

Determinants of chorus participation and the effects of size, weight and competition on advertisement calling in the tungara frog, *Physalaemus pustulosus* (Leptodactylidae)

ANDREW J. GREEN*

Animal Behaviour Research Group, Department of Zoology, South Parks Road, Oxford OX1 3PS, U.K.

Abstract. The individual mating success of male tungara frogs is best predicted by the number of nights spent in chorus activity, yet individuals are often absent from the chorus for several nights without calling at another site. To test whether males leave the chorus to forage to pay the energy cost of calling, males were captured in groups of four and their calls were recorded over 3 or 5 nights, while half of them were starved and the others fed. Feeding had no effect on the number of males that stopped calling, or on the changes in call rate, call complexity (number of secondary notes) and chorus leading over time. When they were released, fed males did not return faster to the chorus, and were not more likely to return, than starved males. Playback of a tape of a large chorus increased the number of males present in the small natural chorus. Chorus size in three pools was positively correlated with the minimum temperature, and negatively correlated with the rainfall, over the previous 2 days. These results suggest that males are conservative in their chorusing activity because chorusing increases predation risk, not because they need to forage. Males use variation in chorus size, rainfall or temperature to select those nights that offer reduced predation risk and increased mating opportunities. Playback of a tape of a large chorus caused males in a small chorus to increase their call rate by 104%, their call complexity by 38%, and the net energy cost of calling by 70%. Male size and weight had no effect on the mean call rate, call complexity or the amount of chorus leading, but were positively correlated with the maximum call rate of males; this effect may contribute to the higher mating success of larger males observed previously. Size and weight had no effect on the maximum rate of production of secondary notes, or on the influence of playback on call rate. Weight was correlated with the relative increase in call complexity as a result of playback; larger males use relatively more secondary notes in larger choruses, whereas smaller males use relatively more in small choruses.

The tungara frog has been the subject of extensive studies of sexual selection (Ryan 1980, 1983a, 1985a). It has a prolonged breeding period. Males advertise from choruses in water, using a complex call with a primary whine component followed by up to six shorter secondary 'chucks'. Females can choose males freely in the absence of the fights between males for possession of the female found in some bufonid and ranid anurans (Davies & Halliday 1978, 1979; Howard & Kluge 1985) and interference from non-calling satellites found in various hylids (Perrill et al. 1978; Roble 1985). Males do not defend a territory in which the female lays her eggs as in some ranids (Howard 1978) and do not offer paternal care as in some other leptodactylids (Townsend et al. 1984), but they construct a foam nest during amplexus by beating the jelly matrix of the egg mass with their hind legs as they fertilize the eggs. At high densities, males space themselves and

*Present address: Wildfowl and Wetlands Trust, Slimbridge, Gloucester GL2 7BT, U.K.

compete for calling positions in the chorus using 'mew' calls and occasionally wrestling. Larger males have a higher mating success (Ryan 1983a), and females are able to select large males as mates by using the fundamental frequency of the 'chuck' component of the advertisement call, which correlates negatively with body size. Discrimination trials, in which females were offered a choice of a call with either a high frequency or a low frequency 'chuck', showed that females have a phonotactic preference for low frequencies, and hence larger males (Ryan 1980). Females also prefer complex calls with 'chucks' to simple calls without, and males add more chucks in the presence of other calling males (Rand & Ryan 1981).

Ryan (1983a) found that of the parameters he quantified, the number of nights that a male attends a pond chorus is the most significant determinant of mating success (i.e. the number of females mated with), a result that is in agreement with work on other species (e.g. Greer & Wells 1980; Kluge

1981; Woodward 1982; Arak 1983a; Godwin & Roble 1983; Jacobson 1985; Gerhardt et al. 1987). The important role of chorus attendance is not surprising, especially since any male is limited to a maximum of one mate in any one night by the prolonged duration of amplexus and spawning behaviour. Some positive relationship is expected simply because presence is a prerequisite for mating success. However, given that sexual selection will act to increase the number of nights that males spend in the chorus, it is perhaps surprising that each mature individual is inconstant in his presence in the chorus. Although some chorusing occurs on every night, each male is frequently absent for several nights between nights of calling.

In this study, I examine three hypotheses, not mutually exclusive, that could explain this observation.

(1) The energy cost of calling constrains this activity, so that males absent from a chorus are foraging in order to replenish their energy supplies (Ryan 1985a).

(2) Males selectively join large choruses, in which predation risk is lower and the proportion of females to males, or operational sex ratio (Emlen & Oring 1977) is higher (Ryan et al. 1981b).

(3) Male attendance is determined by other environmental variables (e.g. rainfall or temperature) that might influence predation risk or the number of females arriving to breed.

I also explore the roles of male size and competition in the advertisement calling of the tungara frog. I first consider whether vocal competition causes males to change the rate and the energy cost of their advertisement calling. Many species of anurans call at faster rates in choruses than in isolation (e.g. Wells & Schwartz 1984), while the grey treefrog, *Hyla versicolor*, produces fewer but longer calls in choruses (Wells & Taigen 1986). Second, I consider whether the size and weight of males influence call rate, call complexity and chorus leading, all parameters that are likely to affect the ability to attract a mate. The mating advantage of larger males may not be solely due to the influence of 'chuck' frequency; larger males may be more attractive in other ways. In addition, since the 'chuck' frequency does correlate with size, males of different sizes may have different calling strategies, e.g. small males may attempt to overcome their high frequency disadvantage by calling at a faster rate. Finally, I consider how size, weight and intra-sexual competition interact. The mating advantage

of larger males conferred by the low chuck frequency may depend on the level of competition, since the operational sex ratio increases in larger, denser choruses and since females may be less discriminating in the presence of the background noise of larger choruses (as in the green treefrog, *Hyla cinerea*, Gerhardt 1987; Gerhardt & Klump 1988). Consequently the response of males to competitors might depend on size.

METHODS

Study Area and Species

I studied a population of tungara frogs (male snout-vent length range 25–34 mm, female 27–35 mm) in lowland tropical semi-deciduous forest on Barro Colorado Island, central Panama from 11 July to 19 September 1987. This site and species are described in detail by Ryan (1985a). The frogs mature and breed throughout the year, although breeding is concentrated in the wet season (April–December). The adults live and forage in leaf litter. At night males advertise from calling sites in pools, and females approach and initiate amplexus. Males do not feed while in the chorus. I studied males calling from four cement pools around the laboratory clearing, adjacent to Kodak House, Animal House, the Laboratory and Yellow House. All pairwise distances between these pools are within 100 m. Most calling and pairing occurs between dusk (1830) and 2400 hours. Pairs oviposit after calling has finished, usually between 2400 and 0200 hours at sites in the pool that may be several metres from the calling site used by the male. Observations of marked males during the present study showed that males are largely faithful to one pool, even when other males are calling from other pools within 50 m.

Feeding and Competition Experiments

I collected 86 males over a 9-week period in groups of four (quartets) while they were calling in the early evening. Each male was then placed in a separate plastic bucket of 200 mm diameter, filled with water to a depth of 50 mm, by the side of Kodak pool. The buckets were placed at the four corners of a square of 1 by 1 m. A leaf of semi-aquatic plant was placed on the water surface to provide the grip that calling males adopt with their fore feet while semi-immersed. A screen top of 0.5 mm mesh was placed over each bucket, with a central hole to fit the head of a 'Realistic' 300 ohm

dynamic microphone. The four microphones were connected to two 'Realistic' SCP-17 stereo cassette recorders to allow simultaneous recording onto magnetic tape. The calls of the four males were recorded from 2045 to 2130 and from 2200 to 2245 hours. The tapes were transcribed by hand while played back on the recording machines. I selected 20 min from each 45-min recording in 5-min samples at 10–15, 20–25, 30–35 and 40–45 min from the commencement of recording, and noted the number and complexity (i.e. number of chucks) of calls for each male. There was no significant difference between the four bucket positions used for recording for the rate or complexity of calls produced by the males (using the mean rate or complexity for each of 44 males as one data point and controlling for differences between recording nights; for rate $F_{3,26} = 1.58$, NS; for complexity $F_{3,26} = 1.04$, NS).

After recording, I measured and weighed the males. As a measure of size, the length was taken from the snout to the posterior tip of the urostyle (SUL) rather than to the vent (SVL). Most workers use SVL, which is highly correlated with SUL ($SUL = 0.58 + 0.94 \text{ SVL (mm)}$, $r = 0.98$, $N = 66$), but I found this to be a less repeatable measure.

Effects of foraging intake

To test Ryan's hypothesis that males leave choruses after a few nights because a shortage of food reduces their calling ability after this time, males were housed in individual glass jars of 90 mm diameter with a base of moist tissue and clean dead leaves. These jars were kept in semi-natural conditions in a building with mesh windows, away from direct light. I randomly selected two of the males to be given food, and daily at 0930 hours I gave them adult termites, a major component of the natural diet (Ryan 1985a; personal observation), easily collected on the island and of a uniform size. The major species used was *Nasutitermes corniger*. Observation and faecal analysis showed that this food was digested and egested within 48 h. The four males were placed in buckets by the side of Kodak pool each night from 1900 to 2300 hours and allowed to call, and were recorded again at the same times as above on 2 of the following 4 nights. At 2300 hours they were returned to their jars.

The first four quartets were recorded on nights 1, 2 and 3, and were then released. I then changed the design in two ways to increase the chances of detecting any effect on the males of being fed or starved.

To allow a longer period for an effect, the last 13 quartets were recorded on nights 1, 3 and 5. Because an effect is more likely under increased rates of energy consumption, I also changed the acoustic conditions. While all experimental males were under acoustic stimulation from each other and from any chorus present in Kodak pool ($\bar{X} \pm \text{SD} = 2.23 \pm 2.10$, range 0–9 present on nights during this study), these 13 quartets were also always subjected to continuous playback of a 45-s tape loop between 2015 and 2145 hours, which included the first of the two periods of recording. This loop was a recording of a large, dense chorus of several hundred males, made by M. J. Ryan in Gamboa, Panama in 1986, and had the effect of increasing the net energy cost of calling in the experimental males by 70% (see below).

