Variable Responses to Rainfall by Breeding Tungara Frogs

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Though many amphibians breed in response to rainfall, rainfall can create substantial risks as well as benefits. For species that breed in ephemeral ponds and puddles, heavy rainfall can create many "false" ponds that quickly desiccate, particularly in wet years. As a result, nightly responses to rainfall may vary depending on seasonal or yearly rainfall. I used two years of data and previous studies to demonstrate variation in response to rainfall by breeding Tungara Frogs (*Physalaemus pustulosus*) on Barro Colorado Island, Panama. In 1997, an unusually dry year, breeding tungara frogs were far more abundant on wet nights than on dry nights. In 1998, an average year for rainfall, tungara frogs exhibited no significant response to rainfall and even a trend toward greater abundance on dry nights. In addition, female frogs were more sensitive to the effects of rainfall than were males. As a result, mating system parameters were highly dependent on both nightly and yearly rainfall.

DAY-TO-DAY breeding activity in many amphibian species is tightly linked with rainfall (Duellman and Lizana, 1994; Bevier, 1997; Yanosky et al., 1997). Rainfall may be conducive to amphibian breeding in several respects. Rainfall may fill new breeding ponds, providing opportunities to breed in habitats that are relatively free of competitors and predators and that have reduced risks of desiccation (Wilbur, 1997). In addition, the high ambient moisture provided by rainfall may be necessary for migrations from terrestrial habitats to breeding sites (Semlitsch, 1985; Loredo and Van Vuren, 1996; Palis, 1997) and to prevent excessive water loss during breeding activity. The link between rainfall and breeding activity is generally most pronounced for species with explosive breeding (sensu Wells, 1977), in which virtually all breeding activity may be synchronized with a single heavy rainfall (e.g., Bragg, 1945; Fitch, 1956; Wiewandt et al., 1972).

In contrast, for species that have prolonged breeding seasons and inhabit wetter environments, a positive association between rainfall and daily breeding activity is not necessarily expected (Cousineau, 1990; Bevier, 1997). For these species, breeding during rainfall may present substantial risks in addition to potential benefits. Many pools and puddles form during heavy rains but dry out almost immediately following rainfall. Although some species may be able to assess desiccation risks (Spieler and Linsenmair, 1997), these assessments are not likely to be perfect. As a result, during rainy periods, many potential breeding sites will be highly ephemeral and unsuitable for larval development (Green, 1990). In contrast, during drier periods, all potential breeding habitats are likely to be somewhat more permanent, and a high-er proportion of available breeding habitat may be suitable for reproduction. Thus, for some species, one would expect a negative association between rainfall and breeding activity, or no clear association at all.

However, whether the benefits of breeding during rainfall outweigh the risks likely varies from year to year. In wet years, nightly rainfall may tend to create comparatively many "false ponds" and provide little added benefit in terms of new pond creation or added ambient moisture. Conversely, in dry years, rainfall may be more crucial to ensuring breeding pond persistence and sufficient ambient moisture for breeding. Thus, flexible strategies for deciding when to breed in relation to nightly rainfall may indeed be optimal for many species of amphibians.

One species that may demonstrate this flexibility is the Tungara Frog, *Physalaemus pustulosus.* Tungara frogs inhabit seasonally moist Neotropical forests and have a prolonged breeding season. In the canal zone of Panama, most tungara frog breeding occurs between April and December, during which time males and females may breed multiple times (Ryan, 1985). Tungara frogs breed in stream pools, puddles, and treeholes and regularly move between breeding sites (Marsh et al., 1999). Foam nests containing tungara frog eggs may become stranded on dry land (pers. obs.) such that new but highly ephemeral pools and puddles may present substantial risks for breeding. Consistent with this view, Green (1990) found a negative correlation between rainfall and nightly breeding activity of tungara frogs during the rainy season of 1987. In an earlier study, M. J. Ryan and A. S. Rand (unpubl. data) found no clear effects of rainfall on tungara frog breeding activity.

