Males call more from wetter nests: effects of substrate water potential on reproductive behaviours of terrestrial toadlets

Nicola J. Mitchell†

Department of Environmental Biology, University of Adelaide, Adelaide, South Australia 5005, Australia
(nicola.mitchell@adelaide.edu.au)

Laboratory studies of terrestrial-breeding frogs have demonstrated that wetter substrates produce fitter offspring but the relevance of substrate wetness to adult reproductive strategies is unknown. I hypothesized that male toadlets (*Pseudophryne bibronii*) would select wetter areas for nesting and would advertise wet nests strongly, and tested these predictions by manipulating water potentials at a breeding site. Males preferred to nest in the wettest areas, and called at greater rates on almost twice as many nights as males occupying drier nests. Overall, males that mated called on significantly more nights than unmated males. Hence, because males occupying wet nests called more, they also mated more and in 19 out of 20 cases, oviposition occurred in wet nests that were suitable for embryonic development. Males occupying drier nests may have risked dehydration by calling, and so were less able to signal to females. Hydration states therefore have the potential to influence the reproductive success of terrestrial male frogs.

Keywords: Anura; terrestrial breeding; nest-site selection; water potential; *Pseudophryne bibronii*

1. INTRODUCTION

Choice of males by females is widely acknowledged as a mechanism that drives selection in the Anura (Sullivan *et al.* 1995), but a vital caveat for its adaptive value is evidence of fitness benefits to the female (Halliday 1983). A model of female choice that has received little consideration in the literature is one where females select mates based on a resource contained within the male's territory, such as the oviposition site. Discrimination between oviposition sites can provide a consistent environment for the fittest phenotypes to be expressed (Resetarits 1996), so when the breeding environment is variable, males should attempt to control quality nests. Howard (1978) found that larger male bullfrogs (*Rana catesbeiana*) occupied warmer aquatic territories containing fewer leeches than those of smaller males, and that females preferred larger males and egg survival was high. An experimental study revealed that female *Eleutherodactylus coqui* preferred males that called from elevated terrestrial nests, and egg-hatching success was also greater at elevated sites (Townsend 1989). Therefore characters of male nests can be viewed as phenotypic variables of the male that may be subject to female scrutiny.

The Australian toadlet *Pseudophryne bibronii* provides good evidence of the fitness consequences of oviposition site selection in anurans because several studies have determined how the incubation environment influences embryonic and larval viability (Bradford & Seymour 1988; Geiser & Seymour 1989; Seymour *et al.* 1991). *Pseudophryne* toadlets nest in depressions under rocks, logs or leaf litter, embryos hatch when the nest floods after rains, and thereafter larvae are aquatic and feeding (Woodruff 1976). The water potentials of natural nests are

variable (Bradford & Seymour 1985), and when water potentials were controlled in the laboratory, embryos incubated on wet substrates (0 kPa) increased in mass at a rate 71% greater than embryos reared on drier substrates (−25 kPa, Bradford & Seymour 1988). Therefore, because offspring size potentially relates to adult traits such as size and age at first reproduction, and fecundity (e.g. Semlitsch *et al.* 1988), toadlets breeding in wetter nests should have greater fitness.

Male *Pseudophryne* toadlets mate from zero to three times each season, but females may also mate with multiple partners by depositing their egg component in discrete batches over several days (Woodruff 1976). Given this mating flexibility, *Pseudophryne* are excellent models for examining the relevance of nest quality to mating strategies. The present study focuses on the mating strategies of male *P. bibronii* when offered variable water potentials in a manipulated field experiment. Males were monitored over a ten-week breeding season to determine nest locations and to relate variables such as calling effort and mating success to the water potential of the nest site. Three fundamental questions are addressed. First, do males prefer to establish nests on wetter substrates; second, do males advertise a wetter nest more; and third, is the mating success of males using wetter nests greater than males occupying drier nests?

2. METHODS

(a) Study species and site

Pseudophryne bibronii (Anura: Myobatrachidae) is a small (22–36 mm snout–vent length) cryptozoic toadlet found across temperate south-eastern Australia. Males establish nests after the first autumn rains and call for one to eight weeks with discrete mate attractant and territorial calls. At the study site in remnant eucalyptus woodland in Watt's Gully Reserve, ca. 50 km north-east of Adelaide, South Australia, nests were localized along the banks of a meandering winter creek. Several

†Present address: School of Biological Sciences, Victoria University of Wellington, PO Box 600, Wellington, New Zealand
(nicola.mitchell@vu.ac.nz).