I chose timescales of 3 or 5 nights for the experiments because this is the typical timescale for periods of presence and absence of individual males in the natural chorus. After the final night of recording, I marked the males individually by excising the last of the phalanges from two toes on different feet. A 5-mm square of bright plastic flagging was sewn across the loose mid-dorsal skin of the male to allow easy detection, a technique that seems to have no effect on the behaviour of the male (Ryan 1985a). The males were then released in a pool at 2300 hours to study the effect of being fed or starved on subsequent behaviour. Every night during the study I regularly surveyed the pools and identified any marked males present.

I estimated the amount of calling by males that could be fuelled from the food given, using the average energy content of a call and an estimate of the energy content of food. The energetics of calling by tungara frogs were measured on Barro Colorado Island in August 1980 under similar conditions of ambient temperature (25.0–27.5°C) and on frogs of similar weight ($\bar{X} \pm \text{SD} = 1.67 \pm 0.18$ g) to those of the present study (1.70 ± 0.30 g). The average amount of energy input per call was 0.024 J (Bucher et al. 1982; Ryan 1985b). Dry weights of whole termites and of undigested cuticle fragments collected from faeces were measured and the net weight of digestible food was converted into energy content using an estimated calorific value of 25 kJ/g dry weight of termite (a typical value for insects (range 22–31 kJ/g), Southwood 1978). Males selected to be fed were given 15–30 termites a day, and 76% of these males ate all their food. Males recorded over 3 days were given a mean of 0.33 kJ (range

0.30–0.38 kJ) of digestible food over 2 mornings. If males were 100% efficient at converting digested food into calls, this food would provide the energy for 14 000 calls. On average males call 5000 times a night (Ryan 1985a), hence I was feeding these males enough to convert into up to 3 nights of calling. Males recorded over 5 days were given a mean of 0.69 kJ (range 0.53–0.90 kJ) of digestible food over 4 mornings. With 100% efficiency this would provide enough energy for 30 000 calls and 6 nights of calling.

Effects of size, weight and competition

Quartets that were exposed to playback of the background tape loop were used for analyses of the effect of vocal competition, size and weight on the rate, energy cost and complexity of calling, while all quartets were used in an analysis of the effect of size and weight on chorus leading. I used only data from the first night of recording for each quartet in these analyses, except in studies of the effect of size and weight on the maximum rate of calls and 'chucks' recorded for each individual. On 14 September, an extra four males were recorded under the above conditions with the exception that the chorus loop was played from 2130 to 2245 hours, covering the second recording period instead of the first. These males were simply used to study the effect of changing the timing of playback on the rate, cost and complexity of calling, and were not used in a feeding experiment.

I estimated the net energy cost of calling for frogs in terms of oxygen consumption (VO_2 net (ml/h); VO_2 calling minus VO_2 night-time resting) were obtained using the following equation from Bucher et al. (1982)

$$\log_{10}(VO_2 \text{ net}) = -2.27 + 0.71 \log_{10}(\text{call rate})$$

According to this equation obtained from measurements from nine males, the oxygen expended per call decreases with increasing call rate, although this effect was not significant because the slope is not significantly different from one. The males had a mean call rate of 12.9 ± 8.2 calls per min (\pm SD, range 1.3–22.6 calls per min), very similar to the call rates of males in the present study without playback. Variation in call rate explained 91% of the variance in oxygen consumption between males.

Effects of Chorus Size

To study the influence of chorus size on male calling, I used the tape loop described above of a

very large chorus. This was played at the side of a concrete pool behind Animal House through a 'Realistic' SCP-17 Stereo Cassette Recorder, and its effect on the number of males present in the chorus was observed. Three different sampling procedures were used, and the probabilities from the statistical tests were combined using Fisher's method of combining probabilities (Sokal & Rohlf 1981). From 2 to 8 August the number of males present in the pool chorus was censused twice for 3 min beginning at 1930 and 2015 hours on each of 6 nights. I counted all males seen in the pool, whether I heard them calling or not. On 3 of these nights, selected at random, the loop was played continuously at the pool side between censuses. From 14 to 24 August, on 5 nights, I censused the pool chorus at 1910 hours and then every 15 min until 2010 hours. During alternate census intervals the loop was played continuously. The sequence was alternated between nights, so that for example on night 1 the sequence was on, off, on, off, while on night 2 it was off, on, off, on. From 27 to 5 September, on 4 nights, I censused the pool chorus three times at 1910, 1940 and 2010 hours, and the loop was played continuously during one of the census intervals. This was the first interval on nights 1 and 3, but the second on nights 2 and 4.

Pool Chorus Comparisons

To assess whether or not the fluctuations between nights in the number of males present in different pools are related due to some common environmental determinant, I censused three cement pools within 100 m of each other (adjacent to Kodak House, Animal House and the Laboratory) on 18 of 19 consecutive nights from 1 to 19 September at intervals between 1900 and 2100 hours, the peak period of chorus activity. The maximum number of males observed was used as an estimate of the number of males present on that night. The choruses at the three pools were acoustically isolated from each other to the human ear. Similar censuses on 30 out of 35 nights from 16 August to 19 September were compared with meteorological data collected over the same period by the Environmental Sciences Program on Barro Colorado Island.

Statistical Methods

The data were analysed with GLIM (Generalised Linear Interactive Modelling System) and Minitab

statistical packages. To test statistically for a difference in behaviour between males that were fed and males that were starved, in each analysis below I reduced all the data for each quartet to a pair of data points, one being a mean for fed males and the other a mean for starved males, and then conducted Wilcoxon matched-pairs signed-ranks tests on the list of paired points for all quartets. This is necessary because the observations on behaviour of different males within each quartet are not independent. For example, the calling behaviour of four frogs in their buckets is interrelated because males interact vocally with their neighbours. When conducting analyses on each list of paired numbers, I give $\bar{X} \pm SD$ for the differences between each pair, calculated by subtracting the data point for starved males from that for fed males, as well as the 95% confidence limits for the mean where this is of interest. Similarly, when testing for a difference in calling behaviour with and without exposure to a background tape loop, I reduced all the data for each quartet to a pair of data points, one for playback and one without playback.

In multiple regression analyses of call parameters, the data were corrected for differences between nights by fitting a factor with 17 levels in GLIM, because the conditions of recording are different for each quartet (e.g. size of Kodak pool chorus, temperature, light intensity).

RESULTS

Chorus Attendance

Observation of marked males in the population showed that individuals did not attend the chorus in a pool consistently every night, and that on other nights the males were not calling elsewhere (Fig. 1). The 10 males recorded over 10 or more nights while marked called at four different pools with all pairwise distances within 100 m, but each individual was faithful to one pool. The marking method used was short lived as the plastic labels became detached, so I could collect data on each individual for only a short period, mostly over less than 10 days.

Feeding Experiments

Of 68 males used in the feeding experiment, six (9%) failed to call after being placed in the buckets on the first night and on subsequent nights of

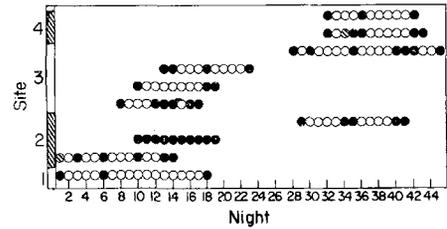


Figure 1. Chorus attendance of 10 marked males recorded over 10 or more nights. Night 1 is 5 August 1987. ●: Presence; ○: absence; ◐: nights when a male was present and is known to have mated. Site 1 is Kodak House, site 2 is Animal House, site 3 is the Laboratory and site 4 is Yellow House.

recording. Of the males that called on the first night 60% also called on the second and third nights of recording. I compared the mean numbers of nights calling by fed and starved males. Starved males were not more likely to stop calling than fed males for the quartets recorded on nights 1, 2 and 3 (one-tailed Wilcoxon matched-pairs signed-ranks test $N=4$ quartets, $T=5$, ns. Difference ($\bar{X} \pm SD$) between matched pairs of means = 0 ± 0.913 , 95% confidence limits for $\bar{X} = -1.452$ to 1.452). Similarly, starved males were not more likely to stop calling than fed males for the quartets recorded on nights 1, 3 and 5 (Wilcoxon test $N=12$, N for test = 9, $T=22$, ns. Difference between matched pairs = 0.028 ± 0.858 , 95% confidence limits for $\bar{X} = -0.158$ to 0.573).

For males that continued to call throughout the experiment, I compared the changes over time in call rate and call complexity (number of 'chucks' per call) between fed and starved males. For the 5-day quartets, I conducted separate analyses for changes between the first and third nights, and changes between the first and fifth nights. For an analysis of the change in call rate between a pair of nights, I considered only those males that called on both nights. I calculated the mean rate for each quartet and for each night, and then I calculated the change in the ratio of individual rate to mean rate between nights for each male, i.e.

$$\frac{\text{individual rate on night } n}{\text{mean rate on night } n} - \frac{\text{individual rate on night 1}}{\text{mean rate on night 1}}$$

This parameter is positive for males that called relatively more as time went on, and negative for males that called relatively less. I calculated the mean value of this parameter for fed and starved males

Table I. Comparisons between fed and starved males in the changes in call rate and complexity over 3 or 5 nights for quartets with and without exposure to a background tape loop

Nights	N	Call rate			Call complexity		
		CRP	T	P	CRP	T	P
1-3 no loop	3	+0.68 ± 0.34	0	NS	+0.22 ± 0.54	1	NS
1-3 loop on	10	-0.21 ± 0.41	41	NS	-0.11 ± 0.30	38	NS
1-5 loop on	7	-0.17 ± 0.66	17	NS	+0.22 ± 0.49	8	NS
1-3 loop off	8	-0.05 ± 0.42	21	NS	-0.05 ± 0.35	19	NS
1-5 loop off	5	-0.11 ± 0.49	0	NS	-0.12 ± 0.40	9	NS

Analyses are with a one-tailed Wilcoxon test, testing the hypothesis that fed males had a higher rate of complexity (number of 'chucks' per call) than starved males. Tests were conducted over 3 nights for quartets never exposed to a background tape loop, and over 3 or 5 nights for quartets that were sometimes exposed to the loop. *N* = number of male quartets for the test. CRP gives $\bar{X} \pm SD$ for the Change in Ratio Parameter, the difference between the matched pairs in the test. The CRP measures the increase over time in the proportion of calls or chucks conducted by fed males at the expense of starved males, and is positive when fed males call/chuck relatively more and negative when fed males call/chuck less. *T* = Wilcoxon statistic.

in each quartet, and then conducted a one-tailed Wilcoxon matched-pairs signed-ranks test between fed and starved means to test the hypothesis that fed males called at a relatively faster rate as time went on. From here on, the difference between matched pairs in the test (i.e. the mean value of the above parameter for fed males minus the mean value for starved males, calculated for each quartet) is called the Change in Ratio Parameter (CRP). The CRP is positive if fed males called relatively more as time went on, negative if fed males called less and zero if there was no difference. If fed and starved males called at the same rate at the start of an experiment, and fed males did almost all the calling at the end, the CRP would converge towards a maximum of +2. Likewise, if starved males did almost all the calling at the end of the experiment, the CRP would converge towards a minimum of -2.