In 1997, a strong El Niño event disrupted the normal rainy season in central Panama. As a result, 1997 was the driest in 60 years in parts of central Panama (Rand and Rand, 1996; S. Paton, unpubl. data). This year provided an exceptional opportunity to test whether the night-to-night responses of breeding tungara frogs to rainfall are relatively fixed or whether they depend on seasonal rainfall. For data from 1997, I compare the observed number of males and females, the operational sex ratio, and the number of egg masses deposited between wet nights and dry nights. I also compare these results to those obtained in 1998, in which the yearly rainfall (2680 mm) was slightly above average. I use these results to show that the responses of tungara frogs to nightly rainfall appear to be flexible rather than fixed and that this flexibility can produce different relationships between rainfall and nightly breeding activity in different years. In addition, I show that responses to rainfall may differ between males and females, such that mating system parameters may be strongly affected by both nightly and seasonal rainfall patterns.

Materials and Methods

Studies were conducted on Barro Colorado Island (BCI), Panama, in a seasonally moist tropical forest that receives an average of 2600 mm of rain per year (Rand and Rand, 1996), with 90–95% of this rain between the months of May and December. I censused tungara frogs and counted egg masses in 1997 and 1998 as part of two other experimental studies (Marsh et al., 1999; DMM, unpubl. data). Data were collected at a series of replicated artificial ponds, plastic basins with a diameter of 30 cm diameter and a depth of 10 cm. These artificial ponds were sunk in the ground, covered with a layer of leaf litter, and allowed to fill with rainwater. Tungara frogs readily breed in these ponds, which are suitable for larval growth and metamorphosis.

Male tungara frogs on BCI begin calling shortly after dusk. Females are attracted to the calls of males, and call characteristics are used to select a mate (Ryan, 1980, 1983, 1985). Pairs in amplexus leave the pond and return in the early morning hours to construct a foam nest containing the fertilized eggs (Ryan, 1985). In both 1997 and 1998, I visited these ponds on alternate nights between the hours of 1800 and 2300 from 4 June to 1 August. I captured all tungara frogs, sexed and marked them, and released them at the pond of capture. The following day, I counted all tungara frog foam nests

deposited the night before. From these data, I determined nightly captures of males, females, the ratio of females to males, and the number of foam nests deposited on each night. Because each pond was only visited once per night, observed numbers of males and females represent only a fraction of the total frogs breeding in those ponds on any given night. However, the high correlation between the number of breeding frogs observed and the total number of foam nests deposited ($r = 0.819$, $P < 0.0001$) suggest that these snapshots provide reliable estimates of the relative abundance of breeding frogs from night to night. To ensure that patterns observed were not an artifact of using artificial ponds, I also collected data on foam nest deposition at six natural breeding sites in 1997.

I divided nights into two categories for data analysis: wet nights and dry nights. Wet nights were any in which detectable rain (> 1 mm) had fallen since breeding activity on the previous night (normally 2400–0200 h). Dry nights were nights in which no rain (< 1 mm) had fallen during this period. These rainfall data were obtained from a rainfall gauge in the laboratory clearing on BCI. However, nights on which the presence or absence of rainfall over the entire study area was uncertain were excluded from the analysis, which left 16 nights in each year for analysis. I used MANOVA to analyze the effects of rainfall (wet vs dry) on four breeding activity parameters: the number of breeding males, the number of breeding females, the ratio of females to males, and the number of foam nests deposited. The significance of the overall model was tested with Wilks' Lambda, whereas effects on individual response variables were tested with F-values corrected for correlations with other variables. I performed this analysis separately for 1997 and 1998. All analyses were performed using SAS (vers. 6.12, SAS Institute, Cary, NC, 1989, unpubl.).

Results

In 1997, I captured a total of 198 males and 92 females. The overall MANOVA model for this year was significant, and the presence or absence of rainfall had significant effects on all response variables (Table 1). Rainy nights had more males, more females, higher female-to-male ratios, and more nests than did dry nights (Fig. 1A). These effects of rainfall on breeding activity were not confined to artificial ponds. In six natural sites censused over the same time period, the number of foam nests deposited was significantly higher on wet nights than on dry

TABLE 1. MANOVA OF RESPONSES (NUMBER OF MALES, NUMBER OF FEMALES, RATIO OF FEMALES TO MALES, FOAM NESTS) TO RAINFALL IN 1997 (A) AND 1998 (B).

