Chapter 6

FLUCTUATIONS IN A NORTHERN POPULATION OF GRAY TREEFROGS, *HYLA VERSICOLOR*

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ABSTRACT.—For 3 breeding seasons (1991 to 1993), we studied a gray treefrog (*Hyla versicolor*) population in southern Ontario. We identified the number of vocalizing males every night of the breeding season and recorded mating events. Breeding seasons varied from 4 to 7 wk in length and number of nights suitable for calling each year ranged from 13 to 37. The total number of calling males varied from 30 to 77, and nightly chorus attendance varied greatly. Variation in number of males chorusing nightly was not explained through air temperature fluctuations, except that when the temperature fell below 8° C, males would not call. Relatively few males mated, resulting in an apparently skewed sex ratio. Number of males calling, breeding season length, number of nights males called, nor proportion of nights within a season suitable for calling were successful in predicting female presence at the pond. We combined our data with data from 2 other intensive field studies on *H. versicolor* populations to find that seasonal population size and number of males seasonally present were positively correlated with the proportion of nights suitable for chorusing (nights that air temperature at dusk was above 8° C and males chorused) in relation to breeding season length. Variation in numbers of males calling and mating in our 3-yr study suggests that establishing decline due to human impact will require long-term intensive study.

RÉSUMÉ.—Pendant 3 saisons de reproduction (1991 et 1993), nous avons étudié une population de rainettes versicolores (*Hyla versicolor*) dans le sud de l'Ontario. Nous avons identifié le nombre de mâles qui coassaient chaque nuit pendant la saison de reproduction et répertorié les accouplements. La saison de reproduction dure entre 4 et 7 semaines et le nombre de nuits propices aux coassements chaque année varie entre 13 et 37. Le nombre total de mâles qui coassent varie entre 30 et 77 et l'assistance nocturne au choeur des mâles varie considérablement. Les fluctuations de la température de l'air ne permettent pas d'expliquer les variations dans le nombre de mâles qui coassent chaque nuit, sauf lorsque celle-ci chutait en-deçà de 8° C puisqu' à cette température, les mâles ne vocalisaient pas. Relativement peu de mâles se sont accouplés, ce qui a donné un proportion mâle/femelle apparemment dyssymétrique. Le nombre de mâles qui coassent, la durée de la saison des amours, le nombre de nuits au cours desquelles les mâles coassent et la proportion de nuits dans la saison propice aux coassements n'ont pas permis de prédire la présence des femelles dans l'étang. Nous avons combiné nos données aux données de 2 autres études intensives sur le terrain correspondant à des populations de *H. versicolor* et avons constaté que la taille de la population saisonnière et le nombre de mâles présents à chaque saison étaient positivement corrélés à la proportion de nuits propices aux coassements (nuits au cours desquelles la température de l'air à la tombée de la nuit était supérieure à 8° C et au cours desquelles les mâles coassaient), par rapport à la durée de la saison de reproduction. La variation dans le nombre de mâles qui ont coassé et se sont accouplés pendant notre étude de 3 ans donne à penser que des études intensives à long terme s'imposent avant d'attribuer le déclin des populations de *H. versicolor* à l'influence humaine.

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Understanding factors that regulate anuran populations during the breeding season is hampered by the intensive human effort required to determine the number of individuals visiting and breeding in a pond on a seasonal basis. To properly assess amphibian population declines (Blaustein et al. 1994; Pechmann et al. 1991; Bishop and Pettit 1992) and future research directions, we need to know the extent of variation in numbers of vocalizing males, the variation in the proportion of males that mate, and what factors influence these numbers.

A number of studies have reported numbers of adult male and female anurans at temperate ponds during the breeding season (for example, Fellers 1979; Howard 1980; Berven 1990; Elmberg 1990; Sullivan and Hinshaw 1992). In these studies, the overall sex ratio (yearly, not operational) appeared skewed toward males in most years. Our study addressed variation in male and female attendance of gray treefrogs, *Hyla versicolor*, at a breeding pond at the northern edge of the species' range.