For those quartets recorded with and without playback of the background tape loop, I conducted separate analyses for these two conditions because a marginal influence of food intake may be detectable only under the higher energy costs of calling induced by playback. These analyses consider the mean call rate over the whole 45 min of a recording period, and I repeated them using the mean call complexity and using the maximum rate recorded over any 5-min period during playback, when calling may have reached a maximum rate. Fed and starved males did not differ in mean rates of calling,

mean complexity (Table I) or maximum rate (one-tailed Wilcoxon test: nights 1-3, *N* = 10 quartets, CRP $\bar{X} \pm SD = -0.093 \pm 0.201$, *T* = 41, NS; nights 1-5, *N* = 6, CRP = -0.190 ± 0.466 , *T* = 14, NS). Similarly, fed males were not more likely to lead chorus bouts (Table II).

Following the recording experiments, I marked and released males four at a time. Seventy per cent of males returned to a natural chorus at a later date, after a median delay of 3 days (range 0-20 days). Males fed before release were not more likely to return than starved males. I calculated the fraction of fed and starved males that returned for each quartet and then conducted a one-tailed Wilcoxon test (*N* = 13 quartets, difference ($\bar{X} \pm SD$) between matched pairs = -0.077 ± 0.479 , 95% confidence limits for $\bar{X} = -0.367$ to 0.213, *N* for test = 9, *T* = 26, NS). Males fed before release did not return faster than starved males. I calculated the mean number of days taken by fed and starved males to return for each quartet, and then conducted a one-tailed Wilcoxon test (*N* = 7 quartets, difference between matched pairs = 1.286 ± 2.360 days, 95% confidence limits for $\bar{X} = -0.897$ to 3.469 days, *N* for test = 4, *T* = 9, NS). Starved males returned more often and returned faster, but not significantly so.

Effects of Intrasexual Competition

Playback of the tape loop of a large chorus clearly stimulated males to call at a faster rate and

Table II. Comparisons between fed and starved males in the changes in the amount of chorus leading over 3 or 5 nights for quartets with and without exposure to a background tape loop

Nights	<i>N</i>	<i>N_i</i>	CRP	<i>T</i>	<i>P</i>
1-3 no loop	2	2	+3.90 ± 0.15	0	NS
1-3 loop off	8	6	+0.76 ± 1.87	6	NS
1-5 loop off	5	4	+0.22 ± 1.59	4	NS

Analyses are with a one-tailed Wilcoxon test, testing the hypothesis that fed males led more chorus bouts than starved males. Tests were conducted over 3 nights for quartets never exposed to a background tape loop, and over 3 or 5 nights for quartets that were at other times exposed to the loop. Chorus leading did not occur during loop playback. *N* = number of male quartets for comparison. *N_i* = *N* for Wilcoxon test, i.e. number of quartets in which there is a difference between matched pairs. CRP gives $\bar{X} \pm \text{SD}$ for the Change in Ratio Parameter, the difference between matched pairs in the test. The CRP measures the increase over time in the proportion of chorus bouts led by fed males at the expense of starved males, and is positive when fed males lead relatively more bouts and negative when fed males lead less. *T* = Wilcoxon statistic. The CRP is exceptionally high in the first test, because the starved males led almost all the bouts at the beginning of the experiment and hardly any at the end.

higher net energy. The mean rate with playback was 24.1 ± 7.3 calls per min ($\pm \text{SD}$, *N* = 57 males), compared with 12.3 ± 6.6 calls per min (*N* = 45) without playback. This is equivalent to an energy cost of 0.93 ± 0.22 ml O_2/h with playback, and 0.56 ± 0.23 ml O_2/h without. Males increased call complexity in response to playback, raising it from 1.00 ± 0.46 chucks per call to 1.39 ± 0.46 chucks.

Of 44 males that called during both the first recording period with playback, and the second period without, 42 males called at a faster rate during playback and 43 males gave more complex calls. Playback increased the mean rate for these 44 males by 104% and the mean complexity by 38%. Using a conversion factor of 20.1 J/ml O_2 (Ryan et al. 1983), the mean net cost of calling was increased by 70% from 11.4 J/h to 19.4 J/h and the total energy expenditure was increased by 36% from 22.1 J/h to 30.0 J/h (males at night-time rest consumed 0.53 ml O_2/h , Bucher et al. 1982). Comparing the mean values for each quartet with and without playback, playback significantly increased the call rate (two-tailed one-sample *t*-test, $t = 9.59$, $df = 14$, $P < 0.0001$), energy cost ($t = 8.71$, $P < 0.0001$) and

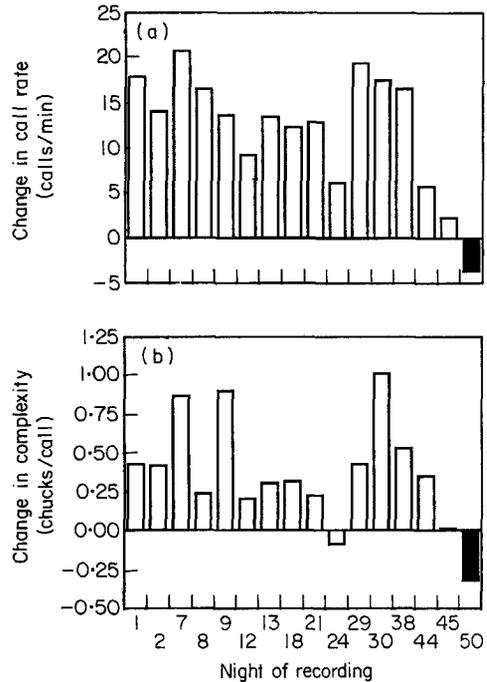


Figure 2. The change in (a) call rate and (b) complexity (means for each male quartet) between recording periods (2045-2130 and 2200-2245 hours) as a function of the night of recording and the timing of playback of a tape loop of a large chorus. The figure shown is the call parameter for the first recording period minus the parameter for the second period. □: Quartets with playback during the first period; ■: the quartet with playback during the second period. Night 1 is 26 July 1987.

call complexity ($t = 5.06$, $P < 0.0001$). Although playback was conducted during the first recording period, the differences in calling between the two periods were not due to changes in calling over time, as was shown by conducting playback during the second recording period on 14 September. Once again the mean call rate and complexity for the quartet were increased during playback. As expected, the timing of playback had a significant effect on the change in call rate from the first to the second recording period (two-tailed two-sample *t*-test, $t = 3.08$, $df = 14$, $P < 0.01$, Fig. 2a), the change in energy cost ($t = 2.76$, $P < 0.02$) and the change in complexity ($t = 2.26$, $P < 0.05$, Fig. 2b).

Playback of the tape loop raised mean call rate and energy cost in two ways. During playback, males called continuously and at a fast rate, while alternating with their near neighbours so as not to call simultaneously. Without playback, males

Table III. Multiple regression of calling parameters

Dependent variables†	<i>S</i>	<i>W</i>	<i>S + W</i>	<i>NR</i>	<i>r</i> ²	<i>F</i>	<i>df</i>
Mean call rate	+1.16	-0.64	(+)1.38	2.44*	0.572	2.26*	16, 27
Maximum call rate	-0.52	+1.83	(+)4.48*	1.68	0.454	1.85	18, 40
Mean complexity	-0.94	+0.94	(-)0.46	1.93	0.538	1.97	16, 27
Maximum chuck rate	+0.12	+0.81	(+)1.92	1.75	0.466	1.94*	18, 40

†The mean call rate for periods with and without playback of a tape loop; the maximum rate of calling over any 5-min period; the mean number of chucks per call (call complexity) with and without playback; and the maximum rate of chucking over any 5-min period. Predictor variables are: male size and male weight (continuous variables), and night of recording (factor). *t*-values are given for the partial effects of size (*S*) and weight (*W*) with + and - denoting the sign of the regression slope. *F*-values are given for the effects of the night of recording (*NR*), and on two degrees of freedom for the effect of size and weight added together in one step (*S + W*). (+) and (-) denote the direction of this combined effect. *r*², *F* and *df* refer to the whole regression.

**P* < 0.05.

chorused together in bouts with silent periods of up to several minutes separating bouts. Furthermore, during these bouts males called at a lower rate than during loop playback, while still alternating with near neighbours. The absence of separate bouts explained most of the increase in call rate and energy expenditure during playback, but males called $21 \pm 36\%$ ($\bar{X} \pm \text{SD}$) faster during playback than they did during bouts without playback. This was calculated from a sample of 17 males in six quartets, and the increase was significant ($t = 3.48$, $df = 5$, $P < 0.02$). Similarly, some of the increase in mean complexity during playback was due to the fact that, without playback, males usually called without chucks as they started a new bout. However, the maximum number of chucks in any one call observed for each male was significantly higher during playback than without, showing that males used more chucks during playback than at any time without. I calculated the mean maximum number of chucks during playback, and the mean maximum without playback for each quartet, and then conducted a two-tailed Wilcoxon test ($N = 16$ quartets, difference ($\bar{X} \pm \text{SD}$) between matched pairs = 0.33 ± 0.50 chucks, N for test = 12, $T = 10.5$, $P < 0.03$).

