (0.43) (0–8)	2.28	0.051
Break lengths	1.8 (0.35) (1–6)	1.9 (0.17) (0–13)	0.09	ns
Stop night	26.6 (1.03) (2–54)	31.1 (3.32) (3–54)	1.56	ns

males present. On nights that the 13 early males mated, 136 out of 303 calling males were present at the pond for their first or second night, whereas on the nights that the 11 other males mated, only 87 of 298 males were present for their first or second night ($G = 15.9, P = 0.0001$).

In 1992 and 1993, we identified individuals that had attended the chorus in previous years (old frogs) and individuals which were new to the chorus (new frogs). Old and new individuals did not differ in any of their attendance parameters. Furthermore, new and old males did not differ in their probability of mating (five of 20 old frogs mated, 10 of 59 new frogs mated, $G = 0.40, df = 1$). Six males that were identified in 1991 returned to the chorus in 1992 and again in 1993. There was considerable variation in the chorus attendance of these six frogs. Using the ranked data, we found no significant added variance component for any variable, because the variance within males was always less than or equal to the error variance. Only stop night was significantly different among years; in 1993 individuals stopped on a later night than in 1991 or 1992 ($F = 4.90, P = 0.03$). However, the 1993 breeding season was over two weeks longer, and the later stop night of those in their third year may be a result of the prolonged end to the season.

Discussion.—The best way for a male gray treefrog to obtain a mate was to be present and calling at the pond for as many nights as possible. Apart from the time spent calling, the pattern and apportionment of calling (start date, bout length, break length, and stop date), although highly variable among males, did not contribute in a statistically significant sense to mating success in this population. Male mating success of common frogs (Elmberg, 1990), spring peepers (Forester et al., 1989), barking treefrogs (Murphy, 1994b), green treefrogs (Gerhardt et al., 1987), and glass frogs (Jacobson, 1985) has also been shown to be correlated with time spent in the chorus.

Because calling often increases a male's chances of mating, there should be strong selection for males to invest a greater amount of energy and call for more nights during the breeding season. Yet, the males that we observed varied greatly in the time they spent in chorus attendance. Males may differ in their abilities to recover lost reserves during the breaks they take from the chorus or during the daytime breaks they have between consecutive nights at the chorus. These events, in turn, may be a matter of natural selection or luck. The male strategy would then appear to be to call

on as many nights as possible, as long as energy reserves are sufficient (Taigen and Wells, 1985) and, therefore, have more chances of being available to mate with females.

From the female's perspective, the sound of chorusing males will lead her to the pond (Wells, 1977b), but we cannot rule out the hypothesis that all males present and vocalizing are equally suitable mates (Bertram, 1993; Sullivan and Hinshaw, 1992). It is unlikely that female hylids visit the pond on any more than one night in the season (Gerhardt, 1991; Morris, 1991; Bertram, 1993). Therefore, it is unlikely that females use previous observations to distinguish males that call on many nights from males that call on a few nights. It is also unlikely that females choose between males by their call parameters. Previous work has also shown that the number of nights spent calling was correlated with mating success in two gray treefrog field studies: call duration, dominant frequencies, and pulse duration were not significantly different between males that mated (called most often) and males that did not mate (Sullivan and Hinshaw, 1992; Bertram, 1993). Random mating by females explains why males that called most often mated; however, if chorus attendance and calling is highly energetically expensive, then random selection of mates really is not random. Females will be more likely to mate with energetically endowed males. Because it is likely that the only critical feature of a male is to maintain the energy necessary for calling, and because all chorusing males appear equally likely to mate, then males that call most often and/or survive to breed another one or two seasons have additional mating opportunities (Elmberg, 1990).

It remains unusual in any prolonged breeding system (Wells, 1977a) for the sex ratio to be so skewed in favor of males and, as a consequence, for most males to never mate. Low overwintering survival may account for the highly skewed sex ratio at our study site. In many anuran systems, females take longer to mature than males (Berven, 1990). If females take one season longer to reach sexual maturity, high overwintering mortality could explain the skewed sex ratio.

Long-term studies are now necessary to determine at what age males and females initiate courtship behavior, what age gray treefrogs attain (Howard, 1988; Elmberg, 1990), whether individuals that mate several times are more common than presently believed, whether surviving to breed another season substantially increases a males reproductive success, and, although our data on returning frogs indicates this unlikely, whether calling performance de-

clines in old age (Avisé, 1993). Telemetry work and a study of the energetics during breaks is needed to determine variance which may help us to understand the underlying causes of variation in chorus attendance and mating success.

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Biology Department, Trent University, Peterborough, Ontario, Canada K9J 7B8. Present address: (SB) Box #37, Department of Zoology, Arizona State University, Tempe, Arizona 85287-1501. Send reprint requests to SB. Submitted: 14 Nov. 1994. Accepted: 8 Nov. 1995. Section editor: S. T. Ross.