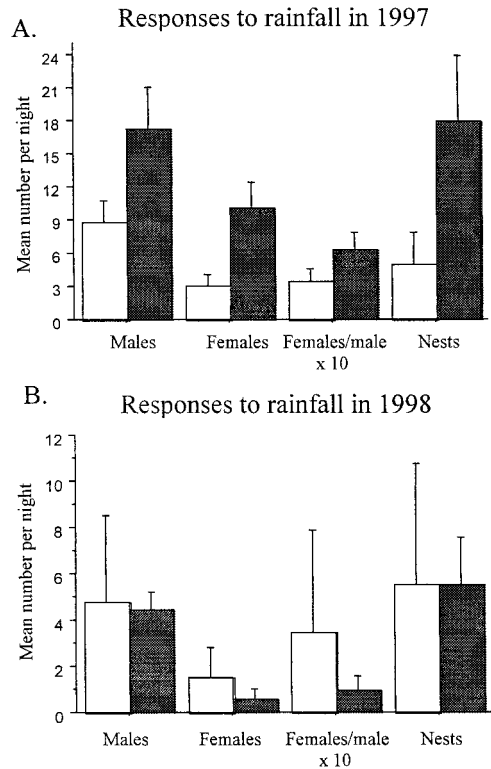| Dependent variable	F-value	df	Wilks' Lambda	P-value
(A) 1997 Responses to rainfall (wet vs dry)				
Full model	8.32	4,11	0.249	0.0024
Males	17.31	1,14	—	0.0010
Females	36.50	1,14	—	0.0001
Females/males	8.50	1,14	—	0.0113
Foam nests	17.50	1,14	—	0.0009
(B) 1998 Responses to rainfall (wet vs dry)				
Full model	1.40	4,11	0.663	0.2980
Males	0.08	1,14	—	0.7873
Females	3.56	1,14	—	0.0801
Females/males	3.69	1,14	—	0.0755
Foam nests	0.00	1,14	—	1.0000

Fig. 1. Tungara frog responses to rainfall in 1997 (A) and 1998 (B). Open bars represent dry nights, and shaded bars represent wet nights. * indicates $P < 0.05$, ** indicates $P < 0.001$. Error bars indicate ± 2 SE.

nights (Mann-Whitney U-test, $Z = -2.079$, df = 1, $P = 0.037$).

In 1998, I captured 72 males and 23 females. The overall MANOVA model for this year was nonsignificant (Table 1), indicating that rainfall had no detectable effects on breeding activity parameters (Fig. 1B). The power for the 1998 analysis was likely somewhat lower than that for the 1997 analysis, because fewer of the 16 included nights were dry and because fewer frogs were captured per night. However, this difference is unlikely to explain the lack of effect in 1998, because all trends in response to rainfall were in the opposite direction from those observed in 1997 (Fig. 1B). Indeed the number of females per night and the ratio of females to males was marginally significantly lower on wet nights than on dry nights in 1998 (Table 1).

DISCUSSION

In 1997, an extremely dry year, tungara frogs exhibited strong responses to rainfall. On wet nights, more males were active, more females were active, and more total nests were deposited than on dry nights. These results are in contrast to those obtained in 1998, a moderately wet year, when there were no detectable effects of rainfall on breeding activity and indeed a trend toward fewer active females on wet nights. The 1997 results are also in contrast to those obtained from previous studies, in which tungara frogs exhibited either negative (Green, 1990) or no clear responses (M. J. Ryan and A. S. Rand, unpubl. data) to nightly rainfall.

