

Mate selection in *Litoria chloris* and *Litoria xanthomera*: Females prefer smaller males

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Abstract It is generally accepted that high quality males are those that succeed in male–male competition: in either aggression or rivalry to attract and be selected by females. Previous studies of amphibians have suggested that the main characters influencing male mating success include variation in call characteristics (e.g. call rate, call intensity), calling behaviour, body condition, age and chorus tenure. In the present paper, several of the characters influencing female mate choice (male body size, body condition, call rate, call frequency and chorus tenure) are investigated in two closely related, explosive breeding frog species *Litoria chloris* and *Litoria xanthomera*. Smaller males of both species are shown to be more successful than larger males and this success is attributed to the increased chorus tenure of smaller males in *L. xanthomera*. This increased chorus tenure was attributed to the lower total energy used per call by a small male calling at a higher frequency. Whether increased chorus tenure explains female mate choice in *L. chloris* is uncertain but is highly probable given the strong similarity between the two species in both ecology and call characteristics.

Key words: body condition, body size, call frequency, call rate, chorus tenure, frogs, male–male competition.

INTRODUCTION

Lek polygyny is one of the mating systems favoured by amphibians (Bradbury 1981) and occurs when males display and compete at a communal site to attract females (Bradbury 1977). Within the lek mating system, female mate choice is often the most important mechanism, as females have the opportunity to actively select a mate once they visit the lek (Bourne 1992). It is generally thought that winners of male–male competition are of superior quality and that it would be in the interest of the female to choose these males (Andersson 1994). Thus dominance *per se*, or traits reflecting it, is expected to be an important cue in female choice (Qvarnstrom & Forsgren 1998). Consequently, studies of the distribution of mating success among males in frog choruses typically seek to identify specific phenotypic attributes that confer a higher mating success on certain individual males (Dyson *et al.* 1998). Previous studies have reported phenotypic attributes influencing female choice that include variation in call characteristics (Forester & Czarnowsky 1985; Klump & Gerhardt 1987; Lopez & Narins 1991), call behaviour (Wells 1977), chorus tenure (Dyson *et al.* 1992; Murphy 1994; Bertram *et al.* 1996), body size (Wells 1979; Elmberg 1991) and body condition (Cherry 1993; Dyson *et al.* 1998).

Variation in acoustic characteristics and calling behaviour is presumed to be an important determinant of reproductive success in anurans (Lopez *et al.* 1988). Previous studies on mate choice in anurans report that females of many species exhibit preferences for certain call characteristics, for example faster call rates, higher call intensities and low dominant frequencies in conspecific males (Arak 1983, 1988; Ryan 1985; Wells 1988; Morris & Yoon 1989; Marquez 1995) with most female preferences being for call properties that involve high energy expenditure (Arak 1983; Sullivan 1983). Males that exhibit these specific call characteristics are thought to be more successful in obtaining mates than males that do not exhibit the specific characters.

Along with attracting mates, vocal interactions are used in many species to establish and maintain calling sites within leks and to maintain intermale spacing in choruses (Wells 1977; Arak 1983). Maintenance of intermale spacing may reduce interference between males, thus potentially enabling females to find males more easily as well as reducing the number of potential competitors by preventing nearby males from calling (Wells 1977).

Endurance rivalry or the ability to remain reproductively active at a lek or other mating site is favoured as it increases the number of matings (Andersson & Iwasa 1996). In other words, by increasing chorus tenure or the number of nights spent at the chorus during the breeding season, a male increases his chances of being chosen by a female (Gerhardt *et al.* 1987; Murphy 1994). As females tend

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to prefer calls with properties that involve high energy expenditure, for example longer calls or faster call rates, competition among males forces them to expend energy at rates incompatible with calling on many nights (Dyson *et al.* 1998). Consequently, males must make a trade-off between these substantial costs and the benefits of prolonged attendance (Dyson *et al.* 1998).

As anuran lek aggregations tend to be characterized by high densities and operational sex ratios skewed toward males, calling behaviour may be accompanied by active searching and struggling with conspecifics for the possession of females (Wells 1977). Males engage in 'scramble competitions' with several males wrestling in an attempt to displace the male most securely fixed to the females back. Larger male anurans are usually more successful in scramble competitions than smaller males because of their greater strength and/or endurance and therefore tend to experience higher mating success (Wells 1979; Olson *et al.* 1986; Telford & Van Sickle 1989).

The two species examined in the present study, *Litoria chloris* (Boulenger) and *Litoria xanthomera* (Davies, McDonald & Adams), are explosive breeders with breeding aggregations forming during or after heavy rain (Barker *et al.* 1995). Contrary to previous studies on explosive breeding anurans (Wells 1977; Howard 1980; Arak 1983; Elmberg 1991), smaller males of both species were consistently observed to be more successful than larger males in breeding congregations. Consequently, we investigated female mate choice and the male characteristics influencing mating success in these two species.

