

SEXUAL SELECTION AND COMMUNICATION IN A NEOTROPICAL FROG, *PHYSALAEMUS PUSTULOSUS*

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Many sexually dimorphic characters have evolved under the influence of sexual selection, either because they increase an individual's ability to compete for access to members of the opposite sex, or because they increase an individual's probability of being chosen as a mate (Darwin, 1871). Some of the most elaborate displays in animal communication are those used by males to attract and court females. Male sexual displays may provide information which allows females to identify males as conspecifics (Mayr, 1963) or possibly to assess mate quality (Fisher, 1958; Trivers, 1972). Other suggested functions of sexual displays, such as synchronizing male and female receptivity (Lehrman, 1965) or persuading a female to approach an aggressive male (West Eberhard, 1979) probably are proximate effects of a signal which evolved to enhance mate discrimination (also see Dawkins and Krebs, 1978).

Most sexual displays seem to contain information far in excess of that needed for species recognition (but see Rand and Williams, 1970). Darwin (1871) maintained that male sexual displays allowed females to pick more vigorous males and that female choice thus caused the further elaboration of male sexual displays. This idea was extended by Fisher's theory of runaway sexual selection (Fisher, 1958; also see Trivers, 1972; West Eberhard, 1979; Lande, 1980, 1981).

Thus there is an important relation between sexual selection and communication. However, few studies have demon-

strated that specific display characters are used by females to choose among conspecific males, and even fewer studies have shown how female choice based on these characters can account for differential male mating success observed in a natural population.

Female mate choice has been demonstrated as an important determinant of male reproductive success in several anuran species. For example, in bullfrogs (*Rana catesbeiana*; Howard, 1978), males vocalize from their territories and attract females, which choose the larger males on the better territories. As with territorial birds (see Searcy, 1979), it is not clear if female bullfrogs use traits of the male, the territory, or both, when selecting mates. This is an important limitation because, in general, males of species with prolonged breeding seasons tend to advertise for mates from defended areas which are later utilized as the oviposition site, while males of species with very short breeding seasons tend to acquire mates by actively searching and clasping anything that resembles a female (Wells, 1977). Therefore, among many anurans in which female choice is important in determining male reproductive success, it will be difficult to elucidate the importance of male traits versus territorial quality as cues used by females to select mates.

The importance of the anuran advertisement call in interspecific mate choice and male-male spacing has been documented extensively (Salthe and Mecham, 1974; Wells, 1977), but there is little direct evidence that variation among conspecific calls affects intraspecific mate choice. Whitney and Krebs (1975) demonstrated

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that the amount of calling by male *Hyla regilla* might influence their reproductive success. Fellers (1979a) showed that when given a choice between calls, female *H. versicolor* preferred the louder call, and he also showed (1979b) that males calling from perch sites where sound was less attenuated were more likely to attract mates. Similarly, Greer and Wells (1980) showed that male *Centrolenella fleischmanni* calling from elevated sites acquired more mates, and they suggested this might be due to better sound transmission from elevated, as compared to lower, call sites. These studies demonstrate that males which increase the total energy content of the vocalization, either by calling more frequently, louder, or from areas with better sound transmission, might attract more mates.

Although their study did not investigate the role of vocalizations in mate choice, Davies and Halliday (1978) demonstrated that intraspecific variation in advertisement calls can play an important role in anuran social behavior. They showed that a vocalization of the common toad, *Bufo bufo*, does contain information specific to the individual: the frequency of the male's call indicates his size. Males are more likely to displace mated males from females when mated males are smaller, and Davies and Halliday suggest that males use the information in the call to evaluate the size of their competitors.

This paper describes an investigation of sexual selection and communication in the túngara frog, *Physalaemus pustulosus* (Leptodactylidae). These frogs are common on Barro Colorado Island (BCI), Panama, where this study was conducted. This species breeds in every month of the year, but breeding is concentrated in the wet season (April to December). Preliminary observations (Ryan, 1980a) showed that males advertise from stationary calling sites which do not later serve as the oviposition site, and that male-male vocal and physical interactions seem to function primarily in maintaining inter-individual distances among males. Females approach calling males and there is little "scramble

competition" (Wells, 1977) among males for mates; that is, males do not acquire mates by searching and clasping, as do many species with explosive breeding seasons (Wells, 1977). Also, female *P. pustulosus* readily approach speakers broadcasting the species-specific advertisement call (Rand and Ryan, 1981). This provides a method to experimentally test hypotheses about the importance of intraspecific variation of vocalizations in mate choice.

