The Costs and Benefits of Frog Chorusing Behavior

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Summary. 1. A number of predators, including a bat (*Trachops cirrhosus*), a frog (*Leptodactylus pentadactylus*), an opossum (*Philander opossum*), and a crab (*Potamocarcinus richmondi*), prey on the neotropical frog *Physalaemus pustulosus*, which calls in choruses on Barro Colorado Island, Panama.

2. Predation rate (no. of frogs eaten/h of observation) and predation risk to individuals (predation rate/chorus size) were determined for choruses of various sizes. There was no correlation between chorus size and predation rate, but there was a significant negative correlation between chorus size and predation risk.

3. There was a significant correlation between the number of females present and chorus size (i.e., number of males). A second order regression indicates that the proportion of females to males, the operational sex ratio, tends to increase with chorus size; thus, males have a higher probability of mating in larger choruses.

4. We suggest that the benefits of lower predation risk and higher mating probabilities associated with larger choruses were responsible for the evolution of communal sexual displays in *Physalaemus pustulosus*.

5. A cost-benefit model predicts that the size of males that join choruses is influenced by the asymmetric benefits related to male size and the behavior of other males in the population.

Introduction

Males of many species aggregate and advertise acoustically to attract mates. Chorusing is especially prevalent among insects and anurans (Alexander 1975; Wells 1977). Males in aggregations might have advantages in attracting females over males advertising alone because (1) aggregations form at resource bases needed by the female for reproduction (Alexander 1975), (2) larger choruses attract females from a larger area (Wells 1977), or (3) females might prefer to select males from larger choruses because they provide a greater range of choice (Alexander 1975; Emlen and Oring 1977; Bradbury 1981). These mechanisms are not exclusive.

There are also potential disadvantages to males who join choruses. Acoustically orienting predators might be attracted to choruses; thus, calling males will have an increased chance of being victimized (Cade 1975; Tuttle and Ryan 1981). But Hamilton (1971) suggested that although larger aggregations might attract more predators, individuals in large aggregations might have reduced predation risk.

Several studies of acoustically chorusing insects have shown that there is increased risk to advertising males. Cade (1975, 1979) demonstrated that the fly, *Ephasiopteryx ochea*, is attracted to calls of the cricket, *Gryllus interger*, and deposits its larvae on males. Similarly, Soper et al. (1976) showed that the cicada, *Okanga rimosa*, attracts a parasitoid fly, *Colcendamyia auditrix*, with its call. Cats (Walker 1964) and herons (Bell 1979) also use acoustic cues to locate calling male crickets.

Previous to our studies, there was little evidence that predators use acoustic cues to locate frogs. Jaeger (1976) reported that the large marine toad, *Bufo marinus*, feeds on the smaller *Physalaemus pustulosus* and probably uses the latter's call to locate the chorus. Recently, Tuttle and Ryan (1981) reported that the fringe-lipped bat, *Trachops cirrhosus*, feeds on a variety of frogs, which they locate by using the frogs' vocalizations. Tuttle et al. (1981) also demonstrated that the four-eyed opossum, *Philander opossum*, uses frog vocalizations to locate prey.

No study to date has quantified the amount of predation on a frog chorus or assessed the predation risk to individual males. There are also few studies

that actually measure the benefit to males joining aggregations of various sizes. The purpose of our study is threefold: (1) to report observations of a variety of predators that feed on one species of frog at one chorus site; (2) to quantify predation risks for males calling in choruses of different sizes; (3) to assess potential costs (predation risk) and benefits (probability of mating) of chorusing for males in choruses of different sizes.

Materials and Methods

We observed predation at frog choruses on Barro Colorado Island (BCI), Panama, from January to April 1980, during our studies of bat-frog interactions (Tuttle and Ryan 1981; Ryan et al., in preparation). On 7 nights between 17 and 28 April we attempted to quantify the amount of predation on a frog chorus, *Physalaemus pustulosus*, at Weir Pond on Lutz Stream.

We made 14.3 h of observations with a Javelin model 221 night vision scope at various times between 1900 and 2400 h. Field notes were recorded on magenetic tape and the total observation time, time spent observing each predator, and the occurrence of predation events were recorded, as was the number of frogs present. The mean chorus size was calculated from the number of frogs present at the beginning and end of each observation period.