Figure 1. Map of study area showing the creekline, the location of experimental plots and distributions of calling males in 1998 and 1999.

nest types were identified in a pilot study in 1998; most were shallow depressions under litter or among grass roots, or were burrows angled into the creek-bank.

(b) *Experimental design and watering procedure*

Fifteen experimental plots of 3 m × 3 m were positioned across sections of creek before the onset of the 1999 breeding season, and were allocated to one of three treatments using a stratified random design (figure 1). Plots were either watered to maintain high soil water potentials, disturbed in a similar manner but not watered (procedural control, PC) or not disturbed (disturbance control, DC).

Watering began immediately before the onset of the breeding season, so that variability in water potential might influence where males chose to nest, and continued every two to three days until natural rains overrode the effects of plot watering (figure 2a). Plots were watered sequentially in the late afternoon using a portable polypropylene frame with 90° irrigation sprayers fixed into each corner. About 100 l of rainwater was pumped from a nearby water trailer onto each plot over 15–20 min. A sham polypropylene watering frame was positioned on a PC plot at the same time an adjacent wetted plot was watered, and DC plots were only entered in the eighth week of the experiment to confirm the identity of resident males.

(c) *Experimental measurements*

Four variables described the responses of toadlets to the experimental plots. These were (i) the number of colonizing males, (ii) male calling effort, (iii) male mating success, and (iv) egg hatching success. Additionally, (ii), (iii) and (iv) were measured for males outside plots, but within the study site. Monitoring began on the night before the first watering (figure 2) and continued approximately every second night for the following ten weeks. Because wetted plots were always watered beyond their boundaries, a male was counted as a resident of an experimental plot if he was located inside the plot or within 0.5 m of the perimeter.

Nesting males were usually found by triangulating on the call, and females were either found near to a calling male or were captured in pitfall traps set around wetted and PC plots.

The uniquely patterned ventral surface of each toadlet was photographed to allow re-identification. Snout–vent length was measured with dial callipers and mass was recorded to the nearest 0.1 g with an electronic balance, after first blotting the toadlet with absorbent tissue.

Once a male entered the chorus, a concerted effort was made to locate it on subsequent nights. Males would indicate their presence in a nest by answering a crude mimic of an attractant call, but when a male called without this stimulus it was scored as a calling night. When a male called consistently his calls were recorded with a digital audio tape-recorder (Sony, Tokyo, Japan) and a microphone (Sennheiser ME66; Sennheiser, Wedemark, Germany) or Sony Professional Walkman and Sony ECM-MS907 microphone. Recordings were digitized and analysed with Avisoft SASLab Pro software (Specht, Berlin, Germany). Temperature at the calling site was measured with a digital thermometer (Fluke model 52; Fluke, Everett, WA, USA).

Call rates of males in wetted and PC plots were measured synchronously on one occasion each week. Four observers positioned themselves in two pairs at either a wetted plot or at the closest PC plot, and a timer was set for 15 min. Observers sat quietly and determined the number of calling males for the first 5 min, and then counted calls for 10 min. The procedure was repeated for the remaining four pairs of wetted and unwetted plots, and the time and the near-ground air temperature were noted on each occasion.

Calling sites were examined for eggs approximately every second night. Matings were attributed to the male attending the eggs. (White (1993) found that when male *Pseudophryne* were placed on unattended eggs of another male, the introduced male would always desert the eggs.) Fresh eggs were counted, and when they reached hatching stage 28 (Gosner 1960) they were carefully excavated from the nest and were flooded the next day in the laboratory. Hatchlings were counted, staged and measured using Optimas image analysis software (Optimas Corporation, Bothell, Washington, DC, USA).

(d) *Measurement of the plot environment*

Soil water potentials of wetted and PC plots were measured weekly using a chromatography paper technique (reviewed by

Figure 2. (a) Watering events and natural rainfalls (rainfall data sourced from the South Australian Bureau of Meteorology Weather Station 23878, 5 km from the study site); (b) number of males calling in experimental plots; (c) number of males calling in the study area each monitoring night; (d) number of female observations and oviposition dates of egg batches, including some outside the study area. The dashed line divides the before and after rain periods.