Although male-male competition and female choice may be complexly interrelated (e.g., Cox and LeBoeuf, 1977), this species seems to offer an opportunity to determine how female choice based on male characters influences differential male mating success.

METHODS AND MATERIALS

I monitored male mating success for 152 consecutive nights at Kodak Pond, a small cement pool (1 × 2 m) on BCI where *P. pustulosus* had been breeding for at least 15 years. From 30 June to 2 December 1979, I measured all unmarked males (snout-vent length) to the nearest 0.5 mm and sizes were rounded to the nearest 1.0 mm for analysis. I then tagged each male with a numbered piece of surveyors' tag stitched to the back. These tags allowed undisturbed observations of the males. Females often were not seen until they were mated because to the observer, they are indistinguishable from males at a distance. To minimize observer interference with mated pairs, females were marked only when they were not mated.

In the shorter pilot study in 1978 (Ryan, 1980a), I analyzed a male's mating success as a function of his size. In this study, a male was not always one size because males grew. Therefore, I analyzed male mating success in terms of the number of matings per male frog-night at each male size (frog-nights are analogous to man-hours). The size of each male at initial capture was known. Most males lost their tags at some time during the study. They were recaptured and remeasured, so their size is known at some date subsequent to their initial capture. When males were

present at the pond between the initial capture and some subsequent recapture, their size was interpolated. Most males were present for at least some nights after their final recapture. In these cases male size was extrapolated using growth rates obtained from the entire male population.

Every hour from 1900 to 2400, all individual males in the pool were noted as calling, not calling, mated or nesting (point sample method, see Dunbar [1976]). Mated and nesting males also were noted when first observed, and when observed after 2400. Observations on each night were continued until all frogs left the breeding site, usually about 0230.

The *P. pustulosus* advertisement call consists of one "whine" and from 0–6 "chucks" (see Rand and Ryan [1981] for call analysis). I previously showed that there was a significant negative correlation between male size and the fundamental frequency of the chuck, and that females were capable of discriminating among males at each extreme of the size distribution by using the size-related information in the chuck (Ryan, 1980a). To further test the extent of female preference based on differences in the chuck, I synthesized calls in which the whine was identical but the fundamental frequency of the chuck was varied. Female choice tests were conducted in 1979 and 1980, and females were usually in amplexus when collected. Females were not collected from Kodak Pond when mating success was being monitored. Female preference among calls was tested with simultaneous choice experiments, and details of the experimental design are in Ryan (1980a).

Physalaemus pustulosus eggs are deposited in foam nests (Heyer and Rand, 1977). To determine the effect of male size on the number of eggs produced by the female, I measured individual males and females and then placed them in buckets in the laboratory. Most pairs (>90%) mated, constructed nests and deposited eggs. Eggs usually hatched in three days. After four or five days the number of tadpoles from each nest was recorded. The foam nest was then dissolved in a solution of water

and chlorine bleach (ca. 5:1), and the number of undeveloped eggs was counted. Nests from the field were treated in a similar way to compare the proportion of undeveloped eggs per nest in the field and in the laboratory.

Data were analyzed by nonparametric statistics (Siegel, 1956) except in the regressions where the parametric assumptions were met (Steele and Torrie, 1960). The multiple regression analysis was computed with the Statistical Analysis System computer package (SAS Institute, No. Carolina). The importance of individual variables in the regression equations was determined by comparing the sum of squares of each variable to the residual mean square with an *F* test (Steele and Torrie, 1960).

RESULTS

Reproductive Behavior.—At Kodak Pond, males arrived around dusk (1830 to 1930) and began calling. Individuals called for various amounts of time, but most calling ceased before 2430 (Fig. 1). Males maintained individual distances with frequent physical encounters, usually kicking and sometimes wrestling. On several occasions during the 4,456 frog-nights a male involved in a prolonged wrestling bout (ca. 20 min) was killed. However, the usual result of an aggressive interaction was that one of the males moved a few cm and resumed calling.