Data were not available on the number of female frogs present each night at Weir Pond. However, during 1978 and 1979, one of us (MJR) conducted a study of the *P. pustulosus* mating system in nearby Kodak Pond (Ryan 1980a and unpublished data). The correlation between the number of females and the number of males (i.e., the chorus size) was determined. These data were then fitted with a linear and a second-order polynomial regression. A second-order regression was used because a linear regression would obscure changes in the proportion of females to males. This proportion, the operational sex ratio (OSR, Emlen and Oring 1977) is needed to determine the probability of mating for males and is also useful in making predictions about mating systems.

Results

Chorus Size

Table 1 shows the number of *P. pustulosus* present each night. The mean number of frogs present was

used to determine the predation risk (predation rate/chorus size) from the predation rate (no. of frogs eaten/h of observation).

Predation at the Chorus

Fringe-lipped bats, *Trachops cirrhosus*, were observed at frog choruses throughout BCI, and were abundant at Weir Pond between January and April 1980. *T. cirrhosus* would fly downstream along the Lutz Stream and circle the pond at less than 0.5 m above the water, quickly swooping to the surface to catch floating frogs (calling *P. pustulosus* always float). Frog capture was indicated in two ways. Either we saw the frog in the bat's mouth or the bat would exhibit typical capture behavior: contacting the water's surface near a calling frog and then flying directly to a nearby tree where it would perch and appear to be manipulating food with its wrists. We saw the frog in the bat's mouth in 45.6% of the predation events.

T. cirrhosus ate 95 frogs in the 14.3 h of observation (6.6 frogs/h). Table 1 shows the total number of frogs eaten during the observation period, the predation rate and the predation risk for each night. There was no correlation between the number of frogs present and the predation rate ($r_s = -0.28$, $P > 0.05$), but there was a significant negative correlation between chorus size and predation risk to an individual male ($r_s = -0.86$, $P < 0.05$).

The South American bullfrog, *Leptodactylus pentadactylus*, is a large frog (max. snout to vent length ca. 200 mm) that often breeds at or near sites of *P. pustulosus* activity. There were at least two, and sometimes three, *L. pentadacylus* present at Weir Pond during our observations. We saw *L. pentadactylus* eat 15 *P. pustulosus* (1.1 frogs/h). There was no significant correlation between chorus size and predation rate ($r_s = 0.49$, $P < 0.05$) and even less of a correla-

Table 1. Night of chorus, chorus size, observation time and the number of frogs eaten, the predation rate (frogs eaten/h of observation), the predation risk (predation rate/chorus size) by each predator and the total predation risk for each night

| Date	$\bar{x}$ number of frogs present	Obs. time (h)	Predation by									Total predation risk
			T. cirrhosus			*L. pentadactylus*			*P. opossum*			
			Obs.	Predation		Obs.	Predation		Obs.	Predation		
				Rate	Risk		Rate	Risk		Rate	Risk	
4/17	425	1.25	6	4.8	0.011	1	0.8	0.002	1	0.8	0.002	0.015
4/18	274	2.47	30	12.1	0.044	1	0.4	0.001	0	0.0	0.000	0.045
4/20	44	1.79	14	7.8	0.178	1	0.6	0.013	0	0.0	0.000	0.191
4/21	50	2.59	16	6.2	0.124	0	0.0	0.000	5	1.9	0.039	0.163
4/22	340	1.98	5	2.5	0.007	11	5.5	0.016	5	2.5	0.007	0.030
4/23	330	2.38	17	7.1	0.022	1	0.4	0.001	7	2.9	0.009	0.032
4/27	130	1.85	7	3.8	0.029	0	0.0	0.000	0	0.0	0.000	0.029
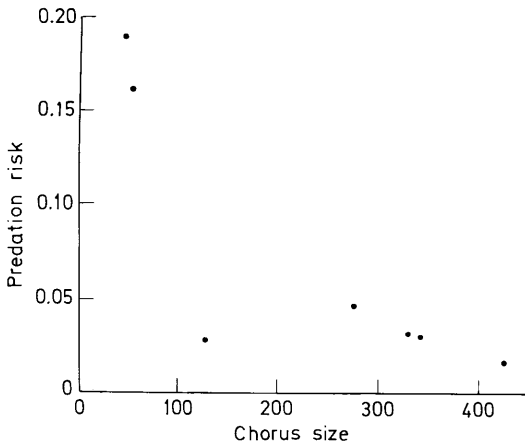
Fig. 1. Predation risk (=predation rate/chorus size; predation rate=no. of frogs eaten/h of observation) for individual frogs in choruses of different sizes at Weir Pond

Fig. 2. Number of females versus chorus size (i.e., number of males) present at Kodak Pond in 1979, with the resulting linear (1) and second order (2) regressions plotted

tion between chorus size and predation risk ($r_s=0.20$, $P>0.05$, Table 1).