Savage *et al.* 1992). Squares of saturated paper (20 mm × 20 mm × 1 mm) were inserted inside dialysis tubing to keep them clean, before being buried in duplicate in each plot under about 1 cm of soil. Papers were removed after five days, their water contents measured in the laboratory and soil water potential was directly inferred from an equilibration curve of paper water content and matric tension (range 0 to −600 kPa).

The physical habitat of plots was scored as the per cent cover of five substrate categories (litter, grass, gravel, soil and bank) using a 1 m square frame divided into four square 0.5 m cells. Litter depth was measured to the nearest 2.5 cm in any cell that contained it, and mean litter depth was calculated for each plot. Substrate cover and litter depth values were fourth-root transformed and the treatment groups were tested for similarity in a one-way ANOSIM procedure using the Bray–Curtis coefficient of similarity and the PRIMER software package (Clarke & Warwick 1994).

3. RESULTS

(a) *Experimental conditions*

The first six weeks of the experiment were unusually dry, but after 12 May rainfalls continued intermittently until the last monitoring day (figure 2a). During the dry weather water potentials of wetted plots averaged about −16 kPa, whereas water potentials of unwetted plots

exceeded −600 kPa (figure 3). After the rains the water potentials of both wetted and unwetted plots were > −2 kPa. Breeding activity waned after 25 May (week 9) when large pools formed in the creek-bed, and had ceased by 18 June when the creek was in full flood.

(b) *Distribution of nesting males*

Fifteen males established nests and commenced calling in wetted plots during the six dry weeks of the experiment, and most left wetted plots during natural rainfalls in week 7 (figure 2b). No male occupied a PC plot, and five males occupied a DC plot following the rainfalls. However, during the dry weather 13 males nested in litter outside of experimental plots (figure 1). Their peak density was about 1 male 76 m^{−2}, compared to 1 male 7 m^{−2}, inside wetted plots.

A two-way analysis of variance was used to test male distribution data, because the effect of watering plots was predicted to be greater in the absence of rain than in the presence of rain (table 1). It was apparent that males preferred to nest in wetted plots before the rains, but not after the rains, because the interaction between treatment and time was significant (table 2).

All males recaptured in 1999 nested between 5 and 130 m from their 1998 nest ($n = 8$), so males were not returning to

Figure 3. Mean water potentials ($\pm$ s.e.) of wetted (filled bars) and PC (open bars) plots during the first seven weeks of the experiment. The water potential scale changes after the rains (indicated by dashed line).

Table 1. *Male distribution data*

treatment ($n = 5$)	number of males ($\bar{x} \pm$ s.e.)	
	before rain	after rain
wetted	3.0 ± 0.9	0.6 ± 0.4
procedural control	0.0 ± 0.0	0.0 ± 0.0
disturbance control	0.0 ± 0.0	1.0 ± 0.5

previous breeding sites. Further, in 1998, there was no difference in the distribution of males in the locations of the wetted, unwetted and control plots (ANOVA, $F_{2,12} = 0.414$, $p = 0.67$). The physical habitat of plots in each treatment was similar (ANOSIM, $r = 0.055$, $p = 0.28$).

(c) *Calling effort of males in wet and dry nests*

Because control plots were not colonized before the rains, I instead compared characters of wetted males to all other males in the study site (henceforth called unwetted males). A wetted male was defined as one that spent 75–100% of its calling nights before the rains within a wetted plot; all other males were classed as unwetted males.

Wetted males called on 46% of monitoring nights before the rains, compared with 15% for unwetted males. After rains, the same, previously wetted males, called on 36% of nights, while calling by previously unwetted males increased to 50% of monitoring nights (figure 4). The difference in calling effort between the two groups of males before and after rains was significantly different (t_{20} , $p = 0.0002$).