There was no obvious noncalling male mating strategy, as has been reported in some other anurans (e.g., Perrill et al., 1978). In fact, the amount of time at the breeding site was an excellent predictor of the amount of calling by a male ($r = .91$, $N = 617$, $P < .001$), suggesting that males did not adopt a noncalling strategy over the season.

Females often were not seen before they mated, but observations of females prior to amplexus suggested that females select mates. The females moved around the breeding site among calling males, but always remained about 10 cm from the nearest male. Males tended to clasp any nearby frog, conspecific or heterospecific,

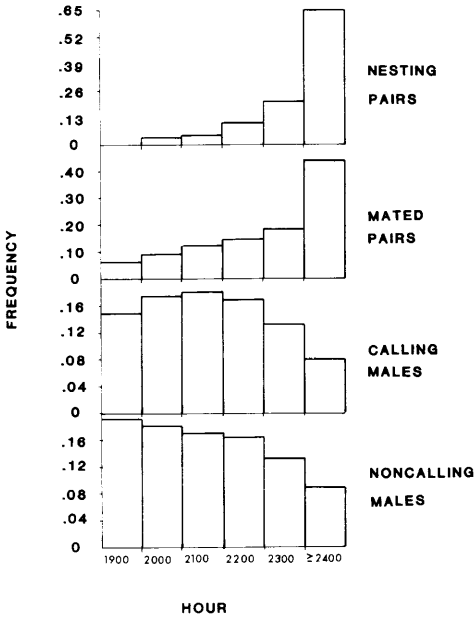


FIG. 1. The average temporal distribution of male and female *Physalaemus pustulosus* behaviors throughout the night at Kodak Pond in 1979.

that came within reach, but they did not search beyond about 5 cm from their calling site. Males which were clasped gave a release call which usually resulted in their release. The female eventually approached a calling male and made physical contact with him. The male then clasped the female. (Up to this point the behavior of the males and females is remarkably similar to other species in which males advertise from stationary calling sites and females choose mates, e.g., bullfrogs, Emlen, 1976; Howard, 1978; Ryan, 1980b.) An unmated male tried to displace a mated male in about 50 of the 751 pairs that were observed. None of these attempts was successful. In fact, often mated pairs sat on the shore only a few cm from from calling males, with no attempted interference by the unmated male. Most of the displacement attempts seemed to take place when mated pairs swam directly into or near a calling male.

Mated pairs usually left the breeding site shortly after the male clasped the female, and often pairs remained in the vegetation

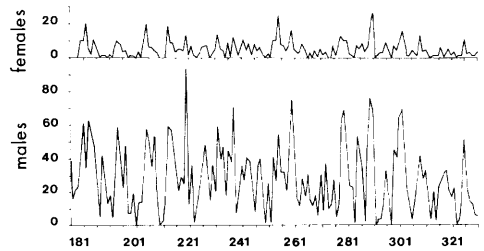


FIG. 2. The number of male and female *Physalaemus pustulosus* present at Kodak Pond from 30 June (day 181) to 2 December 1979 (day 333).

surrounding the pool. They returned several hours later, usually after much of the calling had ceased; nest construction occurred at this time (Fig. 1). The pair did not return to the male's calling site to construct the nest. In fact, *P. pustulosus* frequently nest communally, adding their nests to other nests being constructed.

These behavioral observations suggest that female choice of mates is potentially an important determinant of male reproductive success, and that the quality of the oviposition site will not be considered in mate choice by females.

Male Reproductive Success.—I marked 617 males over 152 consecutive nights (30 June to 2 December) at Kodak Pond in 1979. There were an average of 27.0 ($S = 18.5$) males and 4.9 ($S = 5.1$) females at the breeding site each night (Fig. 2). Females usually came to the breeding site only on the night they mated. Males were present at the breeding site for an average of 7.2 nights ($S = 7.1$) over an average time span (i.e., initial capture to last sighting) of 43.0 days ($S = 40.0$). Although marked males were found breeding at nearby sites only rarely, it cannot be assumed that males did not breed when they were not at Kodak Pond.

Over the 152 nights monitored, the 617 males were present for 4,456 frog-nights and obtained 751 matings ($\bar{x} = 1.2$ matings per male; Fig. 3). The number of nights a male spent at the breeding site strongly influenced his mating success there ($r = .74$, $N = 617$, $P < .01$).