METHODS

Study species

The southern orange-eyed tree frog, *L. chloris* is a moderately large arboreal frog (snout-urostyle length, (SUL): females 58–68 mm, males 54–62 mm) that is associated with coastal rainforest or wet sclerophyll forest and has a scattered distribution along the Queensland–New South Wales coast between Proserpine and Sydney (Barker *et al.* 1995). Males usually call between October and March, with a peak in activity between November and February (Davies & McDonald 1979; pers. obs.). Calling, amplexus and oviposition occur in flooded areas or in shallow pools in or beside rainforest streams (Barker *et al.* 1995).

The orange-thighed frog, *L. xanthomera*, also an arboreal species, is smaller than *L. chloris* (SUL: females 43–55 mm, males 40–56 mm), and is associated with dense rainforest between Cooktown and Townsville in north Queensland (Barker *et al.* 1995). Calling,

amplexus and oviposition also occur in flooded areas or shallow pools in or beside rainforest streams (Barker *et al.* 1995; Hero & Fickling 1997).

Field methods

Litoria chloris

Four sites in south-east Queensland, Australia, were surveyed at 2–3 week intervals between September 1997 and April 1998 and between September 1998 and April 1999 (Mundora 28°13'28S, 153°17'02E; Austinville 28°10'35S, 153°18'22E; Currumbin 28°14'23S, 153°20'53E; Natural Bridge 28°13'58S, 153°14'36E). The SUL, weight and breeding condition (e.g. calling male, gravid female, amplexant, etc.) of all *L. chloris* individuals found along a 200 m transect were recorded. Weight was measured to the nearest 0.5 g by using a Pesola 100 g spring balance, while SUL was measured to the nearest 0.1 mm by using Vernier calipers. If amplexant pairs were not already in the process of laying eggs (majority of pairs found out of water), they were separated, measured and weighed and then released together back into the field. In the one case where they were in the process of laying eggs, they were left undisturbed until they had finished, at which time they were weighed, measured and released.

Litoria xanthomera

One site was surveyed at a disused quarry 2.6 km west of Paluma in north-east Queensland, Australia (19°00'S, 146°10'E). This site was monitored for the duration of the wet season (103 of a possible 139 nights) between 10 November 1995 and 27 March 1996. Nights when the chorus was not surveyed corresponded with unfavourable weather conditions (i.e. hot and dry for several days). All animals captured were weighed to the nearest 0.2 g by using a Pesola 50 g spring balance and SUL was measured to the nearest 0.1 mm by using Vernier callipers. The breeding condition of each individual was also recorded. Amplexant pairs were dealt with in the same way as reported for *L. chloris*.

All individuals were given a unique toe clip code, which facilitated the identification of recaptured males and allowed calculation of chorus tenure (number of nights spent at chorus of 103 nights surveyed) for each individual male.

Call recordings and analyses

Calls were recorded for *L. xanthomera* only. In the 1995/1996 season, at least three calls from each of 52

males were recorded opportunistically by using a Sony WM-D6C professional stereo cassette recorder (tape speed 4.76 cm s^{-1}) with a Tandy Dynamic Highball-8 directional microphone. All recordings were made at a distance of 1 m from the frog by using a fixed recording level setting. Calls were digitized by using the Canary 1.1 bioacoustics package (Charif *et al.* 1991). Waveforms (energy *vs* time), spectrograms (frequency *vs* time) and power spectra (energy *vs* frequency) were generated for each recording.

The advertisement call of *L. xanthomera* (and *L. chloris*) consists of a number of 'moans' followed by a number of 'trills' (Barker *et al.* 1995; Fig. 1). Field observations by Smith (1996) suggest that the trill component of the calls is aggressive while the moan serves as a location advertisement for both species. Consequently, the present study focused on the moan component of each call. As the sound energy of the moan is concentrated at two dominant frequencies (lower = F1 and upper = F2; Fig. 2), values of F1 and F2 were recorded (temporal resolution $< 1 \text{ ms}$, frequency resolution $< 20 \text{ Hz}$) for each male. The call rate (number of moans s^{-1}) was determined from three calls of every male recorded and the mean used in statistical analyses.

Statistical analyses for field data

All data were tested for normality and equality of variances. A Komolgorov–Smirnov (KS) two-sample test was used to compare the observed distribution of male size classes found in amplexus to the distribution expected if size had no effect on mating success. The expected distribution was generated by multiplying the total number of males in each size class by the ratio for overall mating success (i.e. 43/175 for *L. chloris* and 23/129 for *L. xanthomera*).

The hypothesis that females select smaller males can also be tested on a nightly basis rather than a seasonal one (Ryan 1983). This may be more appropriate as it not only determines the males that were selected but also those that were not selected, thus allowing us to determine female preference. Female choice of smaller males was tested by comparing the size of each mated male to the median size of males present on that night (Ryan 1983). If females do not have a size preference then half the mated males should be larger and the other half smaller than the median size.