Effects of Size and Weight

A male's chance of attracting a mate might be influenced by a number of call parameters (mean and maximum rates of calling, mean complexity of calls, maximum rate of chucking and whether he leads in chorus bouts). These were analysed in turn for an effect of size and weight, using multiple

regression analyses. Size and weight were highly correlated ($r = 0.85$, $N = 58$, $P < 0.0001$), so their partial effects and their combined effect on two degrees of freedom were used in the analyses.

Call rate

Since call rates with and without playback were highly correlated (controlling for differences between recording nights, $r = 0.58$, $N = 44$, $P < 0.001$), a mean rate was calculated for each male that called under both conditions (squared to remove heterogeneity of variance). Neither the combined effect of size and weight nor their partial effects were significant predictors of mean call rate (Table III). The influence of size and weight on the maximum rate of calling was considered by using the maximum rate observed for each male over any 5-min sample ($\bar{X} \pm \text{SD} = 29.0 \pm 3.7$ calls per min, $N = 59$) as the dependent variable in a multiple regression (squared to remove heterogeneity of variance). Three outlying males that never exceeded 12 calls per min were excluded, because they were not considered to have approached a maximum rate. The partial effects of weight and size were not significant, but the combination of size and weight had a significant positive effect, i.e. larger, heavier males had faster maximum call rates ($P < 0.02$, Table III). Weight was more highly correlated with maximum rate ($t = 2.98$, $N = 59$, $P < 0.005$, Fig. 3a) than was size ($t = 2.30$, $P < 0.03$, Fig. 3b).

Call complexity

Since the number of chucks per call with and without playback were highly correlated ($r = 0.71$,

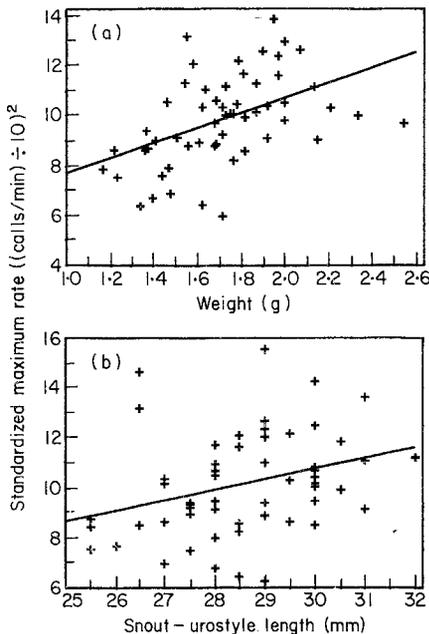


Figure 3. Maximum call rates of males versus weight and snout-urostyle length. The rates are standardized for variation between nights by subtracting the estimates in the multiple regression equation for the effects of each night from the actual rates measured. This corrects for differences between nights in the distribution of call rates and the weight or size of males. (a) $Y = 4.660 + 2.975 X$, $R = 0.42$; (b) $Y = -3.771 + 0.476 X$, $R = 0.34$. The R values are calculated from the original multiple regression rather than the scattergram.

$N = 44$, $P < 0.0001$), a mean complexity score was calculated for each male that called under both conditions. The maximum rate of chucking observed for each male over any 5-min sample ($\bar{X} \pm \text{SD} = 45.2 \pm 12.3$ chucks per min, $N = 59$) was also calculated. Neither of these two functions of call complexity was significantly influenced by size and weight, either for the partial or the combined effects (Table III).

Bout leading

The number of chorus bouts led by each male in the absence of playback is not suitable for parametric analysis because one or two males frequently led all the bouts. Hence I did a non-parametric analysis, first doing a Spearman rank correlation, for each quartet, between size or weight and the number of bouts led. Then the correlation coefficients from each of the quartets were analysed with a two-tailed Wilcoxon one-sample signed-

Table IV. Relationships between amount of chorus leading by males and size, weight, call rate and call complexity

	N	N_i	r_s	T	P
Male size	18	14	-0.01 ± 0.69	52	NS
Male weight	18	17	$+0.06 \pm 0.75$	68.5	NS
Call rate	18	16	$+0.51 \pm 0.64$	25	0.03*
Call complexity	18	16	-0.24 ± 0.71	40	NS

Separate correlation coefficients for each quartet with the number of chorus bouts led are collectively tested for a significant difference from zero, using a two-tailed Wilcoxon one-sample signed-ranks test. N = number of male quartets for comparison. N_i = N for Wilcoxon test, i.e. number of quartets in which the $r_s \neq 0$. $r_s = \bar{X} \pm \text{SD}$ of Spearman rank correlation coefficients. T = Wilcoxon statistic. The coefficients are calculated from two to four males, because in some quartets one or two males did not call at all and were excluded from the correlation.

*After weighting the coefficients according to their reliability by multiplying them by the number of males calling $T = 13$, $P < 0.005$.

rank test for a significant deviation from zero. This method of analysis is appropriate because it reduces data for one quartet to one number, since multiple observations from each quartet are not independent. There was no evidence for a significant relationship between size or weight and chorus leading. Chorus leaders called at a significantly faster rate than the other males, but their calls were not significantly less complex (Table IV).

Interactions between Competition and Size/Weight

For males that called both with and without playback, the interaction between size/weight and competition was first considered by calculating for each male the ratio between his call rate during playback and his mean call rate during both conditions, and making this the dependent variable in a multiple regression. This value is higher for males in the quartet that called relatively more during playback, and lower for males that called relatively more without playback. The effects of size and weight were non-significant, whether partialled or combined (Table V). The ratio for each male between his call complexity during playback and his mean complexity during both conditions was then used as a dependent variable in a second regression, this value being higher for males that added relatively more chucks during playback. To overcome heterogeneity of variance in the model, the ratio was changed to (complexity during playback) \div (mean complexity + 1). The partial effects

Table V. Multiple regression of ratios of calling parameters with and without playback of a tape of a large chorus

Dependent variables†	<i>S</i>	<i>W</i>	<i>S+W</i>	<i>NR</i>	<i>r</i> ²	<i>F</i>	<i>df</i>
Call rate ratio	-0.58	+0.48	(-)0.18	2.65*	0.581	2.34*	16, 27
Complexity ratio	-1.10	+1.97	(+)3.86*	3.72*	0.731	4.58**	16, 27

†Call rate ratio (rate during playback ÷ mean rate with and without playback) and call complexity ratio (complexity during playback ÷ (mean complexity + 1)). Predictor variables are: male size and male weight (continuous variables), and night of recording (factor). *t*-values are given for the partial effects of size (*S*) and weight (*W*) with + and - denoting the sign of the regression slope. *F*-values are given for the effects of the night of recording (*NR*), and on two degrees of freedom for the effect of size and weight added together in one step (*S+W*). (+) and (-) denote the direction of this combined effect. *r*², *F* and *df* refer to the whole regression.

P* < 0.05; *P* < 0.001.

of size and weight were not significant, but size and weight combined had a significant positive effect on the ratio (*P* < 0.04, Table V). Larger, heavier males added relatively more chucks during intense competition (playback) while smaller, lighter males added relatively more chucks during weak competition (no playback). Weight (*t* = 2.54, *N* = 44, *P* < 0.02, Fig. 4a) explained more of the variance than size (*t* = 1.86, NS, Fig. 4b). This result is not caused by larger, heavier males giving less complex calls as time went on, relative to smaller, lighter males as the change in complexity over time from the first to the last 5-min sample during playback was not related within quartets to size (*r* = 0.11, *N* = 42, NS) or weight (*r* = 0.06, NS).

Chorus Size Experiments

The effect of playback of a tape loop, which simulates a large, dense chorus, on the number of males in a natural chorus was compared with control periods without playback. When the different sampling protocols are considered separately, the results are variable. When the change in the size of a chorus over 45 min was compared for 3 nights with playback and 3 control nights without, the increase in chorus size during playback was not significantly greater than during a control (Fig. 5). However, the chorus size increased following playback on all 3 nights, but decreased following a control on 2 out of 3 nights. When the change in the chorus size over 15-min periods was compared for two periods with playback and two control periods without, within each of 5 nights, the mean increase during playback was significantly greater than during a control

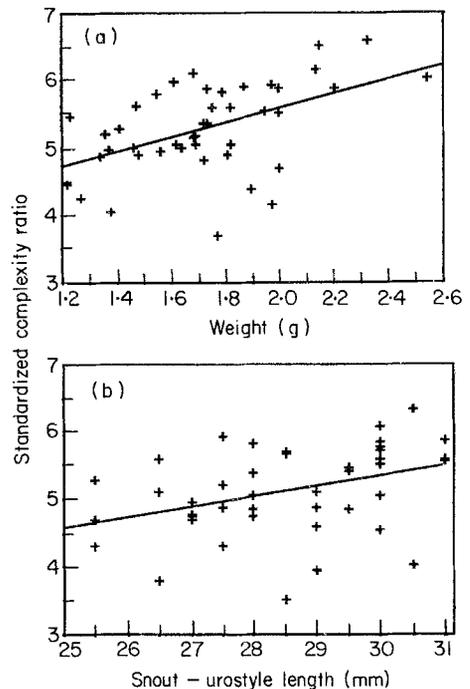


Figure 4. The relationship between weight and snout-urostyle length of males and the effects of playback of a tape loop of a large, dense chorus on the complexity of calling. The *Y* variable is a call complexity ratio ((10 × complexity during playback) ÷ (mean complexity with and without playback + 1)), standardized for variation between nights by subtracting the estimates in the multiple regression equation for the effects of each night from the actual ratio measured. This corrects for differences between nights in the distribution of ratios and the weight or size of males. (a) $Y = 3.431 + 1.073 X$, $R = 0.43$; (b) $Y = 0.678 + 0.155 X$, $R = 0.33$. The *R* values are calculated from the original multiple regression rather than the scattergram.

