

# Female choice of large males in the treefrog *Hyla chrysoscelis*: the importance of identifying the scale of choice

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**Summary.** In this study, I detected the presence of female choice for larger males in the treefrog *Hyla chrysoscelis*. Mated males were larger than unmated males at the scales females could have assessed males: local groups (males found within 2 meters of a mated pair) and the nightly chorus. In addition, females were observed to initiate amplexus with the larger males in local groups. Mated males were larger than unmated males for two of the four seasons studied. Seasonal mating success was also analyzed with a multiple regression model that included size and chorus attendance (nights spent at the breeding site). The partial selection coefficients, which represent the relative magnitude of directional selection, were significant for size in only one season and for chorus attendance in all four seasons. Therefore, there are two possible advantages to being a large male: increased likelihood of obtaining a mate due to female preference, and increased likelihood of mating even if no female preference because of a greater number of opportunities to obtain a mating if matings occurred at random.

## Introduction

Recent theoretical and empirical studies have focused on the methods of measuring selection (e.g. Arnold and Wade 1984; Lande and Arnold 1983; Koenig and Albano 1986), however, it is equally important to be able to detect the mechanisms behind selection (Endler 1986). One reason for identifying the mechanisms of selection, as well as understanding how they interact with one another and other influential factors (e.g. operational sex ratio),

is that this information can aid in predicting the conditions under which selection will be operating.

Anurans have been studied extensively in relation to sexual selection. Both male-male competition and female choice have been identified as mechanisms that effect selection on male body size in anurans (see Howard and Kluge 1985). However, separating the effects of these two components of sexual selection can be difficult, and therefore their relative importance is often not determined. Using the pattern of mating success (size-dependent mating success versus size-assortative mating success) to infer which mechanism is operating has been discredited in anurans (Arak 1983a). Instead, intensive field observations of individual males and females prior to mating can be used to indicate the influence these two mechanisms have on mating success (see Howard 1988). The behaviors that have been attributed to male-male competition include males seeking out and initiating amplexus with females and males displacing one another from amplexus. Behaviors that suggest female mate choice include females moving freely through a chorus of males and initiating amplexus with certain types of males.

In this study I examined the influence of female choice on male mating success in the treefrog *Hyla chrysoscelis*. *H. chrysoscelis* is a particularly good species to study in relation to female choice as the males do not defend resources (e.g., Fellers 1979), and so it is impossible to confuse female choice based on a male's resource with choice based on a male's phenotype. While many different male characters could influence male mating success, I elected to measure male size and chorus attendance (the number of nights a male spends in the chorus). In several species of anurans these two characters have been shown to influence male mating success (male size: Davies and Halliday 1979; Wells 1979;

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Howard 1980; Ryan 1980; Fairchild 1981; Gatz 1981; Robertson 1986; chorus attendance: Greer and Wells 1980; Kluge 1981; Woodward 1982, Arak 1983 b, Godwin and Roble 1983, Ryan 1983).

Behavioral observations of males and females prior to mating can be used to identify the scale at which female choice is acting. If females spend only one night assessing all available males, females have assessed males at the nightly scale, but not at the seasonal scale. The criteria for female choice is best detected by comparing mated and unmated males at the same scale females assess males. Therefore, to examine the criteria for female choice and the extent to which choice resulted in a mating advantage for the males of choice, I used behavioral observations to identify the scales at which female choice was acting, and then compared mating success data analyzed at three scales over four breeding seasons. The first two scales, local groups of males (males found within 2 m of a mated pair) and the nightly chorus, are scales at which females could assess males. The third scale of analysis compares mated and unmated males over a breeding season; this scale is often used in estimating phenotypic selection (Arnold and Wade 1984).

## Methods

I studied two populations of the gray treefrog, *H. chrysoscelis*, in central Indiana. Pond #1, located 11.5 km east of Bloomington, Indiana, was approximately 40 m in diameter, bordered on one side by pines and on the other side by open field. A small pond, located 1 km from the study pond, was checked periodically throughout the breeding season. Two or three males called at this second pond, but were not males that had been marked at the study site. No other choruses of *H. chrysoscelis* were known to occur within 10 km of this pond. Pond #1 was observed from April 28th to July 5th 1984. An alternate study site was selected in 1985, because no frogs bred at Pond #1. Pond #2, located in Yellowwood State Forest (23 km east of Bloomington, Indiana), was approximately 20 m in diameter and completely surrounded by trees and shrubs. The closest chorus of *H. chrysoscelis* to Pond #2 was 2.5 km. Pond #2 was observed from 3 June to 30 June 1985, 7 May to 16 June 1986 and from 5 May to 2 July 1987. The observation periods in 1984, 1986 and 1987 reflect fairly accurate estimates of the length of the breeding seasons, as the study sites were checked for several weeks before and after males were observed calling. In 1987, however, 2 males were known to call from Pond #2 near the beginning of August, and one clutch of eggs was observed. The 1985 observation period represents only a portion of the breeding season, as the first few weeks were spent searching for a new study site.