Because the conditions in 1997 were extreme and somewhat rare, it is not possible to compare responses to rainfall between multiple wet years and multiple dry years. As a result, the relationship between nightly responses to rainfall and yearly rainfall cannot be established with rigorous statistical certainty. However, in addition to being consistent with the 1997 and 1998 data, the hypothesis that yearly rainfall influences nightly responses is also consistent with the results of Green (1990). Green found an inverse correlation between rainfall and tungara breeding activity in 1987, which was the 10th wettest year on BCI since data collection began in 1929 (Rand and Rand, 1996). Furthermore, aside from the extreme weather of 1997, there are few potential alternative explanations for the difference between the responses to rainfall observed in 1997 and those observed in 1998 and in previous studies. As explained above, differences in statistical power are unlikely to account for this difference in response. In addition, experimental methods were standardized between 1997 and 1998, and responses in 1997 were similar to those observed in natural breeding sites,

so experimental methodology is unlikely to be responsible for any differences in results.

The results obtained in 1997 indicate that the responses of tungara frogs to rainfall are not fixed but flexible. Tungara frogs do not always breed, or avoid breeding, in response to rainfall. Instead, tungara frog breeding may be tightly linked to rainfall in some years but relatively independent of rainfall in other years. This flexibility makes sense in the context of costs and benefits to breeding during rainfall, which are likely to vary considerably depending on whether a year is wet or dry.

Interestingly, the effects of rainfall observed in 1997 differed between males and females. The effect of rainfall on female activity was much stronger than the effect on male activity, such that the ratio of females to males was significantly higher on wet nights. These results are similar to those of Henzi et al. (1995), who found that male and female painted reed frogs (*Hyperolius marmoratus*) responded to different environmental cues in deciding when to attend a breeding chorus and that females appeared to be more sensitive than males to environmental cues. The results for both tungara frogs and painted reed frogs suggest that females may be more cautious than males in deciding when to breed. In tungara frogs, males may breed nightly, whereas females have been observed to breed at most every 2.5–3.0 weeks (DMM, unpubl. data). Thus, males may have substantially less to lose by breeding on a night when the risks of desiccation or choice of a poor oviposition site may be higher.

It is also interesting to note that differences between sexes in response to environmental conditions may produce a misleading relationship between male activity and male breeding success (Tejedo, 1993; Henzi et al., 1995). For example, in Figure 2, I present data from 1997 showing the number of males observed on a given night relative to the ratio of females to males observed on that night. Although the one outlier renders the correlation nonsignificant (randomization test, $r = 0.23$, $P = 0.09$), the generally positive trend between male activity and sex ratio could be taken to indicate that larger choruses attract proportionally more females and that this represents a benefit of aggregation. However, the actual data are meaningless in this context, because they were collected across many separate ponds, most of which contained no more than a single male. Rather, this correlation results from males being somewhat more likely to come out on wet nights and females being much more likely to come out on these nights. Although these results were ob-
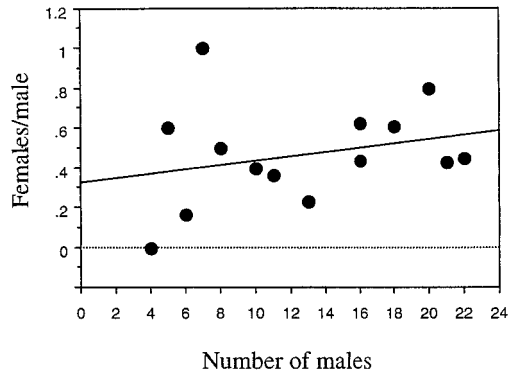

Fig. 2. Relationship between the nightly ratio of females to males and the nightly number of males observed at a series of artificial ponds.

tained in an unusual year, they demonstrate that correlations between chorus size and operational sex ratio (e.g., Ryan et al., 1981; Wagner and Sullivan, 1992; Tejedo, 1993) should be treated with caution.

Finally, the results presented above highlight the value of multiyear studies for examining amphibian mating systems and ecology. Mating systems are often dependent on a range of ecological conditions that may change from year to year (Slobodchikoff, 1988; Lott, 1991). As a result, single-season studies may often provide an incomplete, or even misleading, picture of a species' behavior or ecology. Given that we know very little about the degree to which amphibian mating systems vary or the ecological or evolutionary basis of such variation, multiyear studies assume a particular importance for these organisms.

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