Hyla versicolor ranges from the southern United States northward to central Ontario. It breeds over 4 to 6 wk in late spring and early summer. Both males and females remain in trees surrounding the pond during the day and males move to the pond on each night suitable for chorus attendance. Males select calling sites and vocalize to attract females and maintain inter-male distances (Fellers 1979). Females enter the pond silently, approach a calling male, and induce amplexus, which lasts most of the night. The pair adhere their eggs to vegetation in small scattered clumps just before dawn. Tadpoles undergo metamorphosis by mid-summer but the age at which adult frogs enter a pond to breed for the 1st time is unknown.

We monitored breeding behavior of a population every night of the breeding season over 3 yr. We tested 2 hypotheses. Because temperature is highly variable during the spring and anurans are ectothermic, the length of the breeding season, the number of evenings males chorus, and the number of males chorusing each evening, should vary. Second, because females are thought to be drawn to the chorus through male attraction vocalizations (Wells 1977a), the number of females found mating is likely to be related to the number of males vocalizing.

*Gray treefrog (*Hyla versicolor*). Photo by John Mitchell.*

MATERIALS AND METHODS

Our study site was a small pond located on Trent University property, 6 km north of Peterborough, Ontario (44°22' N, 78°17' W). The pond is permanent, measuring 80 × 45 m in spring, and 20 × 15 m at summer's end, with a maximum depth of 1 m. The pond has adequate vegetation for use as calling perches by males and for females to adhere eggs, but not enough to hinder our movements. Although treefrog immigration into the pond is possible, we believe it is unlikely because the pond is unusually isolated, with the closest pond located 2 km away.

Beginning in the 1st week of May in 1991, 1992, and 1993, we arrived at the pond at dusk every night to listen for calling males. Once vocalizations began, we systematically circled the pond at least twice and located every calling male using both auditory and visual cues. One person would move into an area of the pond, identifying each individual and tagging its location, and searching for non-vocalizing or satellite males. A 2nd person followed, confirming frog identities and searching for frogs that were missed. We identified all vocalizing males by making accurate sketches their natural dorsal markings. These markings are complex and it is unlikely that 2 individuals would have the same

patterns. Dorsal markings have also been used in field studies of other anurans (Wells 1977b; Tuckerman 1982). We reared 1 *H. versicolor* in a lab for 3 yr and the frog was re-sketched annually without access to the previous sketches; its back pattern remained unchanged through time. Furthermore, all field and lab sketches were completed by 1 person who also confirmed the identity of any frog identified by any other observer. The sketch of each individual new to the chorus was added to an album containing the sketches of all individuals' back patterns thus allowing us to determine whether each male was returning or new to the chorus. During the 1992 and 1993 field seasons, sketches from prior seasons were used to identify individuals returning for a 2nd or 3rd year. Therefore, we have assumed that our technique located all males present, clearly identified each male, and that each individual's back pattern remained unchanged through time.

Due to the silent nature of female treefrogs, our attempts to identify females at the pond were limited to locating females already in amplexus. In 1991, while thoroughly searching the pond each night, we recorded all amplexed pairs found. In 1992 and 1993, upon locating and identifying a vocalizing male, we marked its vocalization site with fluorescent flagging tape, allowing rapid relocation. As each evening progressed, we returned to every individual's vocalization site to relocate the individual. If a male was no longer vocalizing, we thoroughly searched an area of at least 2 m in diameter from where the chorusing male was last seen to determine if he was in amplexus with a female. At the end of each chorus we remained at the pond until we had either located all mating pairs, or ensured ourselves that the males had left the chorus for the evening. As a result we have assumed that we observed all matings that occurred over the 3 yr. Our technique did not allow for the identification of females that may have been present at the chorus that did not mate.

Nightly maximum and minimum air temperatures were obtained from the Trent University weather station, located within 1 km of the study pond. The weather station recorded air temperature every minute, giving hourly means. From the hourly means, we determined the maximum and minimum air temperatures for each night during the 3 breeding seasons. To determine whether there was a temperature switch (an air temperature indicative of non-chorusing male behavior), we completed a Chi-square analysis for temperatures from 5 to 15° C and identified the temperature that had the highest significant level indicative of chorusing male presence. All other analyses were completed using regressions.