Female preference for male body size is not always absolute. Some species use male advertisement call frequency to select males that are a fixed proportion of

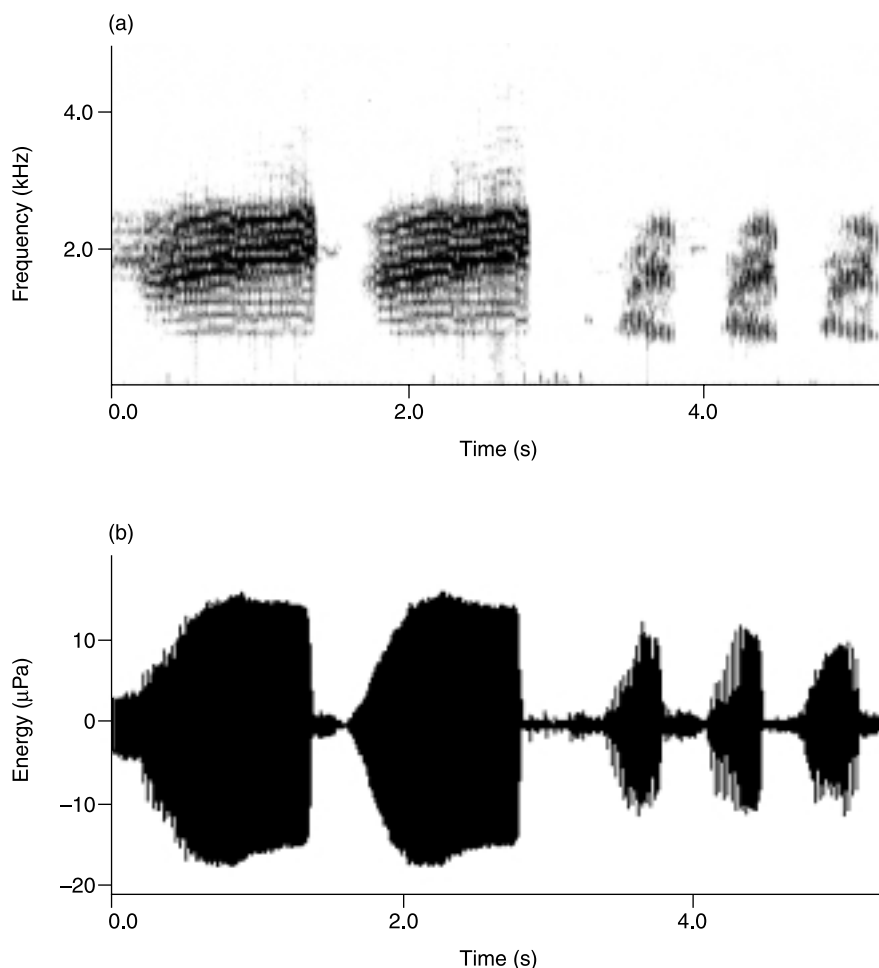


Fig. 1. (a) Sonagram and (b) waveform of two 'moans' followed by three 'trills' in the complex call of *Litoria xanthomera*.

their body length in order to maximize fertilization by optimizing cloacal apposition (Davies & Halliday 1977; Robertson 1986, 1990). To determine whether assortative mating was occurring, the ratio of male : female body size for each amplexant pair was calculated. A one-sample KS test was used to compare the observed cumulative distribution function to that of a normal cumulative distribution.

To test whether females mated with males that were in better condition, a condition index was calculated for each male. The linear residuals of a linear regression of the cube root of body mass on SUL were divided by the SUL to provide an index of weight condition relative to this length (see Dyson *et al.* 1998). Because of unequal variances, the condition of amplexant and non-amplexant males (for both *L. chloris* and *L. xanthomera*) were compared by using a Mann–Whitney *U*-test. A simple linear correlation between SUL and body condition was performed to determine whether there was a relationship between male body size and body condition.

Statistical analyses for calling behaviour of *L. xanthomera*

Previous studies have linked call characteristics to male body size (Ryan 1980; Robertson 1986). Linear regressions were used to explore the relationships between call characteristics (F1, F2 and call rate) and male SUL. As variances were unequal for the

comparisons between call characteristics in amplexant and non-amplexant males, Mann–Whitney *U*-tests were used for these comparisons.

Some call characteristics, for example call rate, are elastic properties that vary with a male's short-term condition and motivation (Gerhardt 1991). A simple linear regression was used to determine whether male body condition had an effect on call rate in *L. xanthomera*.

Statistical analyses for chorus tenure in *L. xanthomera*

A Mann–Whitney *U*-test was used to compare chorus tenure (number of nights spent at the chorus) of mated and unmated males. Spearman's rank correlation was used to detect relationships between the sizes of frogs and chorus tenure.

All statistical analyses were carried out by using SPSS version 8.0 for Windows. In all comparisons, α was set at 0.05.