We frequently observed the four-eyed opossum, *Philander opossum*, at chorus sites on BCI. During the observation periods one *P. opossum* was present at Weir Pond for a total of 23.2 min on 17, 21, 22 and 23 April. With one exception, opossums visited the pond on nights of high frog activity but the predation rate was not correlated with chorus size ($r_s=0.58$, $P>0.05$). As with *L. pentadactylus*, there was an even smaller correlation between chorus size and predation risk ($r_s=0.25$, $P>0.05$, Table 1).

At least three large crabs, *Potamocarcinus richmondi*, (max. carapace length ca. 55 mm) resided in Weir Pond. These crabs were observed eating a total of five frogs from 17 to 28 April. We also observed crabs eating frogs at other BCI sites. These crabs typically caught males floating on the water by approaching the frog from underwater, reaching up, and grabbing a frog with one of its pincers. Several times crabs were seen eating one frog while holding a second in the other pincer.

During a study of the *P. pustulsous* mating system in Kodak Pond (Ryan, unpublished data) 9 of the 185 (4.9%) males marked in 1978 and 26 of the 617 (4.2%) males marked in 1979 were missing portions of at least one limb. Our observations of crab feeding behavior suggest that crab predation could be responsible for at least a portion of these damaged limbs.

Crabs could not be viewed through the night vision scope; sightings of crab predation were made at the beginning and end of each observation period. Therefore, we do not attempt to estimate the amount of crab predation on the frogs; we merely report these observations to indicate the variety of predators at the chorus.
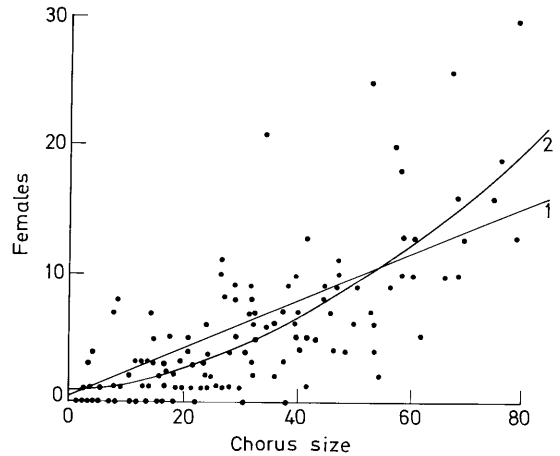
Costs and Benefits of Chorusing

To estimate the cost of chorusing due to predation, which is probably the most important cost of chorusing (Bucher et al. 1981), we combined the predation risks incurred by individual males due to predation by *T. cirrhosus*, *L. pentadactylus*, and *P. opossum* (Table 1). Although there is no relation between chorus size and predation rate ($r_s=0.11$, $P>0.05$), Fig. 1 shows that there is a significant negative correlation between chorus size and predation risk to individual males ($r_s=-0.78$, $P<0.05$).

There is little doubt that the primary benefit of *P. pustulosus* chorusing is mate attraction. The number of receptive females at the breeding site allows us to calculate the mean probability of mating for males in choruses of different sizes.

Females are usually present at the pond only on the night they mate, and amplexed pairs often leave the chorus site immediately after mating and return to construct the foam nest after the chorus has subsided (Ryan 1980a). Females are usually conspicuous to the observer only during nest construction. Since nests may be communal, counting the number of nests does not give a reliable indication of the number of females present. The only accurate measure of the number of females is an all-night survey counting pairs during nest construction.

These data are not available for Weir Pond. However, an ongoing study of the mating system of *P. pustulosus* at Kodak Pond does provide these data (Ryan 1980a and unpublished data). In both 1978 and 1979 there was a significant correlation between the number of females and males present (number of males=chorus size; 1978, $r=0.67$, $P<0.01$, $n=48$; 1979, $r=0.73$, $P<0.01$, $n=146$). Since the data from

1979 were more extensive we fitted these data with a linear and second order regression. An analysis of variance shows that both regressions explain a significant amount of the variability (linear regression, $F = 162.4$, $P < 0.005$; second order, $F = 90.9$, $P < 0.005$). However, the second order regression explains significantly more of the variability than does the linear regression ($F = 9.7$, $P < 0.005$), and Fig. 2 shows that the proportion of females to males, or the OSR, increases with chorus size. This trend is also apparent from the positive β_2 term in the second order regression equation ($Y = 0.82 + 0.05\,X + 0.002\,X^2$).