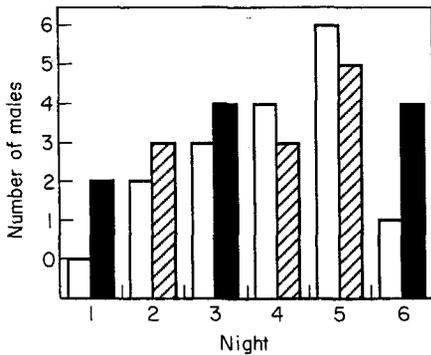


Figure 5. Chorus size results with censuses at 1930 and 2015 hours and playback of a tape loop between censuses on randomly selected nights. □: Initial census; ■: census after playback; ▨: census after a control without playback. (One-tailed Mann-Whitney *U*-test for the difference between the playback and control: $N=6$ nights, $U=0.5$, ns.)

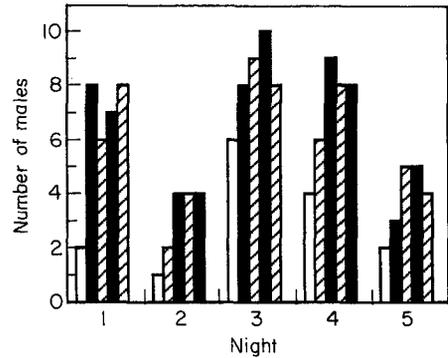


Figure 6. Chorus size results with censuses at 15-min intervals between 1910 and 2010 hours, and playback of a tape loop between alternate censuses. □: Initial census; ■: census after playback; ▨: census after a control without playback. (One-tailed Wilcoxon matched-pairs signed-ranks test for the difference in chorus size between the playback and control: $N=5$ nights, N for test=4, $T=10$, $P=0.05$.)

(Fig. 6). When the change in chorus size over 30-min periods was compared for one period with playback and one control period without, within each of 4 nights, the increase during playback was not significantly greater than during a control (one-tailed Wilcoxon matched-pairs signed-ranks test $N=4$ nights, N for test=3, $T=3$, ns). On 2 of the 4 nights chorus size increased more during playback than during the control, and on one night there was a greater increase during the control.

The combined probability for these three protocols shows that chorus size is increased by the playback of a tape loop of a large, dense chorus (Fisher's method of combining probabilities $\chi^2=12.9$, $df=6$, $P<0.05$). Although males called more during playback, this result is not caused by playback making the males in the pool more conspicuous during a census, because these pools were bare of vegetation so that all males were easily spotted with a torch light. Furthermore, more males were seen on land around the pool edge after the control periods. Some of these males were subsequently seen joining the chorus during playback. Males appeared to respond rapidly to changes in perceived chorus size, and were not drawn from other pools by the tape loop, which was played at a lower volume than the natural call of a single male.

These results are supported by the effects of playback when used in the feeding experiments. Thirteen males from nine quartets called during the first recording period with playback yet did not call at all during the second period without playback.

This is significantly more than the two males from two quartets that called only in the second period (one-tailed binomial test for quartets $P<0.05$), suggesting that some males will join a large chorus, but not a small one. Although playback was always conducted during the first recording period, this result is not due to a decrease in calling over time since most of the 13 males called more as time went on during the first period. Furthermore, in those quartets in which playback was not used, an effect of time would cause some males to call only during the first period. On the contrary, no males called only during the first period ($\chi^2=3.59$, $df=1$, ns), suggesting that the time difference between these periods had no effect on a male's decision to chorus or not.

Whether a male will join a small chorus or only a large one does not seem to depend on his size or weight. These 13 males that chorused only under intensified competition during playback were not significantly larger (two-tailed one-sample *t*-test, $t=0.496$, $df=8$, ns) or heavier ($t=-0.162$, ns) than males in the same quartet that called under both conditions.

Pool Chorus Comparisons

The fluctuations in chorus size in three pools over 19 days are shown in Fig. 7. If these fluctuations were in synchrony due to some common environmental determinant, there would be a statistically significant difference between days in an analysis of

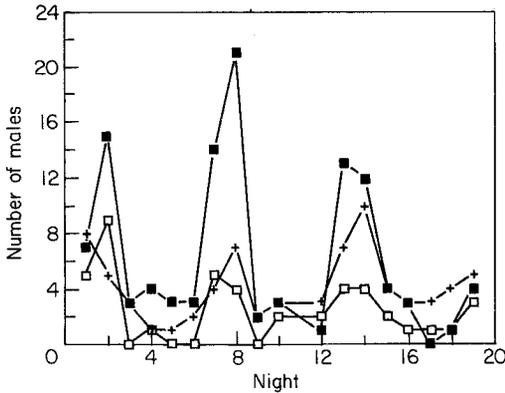


Figure 7. Chorus size in three pools over 19 nights. Night 1 is 1 September 1987. □: Chorus size at Kodak House; ■: at Animal House; +: at Laboratory.

variance including 'pools' as a factor of three levels. This was the case when I used the GLIM package with chorus size as the dependent variable, a log 'link' (a function in GLIM similar to a log transformation of the dependent variable) and a Poisson error distribution ($F_{17,34} = 6.44$, $P < 0.0001$). The data were independent between days so there is no serial dependency in chorus size (combined regression controlling for differences between pools, $r = 0.202$, $N = 48$, NS).

I compared the total number of males observed in the three pools on 30 out of 35 nights with meteorological data over this period. There was no relationship with relative humidity, maximum air temperature, dry bulb temperature or wet bulb temperature. However, there were significant relationships between the total number of frogs and both the minimum daily air temperature (range 22.2–26.1°C, $\bar{X} \pm \text{SD} = 24.4 \pm 1.1^\circ\text{C}$) and the daily rainfall (range 0–162.1 mm, median = 4.1 mm). Regressions were conducted with number of males as the dependent variable and using a log transformation and a Poisson error. There was no significant correlation between the number of frogs and the minimum temperature that day ($r = 0.057$, $N = 21$, NS), but there were significant correlations with the minimum temperature on the previous day ($r = 0.517$, $N = 22$, $P < 0.02$) and on the day before that ($r = 0.578$, $N = 22$, $P < 0.005$, Fig. 8a). There was no correlation with the temperature 3 or more days before. In a multiple regression, while controlling for the temperature on the previous 2 days, there remained no effect of the temperature that day on the number of frogs ($r = 0.028$, $N = 13$, NS).

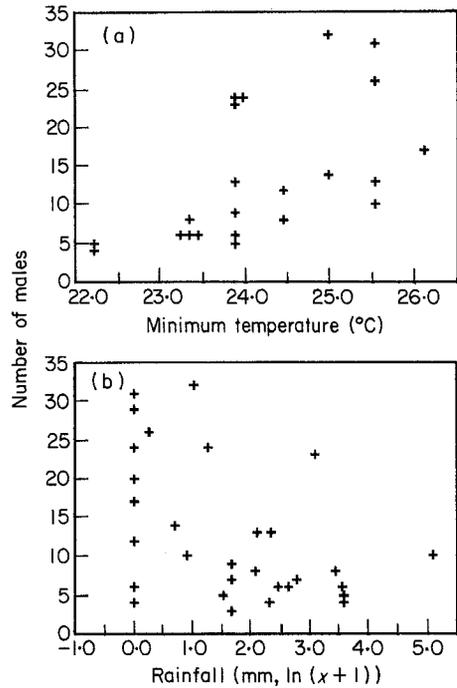


Figure 8. The relationship between (a) minimum temperature 2 days before and (b) rainfall 2 days before ($\log_e(x+1)$) and the total number of males observed in choruses at three pools between 16 August and 19 September 1987.

In regressions with the log of rainfall as the predictor variable, there was no significant correlation between the number of frogs and the rainfall that day ($r = 0.328$, $N = 30$, NS), but there were significant correlations with the rainfall on the previous day ($r = -0.368$, $P < 0.05$) and on the day before that ($r = -0.504$, $P < 0.005$, Fig. 8b). There was no correlation with the rainfall 3 or more days before. In a multiple regression, while controlling for the rainfall on the previous 2 days, there remained no effect of the rainfall that day on the number of frogs ($r = 0.327$, NS).

Rainfall and minimum temperature were highly correlated with each other ($r = -0.451$, $N = 32$, $P < 0.01$) and there is no evidence that they had separate effects on the number of frogs present. In a multiple regression, with the number of frogs as the dependent variable and controlling for minimum temperature 2 days ago, there was no longer an effect of rainfall 2 days ago ($r = -0.279$, $N = 22$, NS). Likewise, while controlling for rainfall 2 days ago, there was no longer an effect of temperature 2

days ago ($r=0.408$, $N=22$, NS). The minimum temperature and rainfall over the previous 2 days together explained 51% of the variance in the number of males present ($F_{4,13}=3.41$, $P<0.05$). There is potential for frogs to use present temperature to predict future temperature, as there was a strong correlation between minimum temperature on day n and on day $n+1$ ($r=0.571$, $N=25$, $P<0.005$). However there is no significant correlation between rainfall on day n and on day $n+1$ ($r=0.141$, $N=41$, NS).

DISCUSSION

Chorus Attendance

Ryan (1985a) said of the tungara frog 'That males are present at the breeding site for only a small proportion of the nights they are known to be alive and that males probably do not feed while they are at the breeding site suggest that males cease reproductive behaviours in order to replenish energy supplies'. Observations during the present study verify Ryan's assumption that males absent from the chorus in one pool are not calling at other pools. It is also clear that males absent from the chorus are not recovering from energy or sperm depletion due to mating, since the frequency of withdrawal from the chorus greatly exceeds the frequency of mating, which was one mate for every 5 nights of attendance at Kodak pool in 1979 (Ryan 1985a). Also, mating success is not consistently followed by chorus absence (Fig. 1). For the green treefrog, another prolonged breeding species in which chorus attendance is the best known predictor of individual mating success, Gerhardt et al. (1987) found that mating success has no effect on a male's attendance or calling behaviour on the following night.