It is necessary to know the size of the male and his probability of mating when

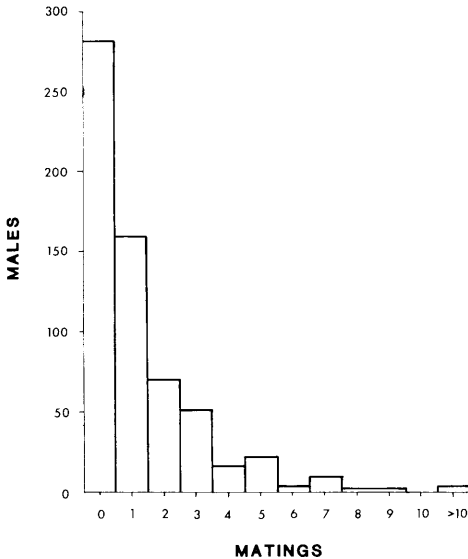


FIG. 3. The distribution of the number of matings per male for 751 matings and 617 *Physalaemus pustulosus* males at Kodak Pond in 1979.

at the breeding site to determine the influence of male size on female choice. Most males were not one size during the study, and were present at Kodak Pond for different numbers of nights. Therefore, I determined the probability of mating for males in each size class by dividing the number of matings in each size class by the number of frog-nights in that size class. There was a significant positive correlation between a male's size and the probability of obtaining a mate ($r_s = .71$, $N = 11$, $P < .05$; Fig. 4). This suggests that over the season, females were more likely to select larger males as mates.

The hypothesis that females select larger males also can be tested on a nightly, rather than a seasonal, basis. This type of analysis probably is more appropriate, because to determine female preference we should know not only the male selected by a female, but also the males not selected. I do not know the precise males sampled by each female, but the males that were present on the night she mated surely is a more accurate approximation of this sample than are the males that were present over the entire season. Female choice of

larger males was tested by comparing the size of each mated male to the median size of males present on that night. The null hypothesis of no preference predicts that half of the mated males should be larger than the median male size. Significantly more mated males were larger than the median male size (363 > median, 288 < median, 100 = median; $\chi^2 = 8.6$, $d.f. = 1$, $P < .005$). Because this test did not take into account the fact that the median male size available to females decreases when subsequent females choose mates, this is a conservative test of female preference for larger males since it is biased towards a type II error. These results are in concordance with previous results (Ryan, 1980a) demonstrating that at the breeding site, larger males are more likely to acquire mates.

I examined the data to determine whether size-dependent differences in behavior might be responsible for the increased probability of larger males mating. Although the point sample method at 1 h intervals provided only a gross description of behavioral repertoires, it did provide an unbiased estimate. There was no correlation between a male's initial, mean, or final size and the number of nights he was calling ($r = -.06$, $r = .03$, $r = .01$, $N = 617$, $P > .05$) or the proportion of nights present on which he called ($r = -.06$, $r = -.04$, $r = -.03$, $N = 617$, $P > .05$). There also was no correlation between male size and call intensity ($r_s = .005$, $N = 7$, $P > .05$). Call repetition rate was constant among males and the total number of calls produced in one night (as many as 7,000) was not size dependent (Ryan et al., in press). This suggests that larger males do not have greater mating success because they call more often or louder.

Female Mate Choice Based on Call Characteristics.—Previously (Ryan, 1980a), I showed that there was a negative correlation between male size and the fundamental frequency of the chuck, and that females preferred calls with a chuck fundamental frequency of 200 Hz over a 260 Hz call (Table 1). The experiments re-

TABLE 1. Numbers of female *Physalaemus pustulosus* responding to calls with chucks of different fundamental frequencies in simultaneous choice tests.

200 Hz	260 Hz	P
8	0	.004
210 Hz	250 Hz	
9	2	.032
220 Hz	250 Hz	
10	6	.237

ported here were conducted to further substantiate the claim that females can discriminate among males of certain sizes based on differences in the chuck, and to gather data suggesting the extent to which females are capable of discriminating. In simultaneous choice tests, females preferred 210 Hz calls over 250 Hz calls, but did not discriminate between calls of 220 Hz and 250 Hz (Table 1; Ryan, 1980a).