Statistical tests were not appropriate for call data obtained from recordings, because both spatial (e.g. a calling neighbour) and temporal (e.g. time of night) variables influenced call parameters. However, recordings suggested that wetted males produced attraction calls at about twice the rate of unwetted males, and that wetted males produced more territorial calls (table 3). Deep litter piles in particular attracted multiple males and territorial calling could be frenetic, as occurred when five out of six males in a wetted plot occupied a single large litter pile ($1\text{ m} \times 0.5\text{ m} \times 0.2\text{ m}$). If territorial calls are included in the measurement of call rate, then wetted males produced $10.3\text{ calls min}^{-1}$ before rains, compared to $4.5\text{ calls min}^{-1}$ for unwetted males before rains. After rains the call rate of all recorded males was $7.5\text{ calls min}^{-1}$.

Table 2. *Results of two-way ANOVA for male distribution data*

(Variances of $\ln(x+1)$ -transformed data were homogenous (Cochran's test), but data were not normally distributed. However, ANOVA is generally tolerant to deviations from normality when treatments are well replicated (Underwood 1981).)

variable	d.f.	sum of squares	F ratio	p
time (before or after rain)	1	0.1180	0.84	0.3672
treatment	2	1.7568	12.58	0.0002
time treatment	2	1.4083	10.08	0.0007

The weekly synchronous measures of call rates inside wetted and PC plots were confounded by the absence of males in the latter. However, attraction call rates in wetted plots before the rains ($\bar{x} = 2.88\text{ calls min}^{-1}$; range $0.2\text{--}6.1\text{ calls min}^{-1}$) were lower than those measured from recordings, and call rates of males in each wetted plot (data from all weeks pooled) were not related to plot water potential, the number of males in plots, or the time or temperature that measurements were made (linear regression, all $p > 0.3$, $n = 19$).

(d) *Male mating success*

All females located in dry weather were near calling males in wetted plots. Six out of 11 wetted males mated during dry weather, and one out of 12 unwetted males mated (Fisher's exact test, $p = 0.023$). After the rains, two out of the 11 previously wetted males mated, and four out of the 12 previously unwetted males mated (Fisher's exact test, $p = 0.270$), so the difference in mating success between wetted and unwetted males was significant only in the absence of rain.

(e) *Egg hatching success in wet and dry nests*

Egg hatching success ($\bar{x} \pm$ s.e.) of five clutches oviposited in wetted plots before rain was high ($95 \pm 2.3\%$, range $87\text{--}99\%$). The clutch oviposited in unwetted litter before the rain experienced almost complete mortality. Only three larvae hatched, and they were about 45% of the wet mass and 70% of the length of hatchlings from wet nests. The precise hatching success of this clutch was unknown, because the fresh eggs were shrunk and difficult to discern from debris.

Table 3. *Physical and behavioural characters of wetted and unwetted males in the study area*

time	variable	wetted males		unwetted males	
		$\bar{x} \pm \text{s.e.}$	<i>n</i>	$\bar{x} \pm \text{s.e.}$	<i>n</i>
general	snout-vent length (mm)	26.3 $\pm$ 0.53	11	26.5 $\pm$ 0.68	12
	night that male joined chorus	7 $\pm$ 1.3	11	13 $\pm$ 3.1	12
before rain	number of calling nights in wetted plot	14 $\pm$ 1.8	11	1 $\pm$ 0.4	12
	attraction call rate (calls min ⁻¹) ^a	6.1 $\pm$ 0.9	32	3.5 $\pm$ 0.4	8
	territorial: attraction calls ^a	0.68 $\pm$ 0.11	37	0.28 $\pm$ 0.12	8
	mass (g) ^b	1.8 $\pm$ 0.10	7	1.9 $\pm$ 0.05	9
after rain	number of calling locations	1.7 $\pm$ 0.38	11	1.2 $\pm$ 0.24	12
	mass (g) ^b	1.5 $\pm$ 0.07	7	1.8 $\pm$ 0.07	9
	number of calling locations	1.1 $\pm$ 0.16	11	1.3 $\pm$ 0.18	12

^a From call recordings, *n* refers to number of recordings rather than number of males.

^b Only males weighed both before and after rains have been included.