The maximum chorus size used in the above analysis (80) is much smaller than the maximum chorus size at Weir Pond (425). However, we see no reasons not to expect the same qualitative relationship between the OSR and chorus size at Weir Pond, but the precise quantitative relationships at Weir and Kodak Ponds are probably quite different.

Discussion

Applicability of Predation Estimates

In this study we observed predation at one chorus site of one species of frog. In light of the large amount of predation at the Weir Pond, we must consider whether ours was a 'typical' situation and whether *P. pustulosus* might be more susceptible to predation than other species which chorus.

Although we have no predation estimates at other chorus sites, Tuttle and Ryan (1981) showed that the bat, *T. cirrhosus*, was attracted to speakers broadcasting a variety of frog vocalizations, including *P. pustulosus*, at numerous sites on BCI. Also, our observations of predation at Weir Pond did not include the full array of known *P. pustulosus* predators. The marine toad, *Bufo marinus*, was observed eating *P. pustulosus* at Kodak Pond (Jaeger 1976; Ryan, unpublished data) and was seen at Weir Pond, although it was not observed eating *P. pustulosus*. Also, the snake, *Leptodiera annulata*, was observed at Kodak Pond as well as choruses on the mainland. *L. annulata* is a well-known frog predator (Duellman 1958). Thus, *P. pustulosus* appear to be vulnerable to a variety of predators at a number of their breeding sites.

There is also evidence from at least one other species of frog that predation might be quite intense at chorus sites. In his study of the natural history of the gladiator frog, *Hyla rosenbergi*, in Panama, Kluge (1981) saw predation by a frog (*Leptodactylus pentadactylus*) and a snake (*Leptodiera annulata*) and suspected predation by several other species. He also noted no return of permanently marked males between 1978 and 1979. He suggests that *H. rosenbergi*

males live only one year, and are among the shortest lived anurans, owing to predation pressure. It seems that the intense predation on *P. pustulosus* might not only be typical for that species, but might be indicative of the amount of predation on other tropical frogs that chorus.

Benefits of Chorusing and the Evolution of Communal Sexual Displays

Hamilton (1971) suggests that predator avoidance behavior might explain the centripetal tendencies of many species. He further suggests that even if predation increases with aggregation size, predation risk to individuals might still be lower in larger aggregations. It is obvious that as long as predation does not increase with chorus size, predation risk will be lower in larger aggregations. In our study there was no increased predation rate at larger choruses and there was a marked reduction in predation risk. There is no question that males in larger choruses benefit from reduced predation risk.

Data from Kodak Pond indicate that the OSR increases with chorus size. The chorus sizes at Weir Pond are much larger than those at Kodak Pond, but we assume the same qualitative phenomenon occurs at both sites, although probably in different quantitative manners. Therefore, males in larger choruses have a higher probability of mating, although this relationship is not straightforward for all males (see below).

There has been considerable discussion about the selective forces that have initiated communal sexual displays (see review in Bradbury 1981). Male *P. pustulosus* advertise from resources (e.g. water) needed by the female for reproduction (Ryan 1980a), as do many other anurans (Wells 1977). In only a few species of frogs do males actually disperse themselves among the available resources; most tend to be clumped (Wells 1977). Differences in resource quality might be responsible for this clumping in some species, especially those defending resources (e.g. Howard 1978). This does not seen to be the case for *P. pustulosus* (Ryan 1980a). We suggest that when advertising for mates, males join choruses because of the benefits of decreased predation risk and increased mating probabilities associated with larger choruses. Bradbury (1981) suggests that the mating advantage gained by males who join aggregations is due to female preference for larger aggregations and not increased acoustic active space, since the active space of the aggregation, and thus the number of females attracted, does not increase linearly with the number of males added owing to the inverse square law of the spherical spreading of sound. Emlen's

(1976) observations of female bullfrogs bypassing isolated calling males enroute to choruses support such an interpretation. It is not clear if predation pressure, female preference or, more likely, some combination of the two, was the selection force initially responsible for the evolution of chorusing behavior in *P. pustulosus*.