Using the data gathered to test correlation of size and chuck frequency (Ryan, 1980a), I determined the probability of a female "making a mistake"; that is, of selecting a smaller male even though his call has a lower frequency, if she discriminates only to the extent tested in the choice experiments. First, I determined the probability of a female choosing the lower call, but getting the smaller mate, if she only compared calls with chucks at least as different as 200 Hz and 260 Hz. In the population of 132 males sampled (Ryan, 1980a), four males had calls equal to or lower than 200 Hz and five males had calls with frequencies equal to or greater than 260 Hz. In the 20 possible pairwise comparisons a female would never make a mistake; that is, if she chose the lower call she also selected the larger mate. If the female used 210 Hz and 250 Hz as the minimum difference, she would make a mistake with a probability of .06 in the 198 possible pairwise comparisons. Using the difference under which females did not discriminate, 220 Hz and 250 Hz, the probability of making a mistake in the 364 pairwise comparisons is .09.

These results further substantiate the

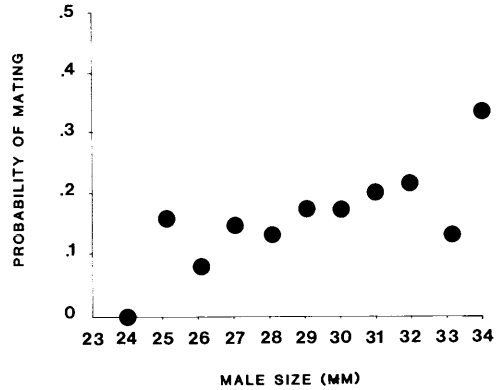


FIG. 4. The frequency of mating versus male size for 4,456 frog-nights in 1979 at Kodak Pond.

claim that females are capable of discriminating among males of certain sizes using the information in the chuck. It also shows that females fail to discriminate as the frequency difference between the calls, and thus the reliability of the information, decreases.

Male Contribution to Female Reproductive Success.—To analyze the influence of male size on female reproductive success, individual males and females were haphazardly paired and placed in small buckets in the laboratory where they mated, deposited eggs and constructed nests. Male size (MS), female size (FS), clutch size (CS), and the absolute value of the size difference between mates (MSD) were recorded. The mean female CS was 234.2 ($S = 97.6$, $N = 68$).

Although most eggs hatched successfully, examination of foam nests showed that this was not always the case; some nests had a large number of undeveloped eggs (Fig. 5). The mean number of undeveloped eggs per nest was 9.1 ($S = 11.4$). Large clutches were not more likely to have undeveloped eggs than small clutches ($r_s = .06$, $N = 68$, $P > .05$), and there also was no significant correlation between MS ($r_s = .11$, $P > .05$) or FS ($r_s = .08$, $P > .05$) and the number of undeveloped eggs. However, Figure 6 shows the relationship between MSD and the number of undeveloped eggs. As MSD increases, so does the mean (and the variance) number of un-

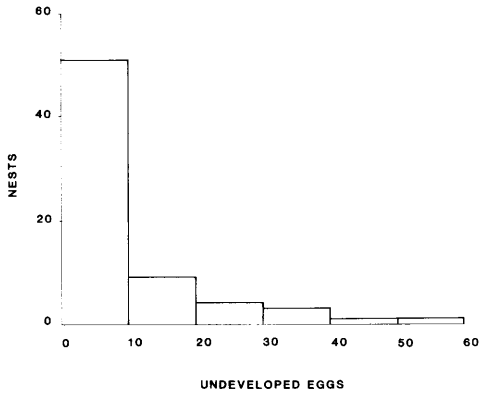


FIG. 5. The distribution of the number of undeveloped eggs per egg mass for 68 *Physalaemus pustulosus* egg masses used in the laboratory experiments.

developed eggs. There was a significant negative correlation between size difference of mates and number of undeveloped eggs ($r_s = .30$, $N = 68$, $P < .05$).