I marked each individual male by tying a small numbered tag around the waist, and recorded snout-vent length (SVL) to the nearest 0.1 mm. Females were marked with different colors of embroidery floss in 1984 and 1985, and toeclipped with a different number code for each night in 1986 and 1987. I also mapped the location of each male's call-site and noted the number of times each male was found in amplexus.

As a first step in separating the effects of female choice from male-male competition, I observed the movements of females through a chorus of males before amplexus, and I observed both natural and experimental initiations of amplexus. For the experimental initiations, I removed females from amplexus and released them near a group of two or more calling males. Each female was released in a position approximately equidistant (50 cm) from all males within the group, and the behavior of the female and males observed until one of the males was in amplexus with the female. I also checked amplexed pairs periodically throughout the night, up until the time that the eggs were fertilized, to determine if males were being displaced from amplexus.

Statistical analyses were performed using Statistix version 1.1 and Systat statistical package (Systat, Inc., Evanston, Illinois). The data were standardized for the multiple regression analysis.

## Results

### *Chorus Organization*

Males congregated at the ponds and called from sites located in the trees or on the ground surrounding pond #1, and from the branches of small shrubs surrounding pond #2. Calling began soon after dusk and continued until approximately 2400 h. In 1984, I marked 163 males over 45 nights of calling. Males spent an average of 1.75 nights at the pond (range=1–14 nights;  $s=1.76$ ), for a total of 285 frog-nights (see Ryan 1983). In 1985, I marked 64 males over 8 nights of calling. Males averaged 1.47 nights at the pond (range=1–5;  $s=0.78$ ), for a total of 94 frog-nights. In 1986, 91 males were marked over 18 nights and males averaged 2.1 nights at the pond (range=1–9;  $s=1.5$ ), totalling 190 frog-nights. In 1987, 157 males were marked over 14 nights and males averaged 2.56 nights at the pond (range=1–12;  $s=2.56$ ), totalling 402 frog-nights. There were more males than females at the ponds each night for all four years. The number of males at the pond on a given night was positively correlated with the number of females (Spearman rank correlation,  $r=0.514$ ,  $n=85$ ,  $P=0.01$ ). Nightly operational sex ratios (OSRs=number of receptive females/number of males, Emlen & Oring 1977) ranged from 0.05 to 0.82, with an average for all four years of 0.22 ( $s=0.23$ ,  $n=45$  nights). Amplexus lasted up to five hours, and no male was observed to mate more than once per night.

The call-sites of individual males changed more often among than within nights. While 81% of the males were within 2 m of the same call-site for all observations on the same night, only 49% of the males observed on more than one night used the same call-site on the second night. In addition, pairs did not start moving towards the pond to

deposit eggs until several hours after the initiation of amplexus. Amplexed pairs were found in the same site throughout several rounds of observations (1–2 h). Therefore, even if the amplexed pair was not found immediately after formation, it was reasonable to assume that the males calling in the area surrounding the amplexed pair were also present at the time amplexus was initiated.

#### *Scale of choice*

Most females mated the night they arrived at the pond and were first observed after they had joined with a male in amplexus. However, in 14 cases (3 in 1984, 2 in 1985, 3 in 1986, and 6 in 1987), I found females prior to amplexus. Twelve of these females were later found in amplexus in the same area (mean area = 1.6,  $s = 1.5$ ) on the same night. Two females (1987) were not found in amplexus until the following night. Based on these observations, it is reasonable to assume that female choice occurred at the scale of local groups or between local groups within a night, but that females, in most cases, could not have assessed males across nights.

#### *Initiation of amplexus*

The initiation of amplexus was observed 28 times throughout the study. Fourteen of these matings were experimental. Females approached males and initiated amplexus more often than males, and they more often chose the larger male available at the local scale (Table 1). The larger male mated in three of the six cases where the male initiated amplexus. Initiation of amplexus by males occurred only after the female remained within three to four cm of the male for four to five minutes. The female's prior close proximity to these males suggests that even when males initiated amplexus some degree of female choice may have occurred.

In three of the 28 observations of the initiation of amplexus (two natural and one experimental in 1985), a nearby calling male jumped on top of the pair during the initiation of amplexus. The second male displaced the male the female had contacted in one of these cases. However, once a male was observed to fully achieve amplexus (arms locked), he stayed in amplexus with the same female throughout the observation period.