Costs and Benefits of Chorusing and Chorus Structure

Our analysis shows that the cost of chorusing (predation risk, but see Bucher et al. (1981) for a measure of energetic costs of calling) decreases with chorus size, while the benefit (probability of mating) increases. There is no noncalling, satellite strategy known in *P. pustulosus* (Ryan 1980a), and all males seem as likely to use the complex mating calls which are more attractive to females (Rand and Ryan, in preparation; Ryan, unpublished data). Also, there is no correlation between male size and amount of calling (Ryan, unpublished data). Therefore, all males at the breeding site should incur the same predation risk. In this sense, costs are *symmetrical* with respect to male size.

Ryan (1980a) showed that female *P. pustulosus* are more likely to choose larger males. Although the mean probability of mating increases with chorus size, due to the increased OSR, males of different sizes are affected in different manners. Thus, benefits are *asymmetric* with respect to male size. An examination of these costs and benefits leads to some interesting insights about *P. pustulosus* chorus structure.

The amount of servicing time required by the female places strict limitations on a male's reproductive success (Emlen and Oring 1977). *P. pustulosus* males mate only once each night due to the prolonged duration of amplexus and nest construction. Servicing time restricts male reproductive success in most anurans, and may suggest why the reported variances of male reproductive success are usually lower for frogs than for birds (but see Kluge 1981 for an alternative interpretation). If female preference for larger males was absolute, then the mating benefit to larger males would increase with the OSR, and presumably with chorus size, and quickly asymptote where the probability of a male maximizing his nightly reproductive success (i.e. mating once) would be 1.0. The stricter the servicing limitations and the stronger the female preference for larger males, the earlier (i.e., at a lower OSR and a smaller chorus size) the benefit curve for large males will asymptote. The benefit curve for the small males will be at its minimum, near zero, during the increasing phase of the large males benefit curve and will begin to increase when the large male's curve asymptotes. The two curves theoretically would
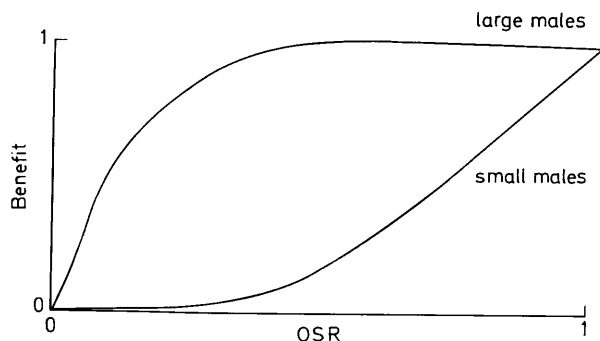

Fig. 3. Theoretical benefit (probability of maximizing nightly reproductive success) versus OSR (operational sex ratio) curves for large and small males

converge when the OSR is one, a situation that does not occur in nature (Fig. 3).

At large choruses males of all sizes have their lowest predation risk and best chance of mating. This leads to the quite obvious prediction that all males should join large choruses. The interesting question is: which males should join small choruses, with their high predation risk and low mating probability? Remembering that costs are symmetrical, first inspection of the asymmetric benefit curves (Fig. 3) predict that small males should not join small choruses; predation is high and they have almost no chance of mating. However, costs should vary among habitats and times of year, and there should be a cost above which large males will not join small choruses. It is not possible to predict the precise cost, but it will depend in part on the probability of males mating in other choruses and how often these choruses occur. As large males drop out of the chorus, the probability of mating for small males increases, perhaps above that which small males experience in most choruses, and small males should now join small choruses. Therefore, we suggest that owing to the size-related asymmetric benefits, the behavior of the large males is strongly influenced by the impending costs and their behavior in turn influences the behavior of the small males. Ryan (1981) proposed a similar model to explain the variability in some lizard social systems.

In order to test this model, we would need to compare habitats or times of year with quite different predation intensities and we would need information on the extent of female discrimination in mate choice, mating probabilities for males of all sizes, and the predation risk to these males.

Our cost-benefit analysis obviously has limited applicability to other species. However, predation has been implicated as a potential factor influencing chorus structure in other anurans (Ryan 1980b), and our

work demonstrates that predation probably is common for at least one frog chorus and might affect chorus structure.

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