RESULTS

Field data

Size distributions of amplexant and non-amplexant males of both species are presented in Fig. 3. As there was no significant difference in the size distributions

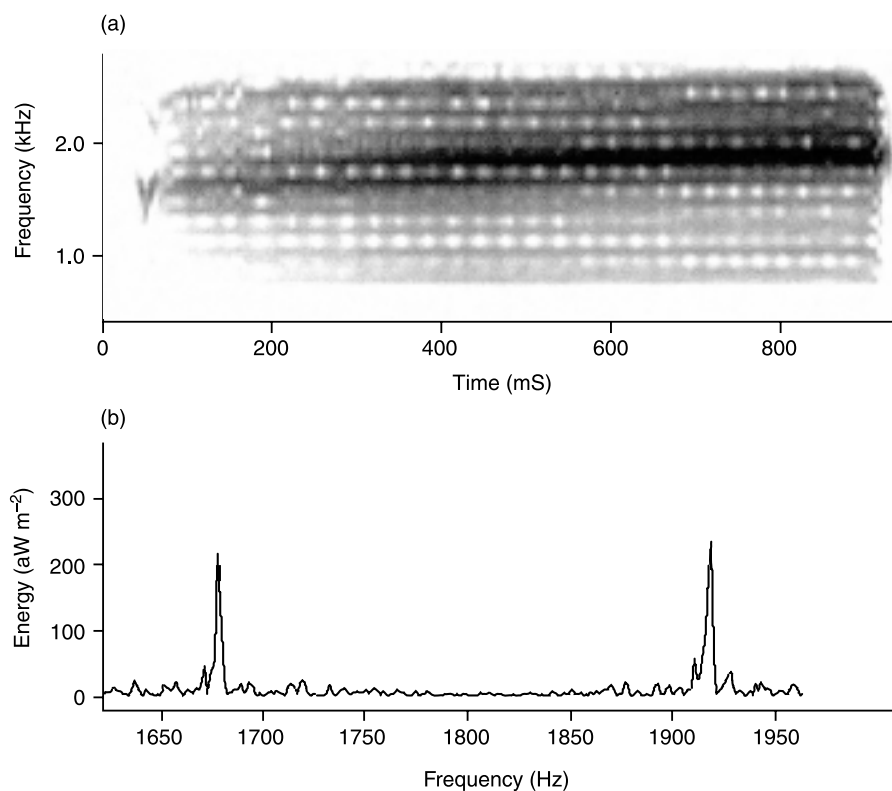


Fig. 2. (a) Sonogram of one moan of *Litoria xanthomera*. The darker shading indicates concentration of energy at the two dominant frequencies, F1 and F2. (b) Power spectrum of one moan of *L. xanthomera*. Peaks correspond with the two dominant frequencies F1 and F2.

of males in the four *L. chloris* populations (Kruskall-Wallis: $\chi^2 = 7.613$, d.f. = 3, $P = 0.061$), the data were combined in the remaining analyses.

There was a significant difference between the distributions of observed and expected SUL for amplexant males in both *L. chloris* (KS two-tail: $Z = 1.911$, $P = 0.001$; Fig. 3a) and *L. xanthomera* (KS two-tail: $Z = 1.88$, $P = 0.002$; Fig. 3b). Males observed in amplexus were smaller than the distribution expected if size had no effect on reproductive success.

When the data were examined on a nightly rather than a seasonal basis, significantly more successful males were smaller than the median male size in both *L. chloris* (seven greater than the median, 34 less than the median, two equal to the median; $\chi^2 = 25.78$, d.f. = 1, $P < 0.0001$) and *L. xanthomera* (six greater than the median, 14 less than the median, three equal to the median; $\chi^2 = 7.338$, d.f. = 1, $P = 0.025$).

The observed cumulative frequency distribution for the ratio of male : female body size was not significantly