It is possible that there is a trade-off between time spent calling and foraging intake for tungara frogs (as for the leptodactylid *Eleutherodactylus coqui*, Woolbright & Stewart 1987), although tungara frogs do at least some of their foraging during the day when calling does not occur (Jaeger & Hailman 1981). Even with such a trade-off, it remains uncertain that a need for short-term foraging intake acts as a constraint on calling activity during the breeding season, whether directly because of the energy cost of calling, or indirectly because of the need to

spend time foraging in order to fuel basic metabolism. I have tested the foraging constraint hypothesis in two ways. First, in a comparison of fed and starved males over 3–5 days, I tested for an effect of food intake on calling behaviour, but failed to find any evidence for a number of calling parameters likely to affect a male's ability to attract a mate. These results offer evidence against the foraging constraint hypothesis because the periods of absence from the breeding site that we are trying to explain are typically similar to the duration of the experiments (Fig. 1). Furthermore, digestion of the food was fairly rapid while analysis of faeces from freshly caught males showed that the species of termites used during the experiments are a major natural component of the frog's diet. In designing these experiments in which males were confined in buckets while recorded, I assumed that starved males that would prefer to forage than to chorus would not call or would call less, even though they were not given the opportunity to forage in the buckets. I consider this a fair assumption, since some males refused to call, left the water and climbed up the sides of the buckets. Furthermore, if starved males resorted to calling only because they could not forage, their energy reserves would be low and their call rates should be limited, which was not the case. However, I overcame this assumption by testing the foraging constraint hypothesis in a second way by simultaneously releasing males that had been fed and starved over 3–5 days. The foraging hypothesis would predict that males that had been starved would spend time foraging instead of chorusing, so that fed males would reappear in natural choruses more rapidly than starved males. This was not the case.

The calling of the tungara frog, therefore, seems not to be constrained by short-term energy reserves, and may be fuelled by medium- or long-term reserves made weeks or months in advance. Intrasexual selection may have adapted males to build up energy reserves in advance, to permit prolonged sexual activity whenever a suitable habitat arises without the need to resort to foraging. While breeding sites in the present study are permanent bodies of water in the wet season, this species usually breeds in temporary pools, the unpredictability of which in time would make reliance on day to day foraging intake inappropriate. If pools only lasted for several nights and males had to spend some of the time foraging, they would reduce their chances of mating. Clearly males can call without feeding

for 5 nights or more, although it is possible that mature males that survive to chorus over a period of several weeks or months do become limited by energetic constraints and withdraw from chorusing for many days or weeks in order to build up energy reserves. If I had continued my feeding experiments for 10 or 20 days, I might have found an effect of foraging intake on chorusing activity, but the frequent disappearance of males from the chorus (Fig. 1) cannot be explained by an energetic constraint.

That males are apparently unconstrained by energetics may explain the absence of non-calling satellites in this species. Satellite behaviour of green treefrogs is common but less successful than calling behaviour, and Gerhardt et al. (1987) suggested that males adopt this alternative strategy when they have depleted their energy reserves. There is no evidence for this, but calling has a higher energy cost in other species of *Hyla* than in the tungara frog (Wells & Taigen 1986). Similarly, energetic constraints may explain the dynamic interchange between territorial calling males and non-territorial satellites in *Uperoleia rugosa* (Robertson 1986). A male loses weight while calling and gains weight while a satellite until heavy enough to oust a caller from his territory.

If energetic constraints are not in action in male tungara frogs, why should individuals ever choose not to attend a chorus and turn down the chance of attracting a mate? Calling greatly increases the conspicuousness of a male to predators, and this predation risk limits the number of nights calling that a male can expect to survive. In 1979 each male was present at Kodak pool for only 7.2 ± 7.1 nights ($\bar{X} \pm \text{SD}$). Calling frogs on Barro Colorado Island are often predated by the freshwater crab *Potamocarcinus richmondi*, the four-eyed opossum, *Philander opossum*, the marine toad, *Bufo marinus*, the South American bullfrog, *Leptodactylus pentadactylus*, the pond turtle, *Pseudemys scripta*, the cat-eyed snake, *Leptodeira annulata*, and the fringe-lipped bat, *Trachops cirrhosus* (Ryan et al. 1981b; Ryan 1985a). The opossum and the bat are known to locate the frogs by using the advertisement call (Ryan et al. 1981a; Tuttle & Ryan 1981). One reason why male tungara frogs may space out their chorus attendance is that if every male began to chorus at the same time at the beginning of the breeding season, and then turned up every night until he was eaten, there would be very few males left by the end of the season. The likely evolutionarily stable strategy (Maynard Smith 1972) is for a

mixed strategy with individual males spacing out their chorus attendance over different periods of the season. A similar problem lies with male post-metamorphic emergence in insects. Males are selected to emerge, on average, before females (protandry), but to space out their emergence over the breeding season (Bulmer 1983; Iwasa et al. 1983). Another likely reason why male tungara frogs space out their chorus attendance is that they may be selected to attend the chorus only on those nights when the risk of predation is relatively low or the chances of attracting a mate relatively high. Thus they might selectively join large choruses, since Ryan et al. (1981b) have shown that the predation risk from a combination of bats, opossums and bullfrogs is significantly lower for an individual as the chorus size increases, and that the proportion of females to males (the operational sex ratio) increases with chorus size.

Data from experiments in the present study, involving the playback of a recording of a large chorus, show that on any night some males will join only a large chorus. It remains unclear whether the cue for a large chorus used by these males was the playback tape, or the calling characteristics of those males present in the natural chorus, which called at a much higher rate, complexity and constancy during playback. The former is the simpler explanation over a short distance, since the males already in the chorus were clearly themselves using the tape as a cue for a larger chorus, although the tape was played at a low volume so that any males assessing chorus size from 20 m or more were probably responding to the natural chorus. Although different males may have different thresholds of the minimum chorus size that they will join on a given night, not all males can be sensitive to chorus size when deciding whether or not to chorus, because at least one male has to begin chorusing on his own.

Males might also be expected to make decisions to join the chorus on the basis of other environmental conditions that may influence predation risk or the number of females arriving to mate. If the fluctuations in chorus size in one pool are determined by environmental variables such as rainfall or temperature, the fluctuations in other pools should be similarly determined and thus synchronized. Data from three pools in this study show that the fluctuations in chorus size are synchronized with a common determinant (explaining 76% of the variance with each site) that appears to be either the minimum temperature or the rainfall over the previous

2 days. It is not possible to say which of these two variables is the important one to the frogs because they are highly correlated and neither has a significant effect while controlling for the other, although temperature remains close to significance. Many males chorus when it has been dry and warm, and few males chorus when it has been wet and cold. Females breed in pools with a depth and area that varies with rainfall, and so might use rainfall as a cue for breeding, while males will be adapted to follow those cues that increase the operational sex ratio and hence their mating success. By breeding when it has been relatively dry, females may avoid laying their eggs on pools that are a temporary product of heavy rain and that will dry up before the eggs have hatched or before the larvae have metamorphosed. If it is the recent minimum temperature that is the key variable, this may be because of its effect on water temperature in the breeding sites. If it has been warm, conditions for egg laying may be improved because eggs will hatch faster from foam nests laid on warm water. Rainfall and minimum temperature explain only 51% of the variation in the number of males chorusing, and there may be other environmental variables affecting chorus decisions which have not been measured during this study. For example, the light conditions are important to predation risk since males can observe the arrival of predatory bats, and stop calling, on a clear night or with a full moon, but not on a cloudy night with no moon (Tuttle et al. 1982). Fluctuations will also be affected by recruitment of newly mature males to the population and by loss of males from predation.

Thus I suggest that male tungara frogs are conservative in their chorusing activity not because of the need to cease calling in order to replenish energy supplies, but rather because chorusing increases predation risk. Males use variation in rainfall or temperature to select those nights that offer increased mating opportunities or reduced predation risk. Males also prefer to join larger choruses with their reduced costs and increased benefits, so that chorus size on any night is controlled by positive feedback. If relatively few males decide to chorus on the basis of, for example, recent heavy rainfall, the chorus will get smaller because males sensitive to chorus size will leave the chorus. If many males decide to chorus on the basis of, for example, recent dry conditions, the chorus will get bigger because the large chorus will attract more males. Clearly, not all males make the same

decisions about chorus participation, otherwise chorus size would be all or nothing each night. The positive feedback is limited by female behaviour. It is not known whether the operational sex ratio is more female skewed in larger choruses because lots of females arrive to breed under dry and warm conditions, or because females prefer to visit larger choruses. In any case, if chorus size becomes very low, it becomes worth it for the males left to stay in the chorus because there is a good chance that one or two females will arrive. On the other hand, if chorus size gets very large, it is not worth it for new males to join the chorus because the number of females arriving has an upper limit, since only a small fraction of the female population is ready to breed at any one time (Davidson & Hough 1969). Chorusing decisions may also depend on the size of individual males, since larger males have a higher mating success (Ryan 1983a), and because this mating advantage may vary with chorus size. The advantage of larger males may decrease in larger choruses because the operational sex ratio increases and because females may be less discriminating in the presence of the background noise of larger choruses (as for green treefrogs, Gerhardt 1987; Gerhardt & Klump 1988). However, there is no evidence that small or large males prefer larger or smaller choruses, since the males that called only during playback (i.e. in a larger chorus) in my experiments were not of a different size from males that called with and without playback, and since chorus size is not significantly related to the mean size of males in the chorus (M. J. Ryan, personal communication).

Effects of Competition

Males of many anuran species call at faster rates in choruses than in isolation (Emlen 1968; Rosen & Lemon 1974; Passmore 1977; Wells 1977, 1978), although playback experiments have been used to show that the increases in rate are caused by vocal competition in only a few species (Lemon 1971; Ramer et al. 1983; Wells & Schwartz 1984). In some species in which males do not normally call in dense choruses, males show no response to playback of conspecific calls (Greer & Wells 1980). The response of female tungara frogs to calls presented at different rates has not been tested, but preferences for fast rates have been found in many anuran species in laboratory tests (Gerhardt 1987, 1988) and in nature in the only study in which the

call rate of individual males has been related to their mating success (*Bufo woodhousei*, Sullivan 1987). Males have been observed to respond to competitors by adding secondary notes to their calls, thus raising complexity, in various hylids (*Smilisca sila*: Tuttle & Ryan 1982; *H. phlebodes*: Schwartz & Wells 1984; *Hyla ebraccata*, *H. minuta*: Wells & Schwartz 1984; *H. microcephala*: Schwartz & Wells 1985), a rhacophorid (*Philautus leucorhinus*, Arak 1983b) and a ranid (*Rana clamitans*, Ramer et al. 1983).