Table 4. *Physical and behavioural traits of mated and unmated males compared with a t-test*

trait	mated males		unmated males		<i>t</i> -test
	$\bar{x} \pm \text{s.e.}$	<i>n</i>	$\bar{x} \pm \text{s.e.}$	<i>n</i>	
snout-vent length (mm) ^a	26.7 $\pm$ 0.35	20	26.4 $\pm$ 0.46	20	<i>p</i> = 0.586, d.f. = 38
mass (g) ^a	1.7 $\pm$ 0.06	20	1.6 $\pm$ 0.08	20	<i>p</i> = 0.321, d.f. = 38
dominant frequency of attraction call (Hz) ^{a,b}	2436 $\pm$ 34.8	14	2496 $\pm$ 52.9	10	<i>p</i> = 0.338, d.f. = 22
number of calling locations	2.6 $\pm$ 0.4	11	2.2 $\pm$ 0.4	11	<i>p</i> = 0.396, d.f. = 20
night of arrival in chorus (1–33)	6 $\pm$ 1.1	12	15 $\pm$ 3.1	11	<i>p</i> = 0.013, d.f. = 21
calling nights (%)	43 $\pm$ 4.6	11	25 $\pm$ 5.4	11	<i>p</i> = 0.019, d.f. = 20

^a Includes 17 males located outside the study area after the rains, eight of which mated.

^b The only call parameter independent of nest temperature ($r^2 = 0.001$, $p = 0.73$) and where coefficients of variation were stable between recordings (see Gerhardt 1991).

4. DISCUSSION

The negligible rainfall in the first six weeks of the experiment (only 9 mm) meant that wetted plots offered markedly different substrate water potentials to control plots (figure 3). As male distributions could not be explained by nest-site fidelity or a preference for a nesting material, then differences in water potential were strongly implicated; males preferred to nest in wetter over drier areas. Further, high substrate water potentials induced behaviours such as male calling and female oviposition, independent of ambient cues such as declining temperature. The large proportion of territorial calls produced by wetted males before the rains, and the tendency of these males to call from more locations (table 3) suggested strong competition between males for territories in wet litter.

Almost all (19 out of 20) females mated in wet nests, either by mating with a male in a wetted plot before the rains, or by mating after the rains. About 50% of males that entered the chorus secured a mate (table 4), and three mated more than once (estimated from the age of egg batches). There was no suggestion that mating success was related to male size or to the dominant frequency of the attraction call (table 4), although this result should be treated cautiously because the size of correlation coefficients depends on the number of males that females sample (Benton & Evans 1998). Instead, mated males tended to call earlier and more often during the breeding

season, a finding consistent with other studies (e.g. Ryan 1983; Wagner & Sullivan 1995).

Because wetted males had both high calling efforts and mating success before the rains, I examined whether mating frequencies predicted from calling effort matched actual mating frequencies (table 5). I made two assumptions: that my 30 observation nights were representative of all nights, and that females should mate with males in proportion to the number of nights each male called (e.g. Greer & Wells 1980). It appeared that wetted males were not directly advantaged by occupancy of a wet nest before the rains, because their observed mating frequencies were similar to expected frequencies ($\chi^2_{0.05,1} = 1.78$, $p > 0.1$). Instead, females probably indirectly selected males in wet nests, because wetted males called more (table 3, figures 2b and 4).

There are many potential explanations of the high calling effort of males occupying wet nests. First, wetted males may have equated the wet conditions with the possibility that females would attend the chorus and responded by increasing their calling effort. Second, the high density of wetted males may have promoted calling competition, but as males were noticed to call antiphonally with neighbours up to 15 m distant, the calling of wetted males should also have prompted nearby unwetted males to call. Third, plot watering may have increased invertebrate abundance (cf. James & Whitford 1994) and so given wetted males an energetic advantage over unwetted

Table 5. *Expected and observed mating frequencies for wetted and unwetted males before the rains*

male type	male identification	number of calling nights	proportion of mating opportunities	number of matings		observed minus expected
				expected	observed	
wetted	98-27	11	0.054	0.376	0	-0.376
	98-40	9	0.044	0.307	0	-0.307
	C1	14	0.068	0.478	1	0.522
	C3	21	0.102	0.717	1	0.283
	C4	9.5	0.046	0.324	1	0.676
	C6	3	0.015	0.102	0	-0.102
	E1	16	0.078	0.546	0	-0.546
	E2	10	0.049	0.341	1	0.659
	O1	19	0.093	0.649	1	0.351
	O2	20.5	0.100	0.700	0	-0.700
	O3	19	0.093	0.649	1	0.351
	98-23	5	0.024	0.171	0	-0.171
	wetted total	157	0.766	5.361	6	0.639
unwetted	I1	6	0.029	0.205	0	-0.209
	98-20	12	0.059	0.410	0	-0.209
	98-23	5	0.024	0.171	0	-0.209
	98-33	3	0.015	0.102	0	-0.209
	98-44	1	0.005	0.034	0	-0.209
	98-8	7	0.034	0.239	0	-0.209
	K1	13	0.063	0.444	1	-0.209
	M1	1	0.005	0.034	0	-0.209
	unwetted total	48	0.234	1.639	1	-1.672
total		205	1	7	7	-1.033