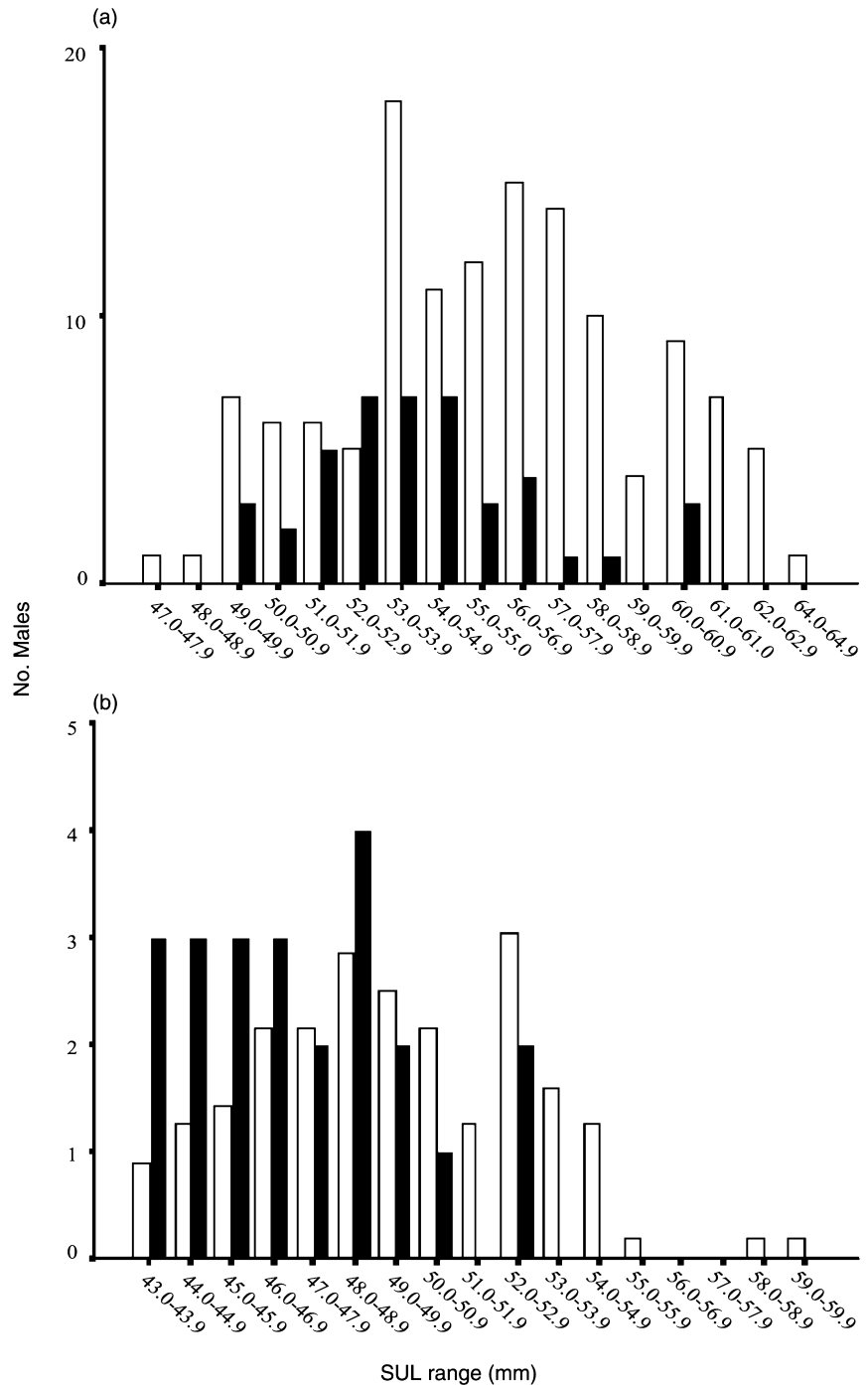


Fig. 3. (■) Observed and (□) expected distributions of the snout-urostyle lengths of amplexant males in (a) *Litoria chloris* and (b) *Litoria xanthomera*.

different from normal for either *L. chloris* (one sample KS: $Z = 0.791$, $P = 0.559$; Fig. 4a) or *L. xanthomera* (one sample KS: $Z = 0.699$, $P = 0.712$; Fig. 4b). These results suggest that no assortative mating was taking place in either species.

There was no significant difference in body condition between amplexant and non-amplexant *L. chloris* males (Mann-Whitney $U = 2544.00$, $P = 0.308$; Fig. 5a). However, the body conditions of amplexant males were significantly better (higher) than non-amplexant males in *L. xanthomera* (Mann-Whitney $U = 437.00$, $P < 0.006$; Fig. 5b).

Call characteristics of *L. xanthomera*

Fourteen of the 52 males with calls recorded were found in amplexus. The mean values, standard errors and ranges of the call characteristics, frequen-

cies F1 and F2 and call rate in amplexant and non-amplexant *L. xanthomera* males are summarized in Table 1. All three call characteristics were negatively related to body size (Table 2). The second dominant frequency (F2) was significantly higher in amplexant males (Mann-Whitney $U = 141.5$, $P = 0.017$; Fig. 6). A similar trend was observed with the first dominant frequency (F1), however, this relationship was not significant (Mann-Whitney $U = 177$, $P = 0.066$). There was no significant difference in call rates between amplexant and non-amplexant males (Mann-Whitney $U = 196$, $P = 0.15$).

Despite suggestions by previous studies that call rate is an elastic property that can be affected by male short-term condition (Gerhardt 1991), call rate in *L. xanthomera* males was not influenced by body condition ($r^2 = 0.001$, $\beta = -1.18$, $P = 0.86$, $n = 41$).