In the present study, vocal competition increased the rate, energy cost and complexity of advertisement calling in male tungara frogs. By increasing the rate and complexity, males presumably raise their chances of obtaining a mate, either directly because of female preferences for faster, more complex calls, or indirectly because these calls space neighbouring males further away from the caller. Adding chucks may make their calls easier to locate (Ryan 1985a), especially in choruses. Females entering a large chorus are typically confronted with an almost continuous din of background noise that may tend to obscure the calls of individual males (Ehret & Gerhardt 1980; Gerhardt & Klump 1988). Calls containing highly stereotyped, repetitive notes with rapid amplitude transitions, such as a series of chuck-like notes (see sonagrams in Ryan 1983b), are the calls most likely to contrast with continuous background noise undergoing random amplitude fluctuations (Schleidt 1973; Green & Marler 1979; Richards & Wiley 1980).

This is only the second study to measure the effects of competition on the energy costs of displays, the first being made on the grey treefrog (Wells & Taigen 1986), in which 'interacting' (2–4 m apart) males consumed significantly more oxygen than those that were 'isolated' (> 4 m apart). Interacting males had a 16% greater total energy consumption, equivalent to an increase in the net cost of calling of 17%. Males in 'dense choruses' (0–2 m apart) consumed 3% more energy than interacting males, but this increase was not significant. In the present study, I found much larger increases in energy consumption when males in a small interacting chorus of from 3 to 12 males (with rivals 1 m apart) were stimulated by playback of a recording of a large, dense chorus of several hundred males. The total energy consumption was raised by 36%, and the net cost of calling by 70%. The increased vocal competition resulted in sharp increases in both the rate of advertisement calling, and the number of chucks in the calls, but

the increased energy cost calculated is due solely to the increased rate, since Bucher et al. (1982) found no evidence for an energy cost of chucks.

In contrast to the tungara frog, the grey treefrog responded to competition by increasing the duration of calls (i.e. the number of secondary notes) but decreasing the rate, so that males in dense choruses gave calls 1.8 times as long as isolated males, but at 0.6 times the rate. Energy consumption is a function of both call rate and duration (Taigen & Wells 1985) and both short and long calls have the same energy cost per s of calling, but Wells & Taigen (1986) suggested that longer calls at lower rates are more fatiguing, more rapidly depleting glycogen reserves in the muscles used during calling. They found that males producing long calls at slow rates called for significantly fewer hours per night than males in the same chorus producing shorter calls at higher rates. They concluded that calling is under energetic constraints, and males free from competition may give shorter, less attractive calls so as to increase stamina and call for longer, while competing males give more attractive calls at the expense of stamina.

In the tungara frog, the effect of competition on energy expenditure may have little or no importance because there is no evidence for an energetic constraint to calling. Males free from competition may call at much lower rates not to conserve energy, but to reduce the risk of predation. The bat *Trachops cirrhosus* is more attracted to calls broadcast at a faster rate (Tuttle & Ryan 1981) and to complex calls (Ryan et al. 1982), which explains why isolated males use no chucks even when single chucks have an insignificant energy cost and increase the chances of attracting a mate. Males call with a faster rate and with more chucks as vocal competition increases in larger choruses largely because the risk per male from bat and opossum predators, which locate frogs acoustically, decreases. Predation risk apparently restricts sexually selected behaviour in male tungara frogs at two different levels, limiting presence in the chorus activity and reducing the rate and complexity of calling once there. The increased investment in calling in large choruses is also explained by a need to produce calls that stand out against the background noise of rival calls, but the role of competitors in causing this increase is obscure because in larger choruses there is actually less competition for mates due to a higher ratio of females to males. Male grey treefrogs invest relatively more energy

than tungara frogs when calling in isolation. They call at 1.6 times the rate and 83% of the net energy cost of males in dense choruses. This may be because chorus size has little impact on the predation risk of calling in grey treefrogs.

Effects of Size and Weight

Whitney & Krebs (1975) found that chorus leaders in the Pacific treefrog *Hyla regilla* had a higher mating success in the field and the laboratory. Brattstrom & Yarnell (1968) found that in a sub-population of four male tungara frogs the chorus leader had the highest mating success, although this result is not statistically significant. While males leading a chorus or giving more complex calls may attract more mates, differences in chorus leading or in call complexity probably do not contribute to the mating advantage of larger males observed in nature (Ryan 1983a), as I failed to find any significant relationship between these call parameters and the size or weight of males. The only significant relationship was between size or weight and the maximum rate of calling produced by a male. While size did not affect mean call rate, this maximum rate may be important and may contribute to a mating advantage of larger males in large choruses, in which maximum rates may be reached. The data on higher mating success of larger males were collected in the presence of much larger Kodak pool choruses (up to 90 males) than in the present study. Even in small choruses, maximum rates may be reached for short periods and males probably call at maximum rates when females are in view, as for *Hyla ebraccata* (Wells & Greer 1981). Hence the mating advantage of larger males may not be entirely a consequence of the correlation between size and chuck frequency and the female preference for lower chuck frequencies. For *B. woodhousei*, a significant large size mating advantage is entirely a consequence of a positive correlation between size and call rate, the parameter important to female choice (Sullivan 1987). The reason for the relationship between size, weight and maximum call rate for the tungara frog is unknown. Larger males are not necessarily older, as males do not survive more than one season and growth rates within a season are highly variable (Ryan 1985a). They may be in better condition than smaller males, with a higher maximum energy output, because they have larger energy reserves made over previous weeks or months, or because they have a lower parasite load.

Interactions between Competition and Size/Weight

By analysing the ratio of call complexity between conditions of small and large choruses for each male tungara frog, larger, heavier males were found to add relatively more chucks in larger choruses, while smaller, lighter males added relatively more chucks in smaller choruses. It is not likely that this result was produced by males responding differentially to the chuck frequencies on the playback tape that mimicked a large chorus, since Ryan (1985a) found that the response of males to a playback call is not dependent on the frequency of the chuck of that call. There are several possible adaptive explanations for my result. Large males may benefit the most from the reduction in predation risk in larger choruses, and so they may add relatively more chucks to their calls. This would be so if those predators that locate males acoustically share the preference of females for lower chuck frequencies, since a lower frequency indicates a larger prey size. An alternative explanation is that a female prefers both more chucks and chucks of a lower frequency, but that her relative preference for these two changes as chorus size and acoustic conditions change. For example, low frequencies may be more attractive in small choruses than in large ones, so that smaller, lighter males try to compensate for this by producing more chucks in small choruses at the expense of increased predation risks. Female green treefrogs can choose only from a small fraction of males as they approach a pond with a large chorus because the background noise from the chorus masks the calls of all but a few males closest to the female, while in a small chorus the female can hear and choose from all the males (Gerhardt & Klump 1988). This means that females are less discriminating on the basis of call frequency in a larger chorus, and this may also be true for the tungara frog. A third possible explanation is that males are responding to the increase in operational sex ratio in larger choruses, e.g. smaller, lighter males may have to compete harder for a mate in small choruses, and so produce more chucks.

It is interesting to note that weight explains more of the variance than size in both the maximum call rate and the complexity ratio of males. In many other studies of anuran call parameters (e.g. Davies & Halliday 1978; Ryan 1980), only size has been considered, whereas in other cases where both have been measured, weight explained more variance in call frequency (Gerhardt et al. 1987; Robertson 1986) and call duration (Robertson 1986). Thus,

despite the fact that the weight of an individual amphibian is rather variable, changing rapidly upon leaving or entering water, it is a measure of more importance to vocalization than size, and should be considered whenever possible by field workers.

ACKNOWLEDGMENTS

This work was conducted at the Smithsonian Tropical Research Institute and financed by a Smithsonian Graduate Student Fellowship and a Christopher Welch Scholarship at the University of Oxford, where I was working for a D.Phil. I would like to pay special thanks to Stan Rand for his boundless help in setting up this project, in discussing its progress and in making it an immense pleasure to conduct. I am also indebted to Alan Grafen for his statistical advice and sagacious comments on an earlier version of this manuscript. Stan, Mike Ryan, Tim Guilford, Tim Halliday, Alan Solomon and Jeremy Robertson also gave helpful comments. I am very grateful to Reinaldo at Barro Colorado Island for his technical assistance. Jae Choe kindly identified the termite species.