Female *P. pustulosus* usually are larger than males (see below). Therefore, MSD was correlated with both MS ($r_s = -.59$, $P < .01$) and FS ($r_s = .44$, $P < .01$) in the expected directions. Since CS is correlated with FS ($r_s = .54$, $P < .01$), CS is also correlated with MSD ($r_s = .29$, $P < .05$). Although only MSD was correlated with the number of undeveloped eggs, it was desirable to consider the effect of these inter-related variables in concert, and especially after the variability explained by MSD was taken into account. The effect of MS, FS and CS was considered before and after the variability explained by MSD was considered. Because the number of undeveloped eggs per nest was distributed

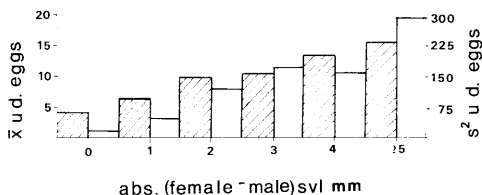


FIG. 6. The relationship between absolute size difference between mates and the mean (striped bars) and variance (open bars) of unfertilized eggs per mass.

TABLE 2. Results of multiple regression determining the influence of male size (MS), female size (FS), clutch size (CS), and the absolute value of size difference between mates (MSD) on the number of undeveloped eggs.

$R^2 = .22$				
	df.	s.s.	F	P
Regression	4	39.99	4.54	<.005
Residual	63	138.63		
S.S. explained by variables in the order listed				
	df.	s.s.	F	P
Regression	4	39.99		
MS	1	2.26	1.03	>.100
FS	1	2.25	1.02	>.100
CS	1	1.55	0.70	>.100
MSD	1	33.93	15.41	<.005

in a Poisson-like manner, the data were transformed by square root (Steele and Torrie, 1960).

The results of the multiple regression indicate that the variables considered in the order MS, FS, CS and MSD are similar to the results of the simple Spearman rank correlations (Table 2); only MSD explains a significant amount of the variability in the number of undeveloped eggs. (The specific order of MS, FS, and CS does not affect the interpretation.)

The number of eggs lost due to MSD is only a small part of the total clutch (mean egg loss = 4% of mean clutch size), and FS is correlated with CS. Therefore, most of the variability in eggs developed is explained by CS or FS. But after the influence of CS on the number of eggs developed is taken into account, MSD, but not FS or MS, does account for a significant amount of the variability in reproductive output (Table 3). Thus MSD significantly influences both the loss of reproductive output (i.e., number of eggs undeveloped) and the total reproductive output (i.e., number of eggs developed) of the pair.

In the field pairs often nested communally, so it was not possible to determine how many pairs contributed to a single nest without observing the nesting. I determined whether the proportion of undeveloped eggs observed in the laboratory reflected the natural situation, rather than

TABLE 3. Results of multiple regression determining the influence of male size (MS), female size (FS), clutch size (CS) and the absolute value of size difference between mates (MSD) on the number of eggs that developed.

$R^2 = .98$				
	<i>d.f.</i>	<i>s.s.</i>	<i>F</i>	<i>P</i>
Regression	4	6,414,551.4	5,829.3	<.005
Residual	63	6,932.7		

<i>S.S. explained by variables in the order listed</i>				
	<i>d.f.</i>	<i>s.s.</i>	<i>F</i>	<i>P</i>
Regression	4	641,451.4		
CS	1	639,489.2	5,811.4	<.005
MS	1	151.6	1.4	>.100
FS	1	62.7	.6	>.100
MSD	1	1,748.0	15.9	<.005

an experimental artifact, by comparing the proportion of undeveloped eggs from nests in the field to the observed proportion in the laboratory. Of the 3,576 eggs observed in ten nests from the field (again the number of nesting pairs was not known), the proportion of undeveloped eggs was .05, while .04 of the 15,929 eggs in the laboratory experiments were undeveloped. This suggests that the results observed in the laboratory were not due to an experimental artifact.

Females usually are larger than males (Fig. 7). Thus for most females, choice of larger males will reduce egg loss by minimizing the size difference between them and their mates. However, smaller females might actually increase egg loss by choosing larger males.