I did not observe satellite male behavior in 1984 or 1986. Satellites were observed four times (out of 94 frog-nights) in 1985, and 6 times (out of 402 frog-nights) in 1987. A male was classified as

**Table 1.** Observations of the initiation of amplexus

	Mated Male Larger		Mated Male Smaller	
	Male init.	Female init.	Male init.	Female init.
1984	1	3	2	0
1985	1	3	1	2*
1986	0	3	0	0
1987	1	7	0	4
<b>totals</b>	<b>3</b>	<b>16</b>	<b>3</b>	<b>6</b>

\* Includes case in which female initiated amplexus with larger male, but smaller male mated (see text). Females initiated amplexus significantly more often than males (22 out of 28, Sign Test,  $P < 0.003$ ), and significantly more often with the larger male (17 out of 22, Sign Test,  $P < 0.01$ )

a satellite if he was observed to be within 10 cm of a calling male, not calling for a period of 5 min, and using a low posture (see Perrill et al. 1978). All males that displayed satellite behavior were also observed calling at some other time during the study. In 1987, the average SVL for the 5 males that used satellite behavior was 39.8 mm, which is significantly less than the average SVL for all males in 1987 (mean = 43.6 mm,  $s = 3.3$ , two-tailed  $t$ -test,  $t = 2.9$ ,  $P = 0.02$ ).

#### *Male mating success*

For the local group analysis, I compared the size of mated males to the average size of the unmated males found within two meters. The distance of two meters was selected based on the average distance females moved through the chorus before amplexus. Not all mated males provided information relevant to this analysis because the analysis required a mated male to be within 2 meters of at least one unmated calling male. Males not used in this analysis were either calling alone or in a group where all males mated. Over all four years, the mated male was larger than the average unmated male in his local group in 47 out of 67 groups (Sign Test,  $Z = 3.3$ ,  $P < 0.001$ ). Mated males were larger than their unmated neighbors significantly more often in 1984 and 1987, but not in 1985 or 1986 (Table 2).

Mated males were larger than unmated males within a night. Over all four years, females were found at the ponds on a total of 45 out of 85 nights. On 29 out of 35 nights, the average size of mated males was larger than the average size of unmated males (Sign Test,  $Z = 3.7$ ,  $P < 0.001$ ). The average size of mated males was the same as the average

**Table 2.** Comparison of the size of mated and unmated males by season and across three scales

	1984			1985			1986			1987		
Fine-grained Spatial												
<i>mated smaller</i>	2			3			9			6		
total pairs	11			11			21			24		
Binomial Probability	0.03			0.08			0.44			0.01		
Nightly												
<i>mated smaller</i>	2			1			6			0		
total nights	9			6			11			11		
Binomial Probability	0.07			0.09			0.23			0.0005		
Seasonal												
	1984			1985			1986			1987		
	Mean	s	N	Mean	s	N	Mean	s	N	Mean	s	N
Mated	42.3	3.1	35	43.9	2.0	16	45.0	3.4	29	44.3	3.0	48
Unmated	41.7	2.8	112	42.6	2.7	50	44.3	3.1	65	43.3	3.4	109
T-Test	1.08			1.78			0.98			1.76		
P	0.15			0.04			0.18			0.04		

**Table 3.** Selection gradients, standardized partial B ( $\pm$ SE), for male size and nights spent in chorus with relative mating probability

Year	1984	1985	1986	1987
Size	-0.003 (0.007)	0.02 (0.01)	0.01 (0.06)	0.04* (0.02)
Nights	0.04** (0.007)	0.03** (0.01)	0.29** (0.06)	0.11** (0.02)
n	146	66	91	157
Multiple R <sup>2</sup>	0.17**	0.14**	0.24**	0.27**