males. However, the effect of feeding on male calling behaviour is inconclusive; some workers have found that feeding increases calling activity (Murphy 1994; Marler & Ryan 1995), while others found no effects (Green 1990; Murphy 1999). Finally, wetted males may have called more because they were not in danger of dehydration.

Unfortunately, although the water relationships of frogs have been under investigation for two centuries (Jørgensen 1997), the precise effects of dehydration on calling behaviour are unknown. Certainly dehydration causes elevated resting metabolic rates (Pough *et al.* 1983) and a 'water-seeking response' where activity levels increase (Hillyard 1999), both of which might hamper calling activity. Some evidence that dry conditions restrict calling behaviour is that significantly more male *E. coqui* adopted water-conserving postures on dry summer nights compared to wet nights, and that the number of vocalizing males increased, respectively, from 20 to 35% (Pough *et al.* 1983). In the present study, light rainfalls that damped the litter could prompt an unwetted male to move to and begin calling from a new nest, which implied that substrate wetting decreased the dehydration risk associated with movement and calling. In contrast, males in wetted plots (at about -16 kPa) must always have been fully hydrated, given that *E. coqui* could absorb water through their ventral surface from substrates as dry as -540 kPa (Van Berkum *et al.* 1982).

If we accept that male hydration at least partly affects calling behaviour, then it tests an assumption of honest signalling, namely, that for a signal to be reliable it must incur a cost (Zahavi 1975). Undoubtedly, calling effort is

Figure 4. Mean % call nights ($\pm$ s.e.) of wetted males (filled bars) and unwetted males (open bars) before and after rains.

an honest signal of male quality, for frog vocalizations are energetically expensive (e.g. MacNally 1981; Bucher *et al.* 1982; Wells & Taigen 1989), and in this study, wetted males lost more weight during the experiment (table 3) and did not call to the same extent after the rains (figure 4). However, if the ability to call (= signal) at any particular time depends on favourable nest water potential, then a male occupying a dry nest is less able to signal to females. In contrast, a male that chances upon a moist site early in the season (in this experiment a wetted plot, but more usually a deep pile of litter) is advantaged because he can begin signalling earlier. Therefore only if

the best males occupied wet nests would call effort truly reflect male quality.

This study highlights the mechanism by which female *P. bibronii* select wet oviposition sites. Males prefer wetter nests because they benefit by increased opportunities to advertise acoustically. Female sampling is therefore biased towards males occupying wetter nests, and a perhaps fortuitous consequence is that oviposition occurs in hydrated sites that enhance embryonic survival. High embryonic mortality was the result of the single oviposition event in a dry nest, because the water potential of the unwetted litter exceeded the viable embryonic limit of -200 kPa determined by Bradford & Seymour (1988). This mating occurred after light rainfall that promoted male calling, but did not penetrate the leaf litter. Consistent calling from a nest during a breeding season should therefore be an honest signal of the persistence of the moisture and the suitability of the nest for embryonic development.

I thank the many people who assisted with watering and fieldwork, especially Oliver Berry, Genny Mount, Dean Newman and James Weedon. I am also grateful to Daniel Rogers, who made many recordings and did half of the call analyses, Helen and Gary Bourne, who generously supplied rainwater and storage facilities, and David Paton, Russell Baudinette and Roger Seymour, who loaned equipment. Earlier drafts of the manuscript benefited from the critical comments of Roger Seymour and Sarah Smith. The study was conducted with the support of Forestry SA and Australian Research Council grant no. A19602654 to Roger Seymour and J. D. Roberts.

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As this paper exceeds the maximum length normally permitted, the author has agreed to contribute to production costs.