RESULTS

Males started vocalizing at dusk during each breeding seasons. Calling individuals moved from the trees to the floating mats of vegetation on the pond or into bushes surrounding the pond. Although some males moved around the pond early in the evening, most remained at the same calling site from their arrival at the pond until chorus end (1930 to 0300 hr). All observed females that entered the chorus initiated contact with males and the amplexed pair then remained in the same general area of the male's calling site for several hours. They laid their fertilized eggs just prior to dawn.

Chorusing activity started between 5 and 10 May in all 3 seasons. Number of males vocalizing on any particular evening was highly variable both within and between breeding seasons. On nights when males called, the mean number of individuals vocalizing was 22 in 1991 (range = 1 to 42), 10 in 1992 (1 to 19), and 12 in 1993 (1 to 37). Although the number of males calling in an evening was positively correlated with the minimum, maximum, and average temperatures recorded for that evening, less than 15% of the variation was explained by temperature (Table 1). However, low air temperatures did hinder chorusing behavior. When the air temperature dropped below 8° C by dusk, males seldom vocalized ($P = 0.001$).

On nights that females were present and mating, chorus size ranged from 5 to 40 males. Maximum, minimum and average temperatures were not correlated with presence of females (Table 1). Although number of females in amplexus each evening was positively correlated with number of males vocalizing ($P = 0.001$, $r^2 = 0.140$), only 13% of the variation in female presence was explained by male presence (Table 1).

Table 1. *Influence of temperature on presence of* Hyla versicolor *at breeding choruses.*

		Nightly temperature		
		Minimum	Maximum	Mean
Total frogs/night	r^2	0.093	0.089	0.135
	F	8.632	8.265	12.564
	P	0.004	0.005	0.001
Males/night	r^2	0.095	0.090	0.141
	F	8.737	8.915	13.172
	P	0.004	0.004	0.001
Females/night	r^2	0.000	0.000	0.000
	F	0.958	0.008	0.257
	P	0.311	0.930	0.614

Table 2. *Numbers of adult male and female* H. versicolor *present during the breeding season.*

Year	Males	Females	Duration of breeding (days)	Chorus nights (proportion)
1978[1]	35	9	50	33 (0.66)
1988[2]	26	6	42	12 (0.28)
1989[2]	36	39	37	23 (0.62)
1990[2]	19	10	30	15 (0.50)
1991[3]	77	10	30	24 (0.80)
1992[3]	30	4	29	13 (0.45)
1993[3]	64	19	54	37 (0.69)

[1]Fellers (1979)

[2]Sullivan and Hinshaw (1992)

[3]This study

Chorusing activity ceased in early June in 1991 and 1992 (7 and 8 June), but chorusing continued until 27 June in 1993 (Fig. 1). There did not appear to be a trend between seasonal air temperatures and length of breeding seasons. Air temperatures during 1992 were cooler than those of 1991 yet the breeding season lengths were similar (Fig. 1). Conversely, daily maximum and minimum air temperatures during 1991 and 1993 were similar, but the 1993 breeding season was three weeks longer than that of 1991 (Fig. 1). The number of nights suitable for male chorusing, i.e. nights when the air temperature at dusk was above 8° C and males were found vocalizing, varied among seasons, with 24 nights in 1991, 13 in 1992, and 37 in 1993.

Numbers of breeding adults fluctuated considerably. In 1991, 77 different males vocalized at the pond, and ten matings occurred. In 1992, only 30 different males attended the chorus and only four matings occurred. During the longer season of 1993, 68 different males joined the chorus and nineteen matings occurred. Thus the sex ratios, based on number of males vocalizing and number of females found in amplexus, were all male biased and varied from 7.7:1 in 1991, to 7.5:1 in 1992, and 3.4:1 in 1993.

New males were the most abundant class in the chorus each year. Of the 77 males at the pond in 1991 only 16 (21%) returned in 1992. In 1993, 9 (33%) of the 1992 chorus returned, including 6 from the 1991 chorus. Because the population in 1993 was so much larger than that of 1992, 83% of the males were there for the first time.