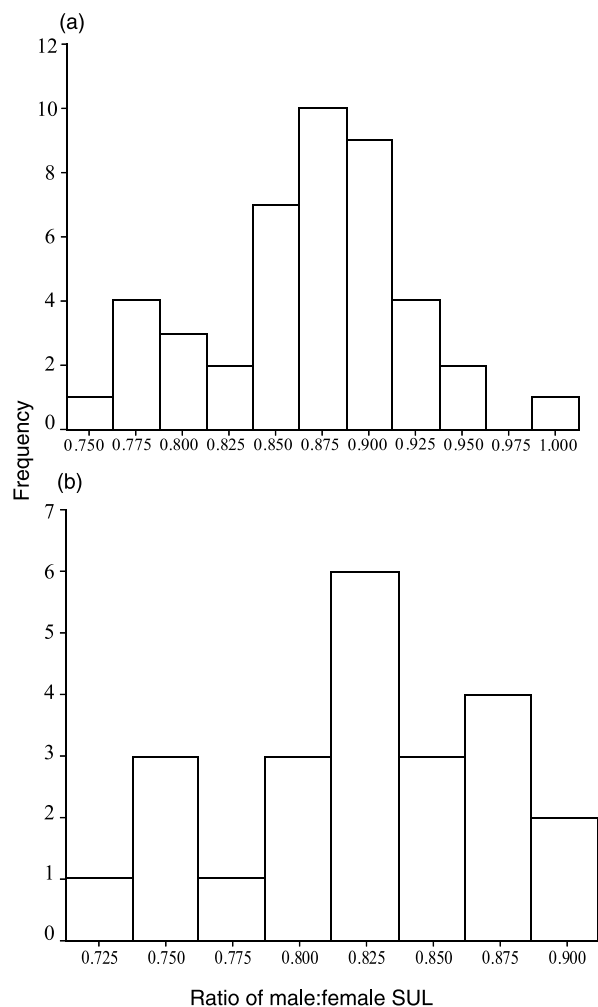


Fig. 4. Distribution of male : female snout-urostyle length ratio in (a) *Litoria chloris* and (b) *Litoria xanthomera*.

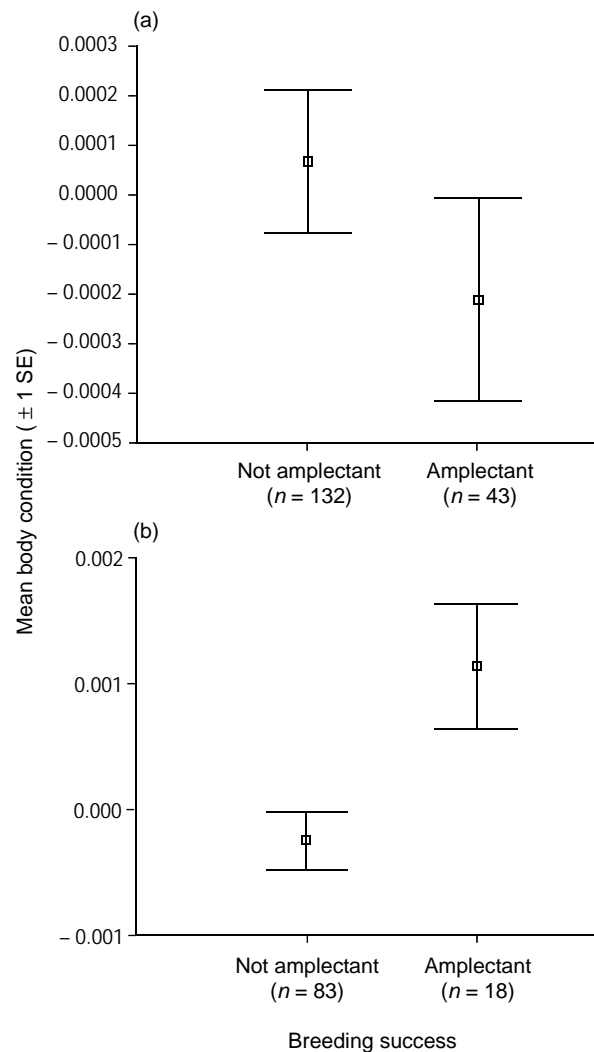


Fig. 5. Mean body condition (± 1 SE) in non-amplexant and amplexant males in (a) *Litoria chloris* and (b) *Litoria xanthomera*.

Table 1. Means (± 1 SE) and ranges for advertisement call characteristics in amplexant and non-amplexant male *Litoria xanthomera*

Call characteristic	Amplexant males ($n = 14$)		Non-amplexant males ($n = 38$)	
	Mean \pm SE	Range	Mean \pm SE	Range
F1 (Hz)	$1.87 \pm 1.85 \times 10^{-2}$	1.73–1.96	$1.83 \pm 9.94 \times 10^{-3}$	1.71–1.95
F2 (Hz)	$2.37 \pm 3.24 \times 10^{-2}$	2.17–2.55	$2.26 \pm 2.52 \times 10^{-2}$	2.02–2.56
Call Rate (moans s^{-1})	$2.37 \pm 3.24 \times 10^{-2}$	2.17–2.55	$0.89 \pm 1.85 \times 10^{-2}$	0.65–1.27

F1, dominant call frequency 1; F2, dominant call frequency 2.

Table 2. Linear regression results for comparisons between three call characteristics and male body size (snout–urostyle length; SUL) in *Litoria xanthomera*

Variables	r^2	β	P	n
SUL vs F1	0.444	-0.664	< 0.0001	52
SUL vs F2	0.286	-0.535	< 0.0001	50
SUL vs Call rate	0.147	-0.38	< 0.005	52

F1, dominant call frequency 1; F2, dominant call frequency 2.