\*  $P < 0.05$ ; \*\*  $P < 0.01$ 

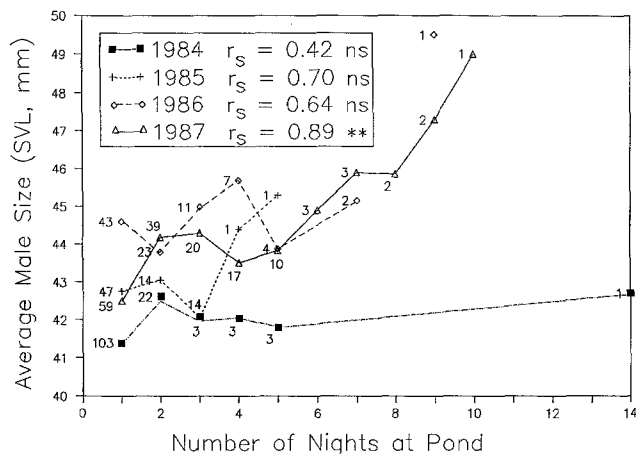
size of unmated males (within 0.1 mm) on ten nights. When the nightly data are analyzed for each season separately, mated males were larger than unmated males on significantly more nights only in 1987 (Table 2). The nightly analysis for 1984 and 1985 and the local group analysis for 1985 do not show a significant advantage for large males. However, sample sizes were small and the  $P$  values are only marginally nonsignificant in these three tests. Therefore, these results still lend some support to the hypothesis of a large-male mating advantage at these scales of analysis.

The seasonal mean sizes for unmated and mated males were compared with a one-tailed students t-test. The average size of males that mated was significantly larger than that of unmated males in 1985 and in 1987, but not in either 1984 or 1986 (Table 2). I compared relative mating success

for each male in a multiple regression that included the two factors suspected to influence mating success: body size and chorus attendance. The standardized partial selection coefficients (Arnold and Wade 1984) for each season are shown in Table 3. These coefficients represent the relative magnitude of directional selection while holding the other measured trait constant, thus controlling for correlations between traits (Lande and Arnold 1983). The effect of large male body size on male mating success was only direct in 1987. Chorus attendance, however, was under direct selection in each year, with the relative magnitude of its effect being greatest in 1986 when no size-related advantage was detected.

The number of nights a male spent at the pond was significantly correlated with male size in 1987, but not in any of the other seasons (Fig. 1). It is not known why large males attended the chorus more often, nor if males were moving between choruses during the season. However, this correlation suggests that at least in 1987, chorus attendance may have indirectly selected for male size.

A large-male mating advantage was detected at the scale of local groups but not in the seasonal scale of analysis for the 1984 breeding season (Table 2). The discrepancy between these two results stems from the use of a subset of the seasonal data by the local group analysis. In 1984, 64% of the observed matings took place on one night, when the operational sex ratio (OSR) was higher than average (0.52 females/males) and it was fairly com-



**Fig. 1.** Average male size (SVL) by the number of nights found at the pond. The total number of males found on a given number of nights is shown. Spearman Rank correlation coefficients are given for each year (ns = non-significant, \* =  $P < 0.05$ , \*\* =  $P < 0.01$ ). The overall Spearman Rank correlation (all four years combined), was significant ( $r_s = 0.56$ ,  $P < 0.01$ )

mon for mated males to only have other mated males as close as two meters. These matings could not be included in the local group analysis, but were included in the seasonal analysis. Mated males with unmated neighbors (42.9 mm,  $s = 3.05$ ,  $n = 11$ ) were larger than mated males with mated neighbors (41.1 mm,  $s = 3.29$ ,  $n = 12$ ;  $t = 1.43$ ,  $P = 0.08$ ), which can account for the detection of the large-male mating advantage in the local group analysis but not the seasonal analysis.

I compared the size (SVL) of males and females from all pairs found in amplexus to determine if size-assortative mating could have influenced mating patterns. Correlations between the body sizes of these pairs were not significant for any of the four years (all  $P > 0.10$ ).

## Discussion

In this study, female choice for larger males could be detected even when an overall male size advantage could not. Mated males were larger than unmated males at the scales females could assess males, and females were observed to initiate amplexus with the larger male in local groups. However, the female preference for large males resulted in net selection for large males in only one out of four study periods. Because size reflects age as well as growth rates in anurans, the comparison of the size of mated and unmated males is not a strict measurement of phenotypic selection within a cohort. However, there was an episode of selection on male size, which will only result in evolution of male body size if there is a heritable compo-

nent to size and the selection across cohorts reflects similar selection within a cohort. In addition, I have not identified the factors responsible for the between season variance in selection on male size, but suggest that both operational sex ratio and the correlation between male size and chorus attendance warrant further investigation.

Male-male competition can take several different forms in anurans. However, neither of the two forms of male-male competition that were observed in this population could account for the large-male mating advantage. Displacement during the initiation of amplexus was not common enough to influence observed mating patterns, and males that behaved as satellites were usually smaller males, which would only dilute a large-male mating advantage. Therefore, my observations suggest that females had the opportunity to choose a mate, and when the initiation of amplexus was observed, chose a larger than average male from within a local group.