Table 3. *Numbers of male and female* H. versicolor *from 3 breeding populations related to number of nights males chorused and duration of season. Data from this study, Fellers (1979) and Sullivan and Hinshaw (1992) are combined.*

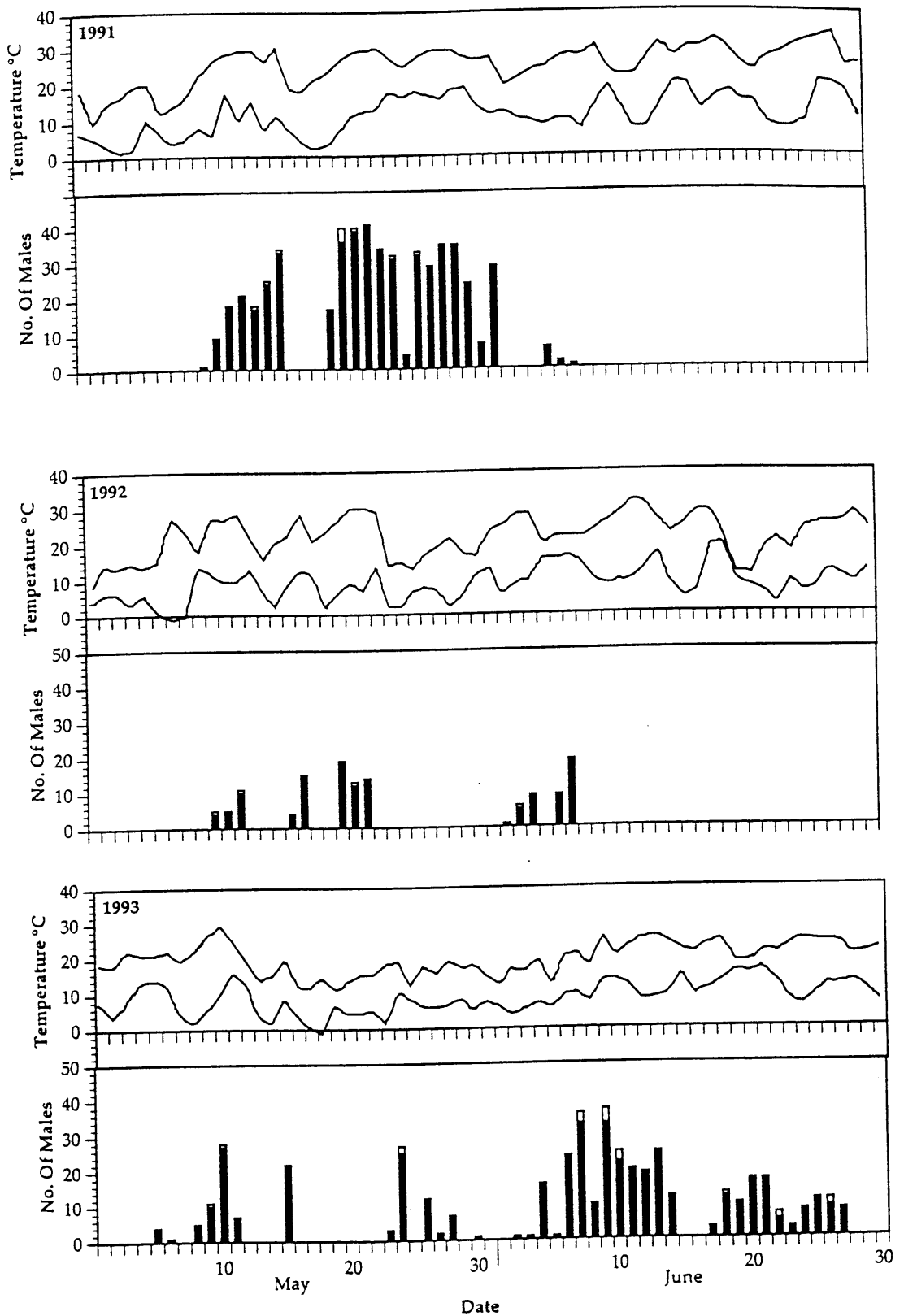|		Number of chorus nights	Duration of breeding season	Proportion of chorus nights to total
Total frogs	r^2	0.228	0.000	0.543
	F	2.768	0.159	8.128
	P	0.157	0.706	0.036
Total males	r^2	0.305	0.000	0.587
	F	3.629	0.225	9.534
	P	0.115	0.635	0.027
Total females	r^2	0.110	0.000	0.000
	F	0.617	0.132	0.657
	P	0.468	0.731	0.657