REFERENCES

- Arak, A. 1983a. Sexual selection by male-male competition in natterjack toad choruses. *Nature, Lond.*, **306**, 261-262.
- Arak, A. 1983b. Vocal interactions, call matching and territoriality in a Sri Lankan treefrog, *Philautus leucorhinus* (Rhacophoridae). *Anim. Behav.*, **31**, 292-302.
- Brattstrom, B. H. & Yarnell, R. M. 1968. Aggressive behavior in two species of leptodactylid frogs. *Herpetologica*, **24**, 222-228.
- Bucher, T. L., Ryan, M. J. & Bartholomew, G. A. 1982. Oxygen consumption during resting, calling, and nest building in the frog, *Physalaemus pustulosus*. *Physiol. Zool.*, **55**, 10-22.
- Bulmer, M. G. 1983. Models for the evolution of protandry in insects. *Theor. Popul. Biol.*, **23**, 314-322.
- Davidson, E. H. & Hough, B. R. 1969. Synchronous oogenesis in *Engystomops pustulosus*, a neotropical anuran suitable for laboratory studies: localization in the embryo of RNA synthesized at the lampbrush stage. *J. exp. Zool.*, **172**, 25-48.
- Davies, N. B. & Halliday, T. R. 1978. Deep croaks and fighting assessment in toads *Bufo bufo*. *Nature, Lond.*, **274**, 683-685.
- Davies, N. B. & Halliday, T. R. 1979. Competitive mate searching in male common toads, *Bufo bufo*. *Anim. Behav.*, **27**, 1253-1267.
- Ehret, G. & Gerhardt, H. C. 1980. Auditory masking and effects of noise on responses of the green treefrog (*Hyla cinerea*) to synthetic mating calls. *J. comp. Physiol.*, **141**, 13-18.
- Emlen, S. T. 1968. Territoriality in the bullfrog, *Rana catesbeiana*. *Copeia*, **1968**, 240-243.
- Emlen, S. T. & Oring, L. W. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science, N. Y.*, **197**, 215-223.
- Gerhardt, H. C. 1987. Evolutionary and neurobiological implications of selective phonotaxis in the green treefrog, *Hyla cinerea*. *Anim. Behav.*, **35**, 1479-1489.
- Gerhardt, H. C. 1988. Acoustic properties used in call recognition in anurans. In: *Evolution of the Amphibian Auditory System* (Ed. by B. Fritsch, T. Hetherington, M. Ryan, W. Wilczynski & W. Walkowiak), pp. 455-483. New York: John Wiley.
- Gerhardt, H. C., Daniel, R. E., Perrill, S. A. & Schramm, S. 1987. Mating behaviour and male mating success in the green treefrog. *Anim. Behav.*, **35**, 1490-1503.
- Gerhardt, H. C. & Klump, G. M. 1988. Masking of acoustic signals by the chorus background noise in the green tree frog: a limitation on mate choice. *Anim. Behav.*, **36**, 1247-1249.
- Godwin G. J. & Roble, S. M. 1983. Mating success in male tree frogs, *Hyla chrysosecelis* (Anura: Hylidae). *Herpetologica*, **39**, 141-146.
- Green, S. & Marler, P. 1979. The analysis of animal communication. In: *Handbook of Behavioral Neurobiology. Vol. 3* (Ed. by P. Marler & J. G. Vandenbergh), pp. 73-158. New York: Plenum Press.
- Greer, B. J. & Wells, K. D. 1980. Territorial and reproductive behaviour of the tropical American frog, *Centrolenella fleischmanni*. *Herpetologica*, **36**, 318-326.
- Howard, R. D. 1978. The evolution of mating strategies in bullfrogs, *Rana catesbeiana*. *Evolution*, **32**, 850-871.
- Howard, R. D. & Kluge, A. G. 1985. Proximate mechanisms of sexual selection in woodfrogs. *Evolution*, **39**, 260-277.
- Iwasa, Y., Odendaal, F. J., Murphy, D. D., Ehrlich, P. R. & Launer, A. E. 1983. Emergence patterns in male butterflies: a hypothesis and a test. *Theor. Popul. Biol.*, **23**, 363-379.
- Jacobson, S. K. 1985. Mate selection and parental care in glass frogs (Centrolenidae). *Herpetologica*, **41**, 396-404.
- Jaeger, R. G. & Hailman, J. P. 1981. Activity of Neotropical frogs in relation to ambient light. *Biotropica*, **13**, 59-65.
- Kluge, A. G. 1981. The life history, social organization, and parental behavior of *Hyla rosenbergi* Boulenger, a nest-building gladiator frog. *Misc. Publ. Mus. Zool. Univ. Mich.*, **160**, 1-170.
- Lemon, R. E. 1971. Vocal communication of the frog *Eleutherodactylus martinicensis*. *Can. J. Zool.*, **49**, 211-217.
- Maynard Smith, J. 1972. *On Evolution*. Edinburgh: Edinburgh University Press.
- Passmore, N. I. 1977. Mating calls and other vocalizations of five species of *Ptychadena* (Anura: Ranidae). *S. Afr. J. Sci.*, **73**, 212-214.

- Perrill, S. A., Gerhardt, H. C. & Daniel, R. 1978. Sexual parasitism in the green treefrog (*Hyla cinerea*). *Science, N. Y.*, **200**, 1179–1180.
- Ramer, J. D., Jenssen, T. A. & Hurst, C. J. 1983. Size-related variation in the advertisement call of *Rana clamitans* (Anura: Ranidae), and its effects on conspecific males. *Copeia*, **1983**, 141–155.
- Rand, A. S. & Ryan, M. J. 1981. The adaptive significance of a complex vocal repertoire in a Neotropical frog. *Z. Tierpsychol.*, **57**, 209–214.
- Richards, D. G. & Wiley, R. H. 1980. Reverberations and amplitude fluctuations in the propagation of sound in a forest: implications for animal communication. *Am. Nat.*, **115**, 381–399.
- Robertson, J. G. M. 1986. Male territoriality, fighting and assessment of fighting ability in the Australian frog *Uperoleia rugosa*. *Anim. Behav.*, **34**, 763–772.
- Roble, S. M. 1985. Observations on satellite males in *Hyla chrysoscelis*. *Hyla picta* and *Pseudacris triseriata*. *J. Herpetol.*, **19**, 432–436.
- Rosen, M. & Lemon, R. E. 1974. The vocal behavior of spring peepers, *Hyla crucifer*. *Copeia*, **1974**, 940–950.
- Ryan, M. J. 1980. Female mate choice in a Neotropical frog. *Science, N. Y.*, **209**, 523–525.
- Ryan, M. J. 1983a. Sexual selection and communication in a Neotropical frog, *Physalaemus pustulosus*. *Evolution*, **37**, 261–272.
- Ryan, M. J. 1983b. Frequency modulated calls and species recognition in a Neotropical frog, *Physalaemus pustulosus*. *J. comp. Physiol.*, **150**, 217–221.
- Ryan, M. J. 1985a. *The Tungara Frog: A Study in Sexual Selection and Communication*. Chicago: University of Chicago Press.
- Ryan, M. J. 1985b. Energetic efficiency of calling in the frog *Physalaemus pustulosus*. *J. exp. Biol.*, **116**, 47–52.
- Ryan, M. J., Bartholomew, G. A. & Rand, A. S. 1983. Energetics of reproduction in a Neotropical frog, *Physalaemus pustulosus*. *Ecology*, **64**, 1456–1462.
- Ryan, M. J., Taft, L. K. & Tuttle, M. D. 1981a. Acoustical location of calling frogs by *Philander opossum*. *Biotropica*, **13**, 233–234.
- Ryan, M. J., Tuttle, M. D. & Rand, A. S. 1982. Bat predation and sexual advertisement in a Neotropical frog. *Am. Nat.*, **119**, 136–139.
- Ryan, M. J., Tuttle, M. D. & Taft, L. K. 1981b. The costs and benefits of frog chorusing behaviour. *Behav. Ecol. Sociobiol.*, **8**, 273–278.
- Schleidt, W. M. 1973. Tonic communication: continual effects of discrete signs in animal communication systems. *J. theor. Biol.*, **42**, 359–386.
- Schwartz, J. J. & Wells, K. D. 1984. Vocal behavior of the Neotropical treefrog *Hyla phlebodes*. *Herpetologica*, **40**, 452–463.
- Schwartz, J. J. & Wells, K. D. 1985. Intra- and inter-specific vocal behavior of the neotropical treefrog *Hyla microcephala*. *Copeia*, **1985**, 27–38.
- Sokal, R. R. & Rohlf, F. J. 1981. *Biometry*. 2nd edn. San Francisco: Freeman.
- Southwood, T. R. E. 1978. *Ecological Methods with Particular Reference to Insect Populations*. 2nd edn. London: Chapman & Hall.
- Sullivan, B. K. 1987. Sexual selection in Woodhouse's toad (*Bufo woodhousei*). III. Seasonal variation in male mating success. *Anim. Behav.*, **35**, 912–919.
- Taigen, T. L. & Wells, K. D. 1985. Energetics of vocalization by an anuran amphibian (*Hyla versicolor*). *J. comp. Physiol. B*, **155**, 163–170.
- Townsend, D. S., Stewart, M. M. & Pough, F. H. 1984. Male parental care and its adaptive significance in a Neotropical frog. *Anim. Behav.*, **32**, 421–431.
- Tuttle, M. D. & Ryan, M. J. 1981. Bat predation and the evolution of frog vocalizations in the Neotropics. *Science, N. Y.*, **214**, 677–678.
- Tuttle, M. D. & Ryan, M. J. 1982. The role of synchronized calling, ambient light, and ambient noise in anti-bat predator behavior of a treefrog. *Behav. Ecol. Sociobiol.*, **11**, 125–131.
- Tuttle, M. D., Taft, L. K. & Ryan, M. J. 1982. Evasive behaviour of a frog in response to bat predation. *Anim. Behav.*, **30**, 393–397.
- Wells, K. D. 1977. The social behaviour of anuran amphibians. *Anim. Behav.*, **25**, 666–693.
- Wells, K. D. 1978. Territoriality in the green frog (*Rana clamitans*): vocalizations and agonistic behaviour. *Anim. Behav.*, **26**, 1051–1063.
- Wells, K. D. & Greer, B. J. 1981. Vocal responses to conspecific calls in Neotropical hyliid frog, *Hyla ebraccata*. *Copeia*, **1981**, 615–624.
- Wells, K. D. & Schwartz, J. J. 1984. Vocal communication in a Neotropical treefrog, *Hyla ebraccata*: advertisement calls. *Anim. Behav.*, **32**, 405–420.
- Wells, K. D. & Taigen, T. L. 1986. The effect of social interactions on calling energetics in the gray treefrog (*Hyla versicolor*). *Behav. Ecol. Sociobiol.*, **19**, 9–18.
- Whitney, C. L. & Krebs, J. R. 1975. Mate selection in Pacific tree frogs. *Nature, Lond.*, **255**, 325–326.
- Woodward, B. D. 1982. Male persistence and mating success in Woodhouse's toad (*Bufo woodhousei*). *Ecology*, **63**, 583–585.
- Woolbright, L. L. & Stewart, M. M. 1987. Foraging success of the tropical frog, *Eleutherodactylus coqui*: the cost of calling. *Copeia*, **1987**, 69–75.

(Received 13 June 1988; initial acceptance
24 August 1988; final acceptance 7 November 1988;
MS. number: 3242)