The mechanism by which females choose larger males was investigated for this population of *H. chrysoscelis* during the 1987 breeding season by Morris and Yoon (1989). We showed that females preferred to approach the lower frequency calls of large males over the higher frequency calls of small males when all other call characteristics were held constant. The degree of female preference for the low frequency calls was great enough to account for the large-male mating advantage detected at the scale of small groups. This provides further evidence that female choice is important in producing the large-male mating advantage.

Wittenberger (1983) stresses the importance of understanding the tactic by which females choose their mates before the criterion for choice can be identified. Because males in most anuran species aggregate into choruses during the breeding season, females could assess all males in the chorus before making their choice. Some anuran studies have included observations of unmated females moving through a chorus past several calling males before initiating amplexus (Ryan 1985; Howard 1978). In comparison, the limited movement of *H. chrysoscelis* females once they arrive at the pond, suggests that females assess only a few males at the pond before choosing a mate. Both Wells and Schwartz (1984) for *H. ebraccata* and Gerhardt et al. (1987) for *H. cinerea* have noted that females behave similarly to *H. chrysoscelis*, in that once at the pond, females do not appear to move through the chorus of males. Further observations of females approaching a chorus are needed to determine if the scale of female choice in *H. chrysos-*

*celis* involves a choice between local groups of males as they approach the pond or only among males in local groups. In addition, it would be useful to determine if the number of males assessed varies in relation to density or OSR. However, the results of this study stress the importance of information about the tactics of mate choice to understanding female mate choice as a selective agent.

Males increased their mating success through chorus attendance for every season of this study. In *H. chrysoscelis*, male-male competition is used to maintain distance between calling males, but call-sites do not appear to be limiting (Fellers 1979, personal observation). Therefore, it is most likely that chorus attendance does not reflect male-male competition over call-sites. More information is needed, however, to determine why some males spend more nights than others at the breeding site, and to determine whether males move between breeding sites. The possibility that males moved from one chorus to another makes it difficult to interpret correlations between chorus attendance and male characters, but does not jeopardize the interpretation of chorus attendance influencing male mating success. Because chorus attendance explained a significant portion of the variance in mating success, mating success does not reflect the effects of female choice alone. The relative magnitude of the importance of chorus attendance, as measured by the partial correlation coefficients, varied from 0.03 to 0.29 between seasons. This suggests that between seasons, other variables can strongly influence the impact chorus attendance will have on male mating success.

Life history theory predicts that when there is lower reproductive success for smaller, younger males, selection will favor males that reduce reproductive effort (Pianka and Parker 1975). Assuming that small males are not more likely to move to another chorus, the significant correlation between body size and number of nights spent at the chorus in 1987 suggests that small males may be facing a tradeoff between growth and reproductive activity. A negative correlation between calling effort and growth rate among small males has been demonstrated for the anuran *Rana virgatipes* (Given 1988). The data from the 1987 breeding season adds further support to this theory. Smaller males, with a lower mating success at every scale of analysis, spent fewer nights at the breeding site.

The large-male mating advantage was detected at the scale of local groups, but did not result in an overall large-male mating advantage in the 1984 breeding season. One possible explanation is that a high OSR on the night when most of the breeding

took place, diluted the effect of female choice. The effect of OSR on mating behavior has been discussed in several studies (e.g. Trivers 1972; Emlen and Oring 1977; Howard and Kluge 1985), however the interaction between OSR and the scope of female choice has not previously been discussed.

It is obvious that a large-male mating advantage, irrespective of the mechanism, must disappear whenever the OSR is so high that all males mate. If females assess all available males and make the correct choices, a high OSR would dilute the effect, but mated males should still be larger than unmated males. However, if females limit their choice to a subgroup of the population of males (e.g. local groups, only males in the chorus the night they breed) then in some situations, a high OSR could negate the effect of female choice. From this hypothesis, one would predict that the larger males in a local group should mate first. Unfortunately, this information was not collected in this study as the matings occurred too rapidly on the night with the high OSR in 1984 to collect accurate enough times for comparison.

Problems can arise in relation to understanding the mechanisms involved in selection when selection fluctuates in intensity or direction. If mated and unmated males do not differ for some characteristic at the seasonal scale, this does not necessarily demonstrate that females do not prefer males with that characteristic. The seasonal scale of analysis combines the effects of many factors, including factors that can hide or dilute the effects of female choice (e.g. OSR). At the same time, showing that females prefer to mate with males that possess a certain characteristic is not sufficient to suggest that there will be selection for that character. Behavioral observations of both males and females aid in comparing the relative effects of male-male competition and female choice as well as determining the tactics of mate choice. In addition, more comparisons of mating patterns over several seasons are needed to shed light on the interaction between those factors influencing mating success (e.g. OSR, male density and scale of female choice), and the selection potential of female choice.

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