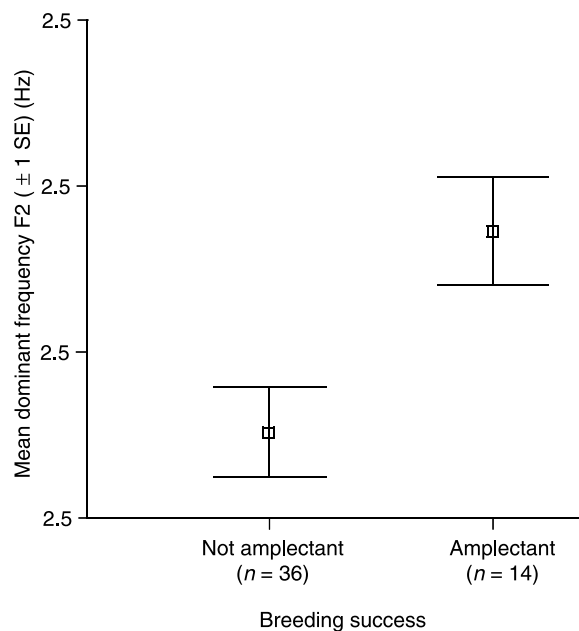
Chorus tenure in *L. xanthomera*

Males that were found in amplexus returned to the chorus more often than non-amplexant males (Mann–Whitney $U = 68.5$, $P < 0.0001$; Fig. 7). Chorus tenure decreased with male body size ($r_s = -0.23$, $n = 78$, $P = 0.04$; Fig. 8), suggesting that smaller males spent more time at the chorus than larger males.

DISCUSSION

Although body size has been invoked as a correlate of reproductive success in a number of explosive breeding anuran species (Wells 1977; Howard 1980; Olson *et al.* 1986; Telford & Van Sickle 1989; Elmberg 1991), female *L. chloris* and *L. xanthomera* were found to prefer smaller males on both a nightly and seasonal basis. There was also no evidence of assortative mating, suggesting that the female mate choice in these two species is not directly based on male body size. Instead, we found that chorus tenure had the most significant influence on male mating success.

A possible explanation for these results is the relationship between call characteristics and male body size in *L. xanthomera*. Calling is undoubtedly the most energetically expensive activity that a male frog undertakes (Taigen & Wells 1985; Pough *et al.* 1992). All other things being equal, calling males expend energy at a rate 6–21 times that of non-calling individuals, with the energetic cost of calling increasing with call rate, pulse rate and call duration (Prestwich 1994). Species or individuals with the greatest calling effort and/or intensity (which correlates with body size) have

**Fig. 6.** Mean dominant call frequency F2 (± 1 SE) in non-amplexant and amplexant male *Litoria xanthomera*.

the greatest factorial increase in their aerobic metabolism while calling (Prestwich 1994). In other words, larger males calling at lower frequencies will use more energy per call than a smaller male. Call frequencies F1 and F2 were found to decrease with increasing body size in *L. xanthomera*, suggesting that the larger *L. xanthomera* males calling at lower frequencies are using more energy per call than a smaller male calling at a higher frequency.

As mating likelihood increases with the amount of time spent at the chorus (Gerhardt *et al.* 1987; Dyson *et al.* 1992; Murphy 1994; Bertram *et al.* 1996; Dyson *et al.* 1998), smaller frogs calling at higher frequencies may be able to sustain chorusing for more nights in the season or for longer on a given night and thereby achieve higher reproductive success. The results of the present study support this theory in that: (i) amplexant *L. xanthomera* males were smaller and had higher F2 frequencies than did non-amplexant males; (ii) the males that spent more time at the chorus were smaller than males that attended the chorus for only 1 or 2

nights; and (iii) successful males attended the chorus on more nights than did unsuccessful males.

An alternative explanation for these results is the one put forward by Dyson *et al.* (1998) that success breeds success. They suggested that mated males are able to conserve energy relative to non-mated males. Their results indicated that the energetic saving that males

gain on a night when they mate successfully (i.e. less time spent calling compared with non-mated males) has a feed-forward effect on their subsequent probability of mating. This feed-forward effect subsequently provides the mechanism for the association between chorus tenure length and mating success. By mating once, males are able to attend the chorus more often or for longer and/or call more energetically, and therefore mate more often. However, although Dyson *et al.* (1998) were able to provide an explanation for the repeated success of certain males, they did not know what feature of these males initially attracted the female and allowed for the feed-forward mechanism to be initiated.

As frogs are ectotherms, temperature can have a significant influence on the acoustic properties of their calls (Duellman & Trueb 1986). Call rates, call frequency and call duration have all been reported to be affected by temperature (Sullivan 1982, 1984; 1992). Individual calling site can also affect temperature and therefore call structure. Consequently, studies involving the influence of call characteristics on male mating success need to take into account the effects of temperature and calling site. Although overall temperature was measured at the beginning and end of each night with *L. xanthomera*, information on individual calling sites and therefore effective temperature when each call was recorded was not noted. Consequently, the results of the call analyses may be biased and should be regarded with caution.