I measured the size of the male and female for 65 pairs from Kodak Pond. I then determined whether females were mating assortatively with respect to size; and especially if smaller females were avoiding the larger males in an attempt to minimize the size difference between them and their mates. There was no significant correlation between the size of mated males and females ($r = -.10$, $N = 65$, $P > .05$). I also divided males and females into small, medium and large size classes (Fig. 8). These data were analyzed by contingency table and the results show that females were assorted randomly with respect to size

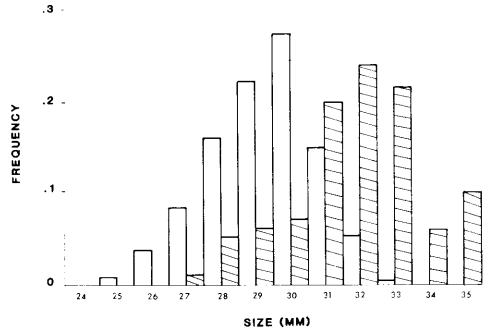


FIG. 7. The frequency distribution of male (open bars) and female (striped bars) *Physalaemus pustulosus* sizes at Kodak pond in 1979.

among the mated male population ($\chi^2 = 2.56$, $d.f. = 4$, $P > .75$). This was also true if small ($\chi^2 = .54$, $d.f. = 1$, $P > .75$), medium ($\chi^2 = .54$, $d.f. = 1$, $P > .75$), or large size classes ($\chi^2 = 1.48$, $d.f. = 1$, $P > .25$) were considered separately (Fig. 8). Analysis of female response during playback experiments also failed to yield any trend suggesting that a female's size influences her choice of mates.

DISCUSSION

Female Choice and Male Mating Success.—Although it cannot be assumed that a male was not breeding when he was ab-

TEST OF ASSORTATIVE MATING BY SIZE

		MALE SIZE (MM)		
		26-27	28-29	30-32
FEMALE SIZE (MM)	33-35	4 3.2	15 12.8	7 10.0
	30-32	3 3.7	13 14.3	13 11.2
	27-29	1 1.2	4 5.0	5 3.9

FIG. 8. The observed and expected (given random assortment of mated males and females) number of matings among size classes of *Physalaemus pustulosus*.

sent from Kodak Pond, based on the data from Kodak Pond we probably can assume that a male's mating success increases with the number of nights he spends at the breeding site. The importance of this phenomenon to female choice has several interpretations. The first is that on any given night a female is presented with a random sample of the male population. If this is true, then the fact that males spending more time at the breeding site mate more has little evolutionary consequence.

However, it is possible that this might act as a screening mechanism for males from which females choose. Predation is quite intense at some *P. pustulosus* choruses (Ryan et al., 1981; Tuttle and Ryan, 1981). Males possess a variety of evasive behaviors that should reduce their predation risk (Tuttle et al., 1982). Obviously, males that spend more time at the breeding site are those that have been able to avoid predation. Also, Bucher et al. (1982) showed that reproductive behavior is an energetically expensive venture for *P. pustulosus*. The mean rate of oxygen consumption for a noncalling male at the breeding site is 1.33 times the nocturnal resting rate, and for a calling male is 2.13 times the resting rate. For the successful male, the energetic cost is even higher; 2.87 times resting for the approximately 1 h of nest construction. (Ryan et al., in press). It is assumed that males at the breeding site also have been able to meet the energetic demands of reproductive behavior, although the corollary need not be true.

If avoidance of predators and energy requirements influence the number of nights a male spends at the breeding site, then females are selecting males from a subpopulation that has been better able to avoid predators and find and process food. Of course, there must be a large stochastic component to not being eaten and finding food—and food might not be a limiting resource. However, to the extent that there is a heritable genetic component to these activities, and that food is limiting, then females might be selecting mates from a

subpopulation of males which are, in some ways, better adapted to the environment.

Alternative Male Mating Strategies.—Male *P. pustulosus* did not adopt noncalling, satellite mating strategies. This might be expected of smaller males, given the high energy and predation costs of advertising and the size-dependent mating success. But reduction in the costs of sexual advertisement is adaptive only if there is a less than proportional decrease in the benefits—the likelihood of attracting a mate. Female choice must be a powerful selection force in this species since it causes males to produce call types that increase their predation risk. Ryan et al. (1982) showed that a whine plus chucks is more likely to attract the bat *Trachops cirrhosus* than a whine only. Isolated males produce calls with only a whine, but add chucks in response to vocal competition from other males, and females are preferentially attracted to calls with chucks (Rand and Ryan, 1981). Perhaps other female behaviors, such as the ability to avoid noncalling males, provide selection against noncalling strategies. Another, and perhaps more important, factor is that although large males are more likely to mate, small males do acquire mates as well, as shown in Figure 4 (see Ryan et al., 1981, for a detailed discussion of this point).