Figure 1. Comparison of numbers of males vacalizing (black bars) and mating (clear bars) each night, 1991 to 1993. Minimum and maximum air temperatures indicate a relationship between low minimum temperature (< 8°) and nights without any calling males.

DISCUSSION

The degree of nightly and seasonal variability in the *H. versicolor* breeding system is immense. Breeding seasons differed in duration as well as in numbers of males and females in attendance. Trends indicate we cannot use overall breeding season air temperatures to estimate breeding season length or breeding population numbers and structure. We are also unable to use nightly air temperatures to predict number of males or number of females present. However, we are able to make predictions on how nightly air temperature fluctuations influence the presence or absence of a chorus. When the temperature fell below 8° C males never chorused. In more southern populations this temperature switch appears to occur at a higher temperature (Fellers 1979), indicating that adaptation to local conditions may occur throughout the range of the species.

We combined our 3 yr of data on population size, length of breeding season, number of nights males vocalized during a season, and the proportion of suitable calling nights (suitable calling nights per breeding season length), with 4 other yr of complete breeding season data from populations of vocalizing gray treefrogs (Table 2; Fellers 1979; Sullivan and Hinshaw 1992). Although sample size is only 7 breeding seasons, there is a positive correlation between total number of males (with or without females) identified at the pond each year and proportion of suitable calling nights (Table 3, Fig. 2). However, we found no such relationships between yearly population size and length of breeding seasons or number of nights males vocalized, nor between number of males present and season length or number of nights males vocalized (Table 3). Female presence at the pond was not correlated with number of nights of male chorusing, breeding season duration, or proportion of nights males chorused (Table 3). It was also not correlated with number of males chorusing ($P = 0.788$).

Over-wintering conditions are likely to influence population sizes and sex ratios. All 3 intensive studies of *H. versicolor* (Table 2) were conducted in areas where over-wintering treefrogs have the possibility of being exposed to harsh environmental conditions. Our data indicate that relatively few males return to the breeding pond for a 2nd or a 3rd season. Sullivan and Hinshaw (1992) reported a similar low rate of return (23% in 1989; 22% in 1990) in a central Maine population. It is possible that non-returning males have migrated elsewhere, but the isolation of our study pond and the evidence that other species return to the same location to breed (Oldham 1966; Gill 1978; Berven and Grudzien 1990) suggests that non-returning males may not survive the winter. Winter survival could be greater in more southern parts of the species range and populations there should provide a means of testing this idea.

Female anurans are notoriously difficult to find at breeding sites and, as a result, male-biased sex ratios are frequently reported (Berven 1990; Pechman et al. 1991; Sullivan and Hinshaw 1992). However, the combination of the ease of accessibility to all parts of our pond, the silence of a male in amplexus, the prolonged amplexus of a mating pair, and our searching technique, which compelled us to scour the area for any male that was identified previously in the evening as vocalizing, gives us confidence that we saw all matings that occurred. Therefore, we believe that the male-biased sex ratios we report for *H. versicolor* are real. Over-wintering mortality may also account in part for such a highly skewed sex ratio years. Since female anurans generally take 1-yr longer to reach sexual maturity than males (Berven 1990), harsh winter conditions occurring for consecutive years may make it difficult for many females to reach sexual maturity before dying.

We conclude that high variability in nightly and seasonal chorus activity, coupled with the low probability of males mating, characterizes *Hyla versicolor* populations. If this treefrog system is indicative of other anuran species, we believe that long term and intensive studies will be necessary to establish whether decline is occurring.

ACKNOWLEDGMENTS

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