Some call characteristics (e.g. call rate) are elastic properties that vary with a male's short-term condition

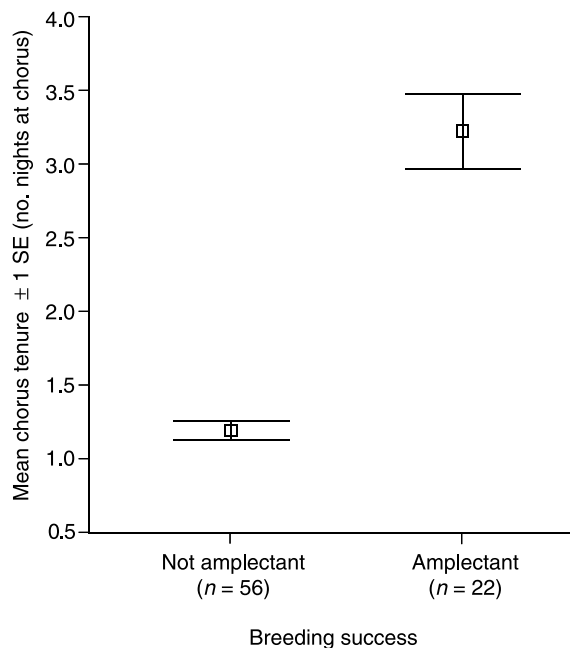


Fig. 7. Mean chorus tenure (± 1 SE) in non-amplexant and amplexant male *Litoria xanthomera*.

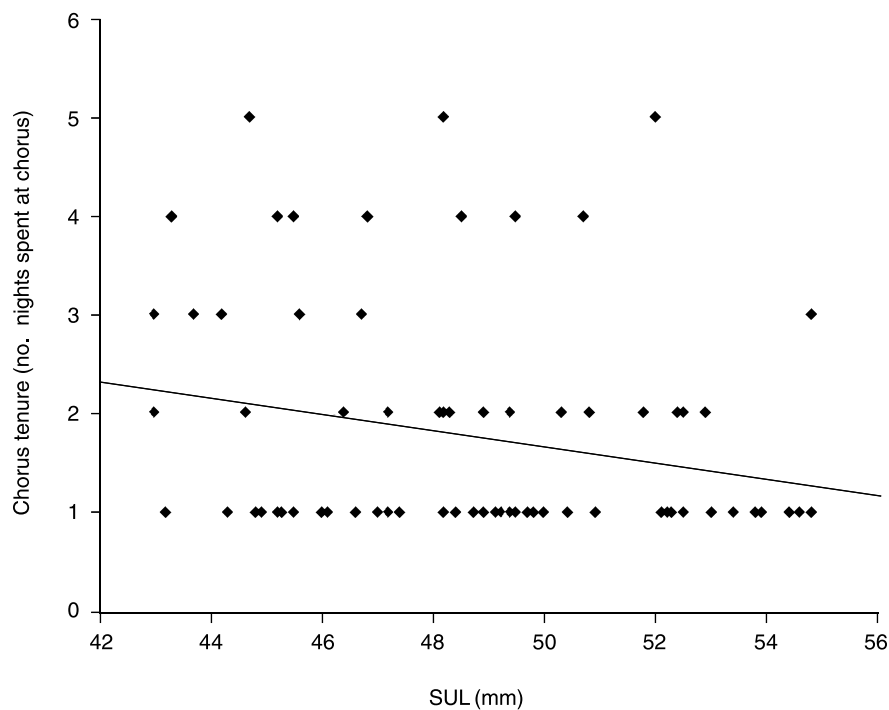


Fig. 8. Relationship between body size (snout-urostyle length; SUL) and chorus tenure in male *Litoria xanthomera*. Each marker represents one male.

and motivation (Gerhardt 1991). Consequently, call characteristics may reflect the body condition of the males, thus allowing females to select mates that are in the best condition and hence increase the fitness of their offspring. Although amplexant *L. xanthomera* males were in significantly better condition than the non-amplexant males, no relationship between body condition and call rate was found. This suggests that female *L. xanthomera* cannot or do not use call rate as an indication of body condition and thus potential fitness. Further studies with larger sample sizes are needed to verify this result.

Most previous studies have emphasized the importance of male phenotypic characters such as large body size (Wells 1977, 1979; Howard 1980; Arak 1983; Telford & Van Sickle 1989; Elmerg 1991), low dominant call frequency (Ryan 1985; Forester & Lykens 1986; Morris & Yoon 1989; Morris 1989), and high call rate (Sullivan 1983; Passmore *et al.* 1992; Sullivan *et al.* 1992) in female choice and male mating success in explosive breeders. However, our results for *L. xanthomera* appear to support those of Gerhardt *et al.* (1987), Gerhardt (1991), Dyson *et al.* (1992), Murphy (1994) and Bertram *et al.* (1996), who suggested that the most important factor influencing male mating success is chorus tenure.

Despite smaller male *L. chloris* being more successful than larger males in securing mates, we cannot say with certainty that the increased success of these smaller males was due to longer chorus tenure. However, because of the high similarity in ecology and call characteristics of these two species (Davies *et al.* 1986; Barker *et al.* 1995), we propose that call frequency and therefore chorus tenure may also influence male mating success in *L. chloris*.

Further studies involving the chorus tenure and call characteristics of *L. chloris*, the effects of temperature and call site on call structure and thus mating success, and female choice as determined through phonotaxis experiments are needed to elucidate the factors determining male mating success in these two species.

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