Sexual Selection and the Advertisement Call.—Larger males at the breeding site were more likely to be chosen by females, and female choice based on differences in the chuck explains some of this variance in male mating success. Do females use other cues to assess male size?

A number of call characteristics were measured but only the fundamental frequency of the chuck was correlated with male size (Ryan, 1980a). Call intensity is one trait that has been shown to correlate with male size in some anurans (Gerhardt, 1975), but it did not in this study. This might be because calls were measured in a variety of habitats under different weather conditions. Both habitat types and microclimatic events affect call attenuation (Morton, 1975; Wiley and Richards,

1978), and this is precisely why we would not expect intensity to be a good predictor of male size.

Spectral properties of the advertisement call can be negatively correlated with male size both among (Martin, 1972; Duellman, unpubl.) and within (Zweifel, 1968; Davies and Halliday, 1978) species, although this is not always the case (Zweifel, 1968). There was a significant correlation between size and frequency for *P. pustulosus* ($r = -.53$, $P < .01$; Ryan, 1980a), but size only explains 28% of the variation in frequency. The data show that when comparing extremes, the chuck provides very reliable information about male size, but as the frequency difference between calls being compared decreases, so does the reliability of the information. At a 30 Hz interval females did not discriminate. It is not clear whether females are not capable of making this discrimination or, given the reliability of the information, the choice would not be meaningful. But choice based on the chuck does explain some of the variability of male reproductive success. I do not suggest that females are not using additional cues to assess male size or that females are not also basing their choice on additional male characters besides size.

It is difficult to test the hypothesis that sexual selection has influenced the evolution of a species' sexual display. But it is interesting to note that this species is the only anuran known to date where a signal functioning in conspecific mate attraction, the chuck, has been uncoupled from the species' recognition signal, the whine (Ryan, in press). The vocal morphology which allows production of the chuck also appears to be unique among anurans (Drewry et al., 1982).

The Adaptive Significance of Female Choice.—Benefits obtained by females from their mates can be of two sorts: those affecting the genetic quality of their offspring, and those affecting their immediate reproductive output. Trivers (1972) suggested that all things being equal, females should select older males because they have demonstrated their ability to

survive. He also suggested that females should select males with faster growth rates because they have demonstrated their resource accrual ability (Trivers, 1976). Larger male *P. pustulosus* are either older or they have grown faster. To the extent that there is a heritable genetic component to growth and survival, these benefits will be passed on to offspring of both sexes. The daughters will benefit because of the correlation between female size and the number of eggs per clutch. Sons will have a higher probability of attracting mates if they are larger. The suggestion that females increase the genetic quality of their offspring through conspecific mate choice is controversial (e.g., Maynard Smith, 1978; West Eberhard, 1979; Lande, 1980, 1981; O'Donald, 1980), and the data needed to evaluate this hypothesis for *Physalaemus* are not available.

A female's mate choice directly, although only slightly, influences her reproductive output. Fertilization and nesting are more elaborate for *Physalaemus* than for most other anurans, and also are energetically demanding (Ryan et al., in press). Perhaps having mates of close to the same size affords some mechanical advantage during nesting (see Davies and Halliday, 1977, for a similar suggestion). But it is not known why small females do not choose mates "optimally" by avoiding larger males.

SUMMARY

The reproductive behavior of a neotropical frog, *Physalaemus pustulosus* (Leptodactylidae), was studied from 1978 to 1980 on Barro Colorado Island, Panama. Males called from small pools of standing water. They maintained individual distances but did not defend an oviposition site. The females entered the breeding site and appeared to select a mate by making physical contact. There was no noncalling strategy among males.

Among the males at the breeding site, larger males were more likely to be chosen as mates. There was a negative correlation between male size and the frequency of

one of the advertisement call components—the chuck. Playback experiments showed that in certain comparisons females were able to choose larger males based on information contained in the chuck. As the frequency difference between the calls decreased, so did the reliability of the information about male size, and the female's ability to discriminate these differences. This suggests that female choice based on chucks explains some of the variability in male mating success.

Females received benefits from choosing larger males. The number of undeveloped eggs per clutch increased with the size difference between a female and her mate. For most females in the population choosing larger males would increase their immediate reproductive output because it decreases the size difference between a female and her mate.

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