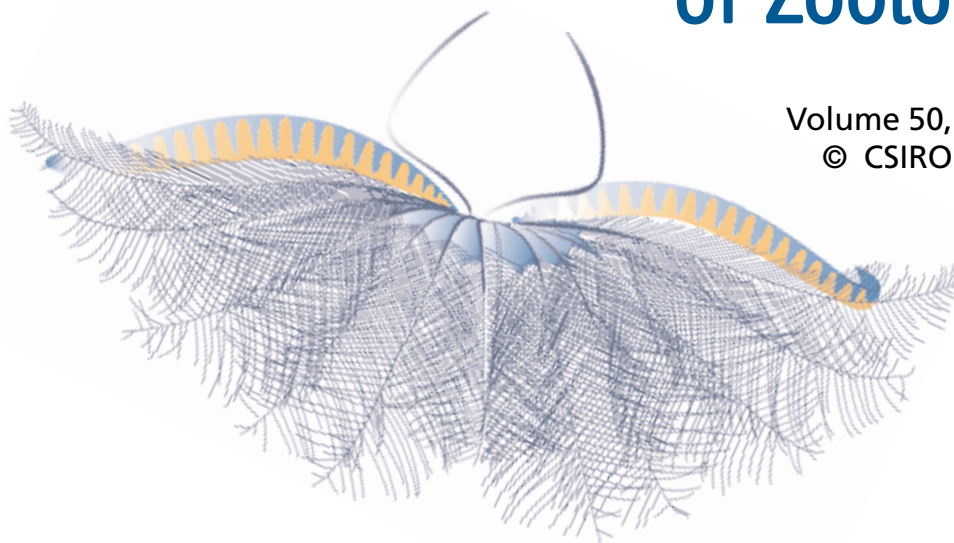


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Nest-site selection in a terrestrially breeding frog with protracted development

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Abstract

Metamorphosis of larvae of the Australian moss frog (*Bryobatrachus nimbus*) occurs in a terrestrial nest approximately one year after oviposition. Neither parent attends the eggs, thus selection of an appropriate nest site is critical to egg viability. This study examined the dynamics of nest-site utilisation over six years and the characteristics of nests chosen as oviposition sites. Nest cavities were located at ground level amongst heath within one of 10 species of bryophyte, lichen and lycopod. On average, 2.6% of nests contained a male *B. nimbus* during daytime monitoring during the breeding season, and 7.3% of nests contained an egg mass. Despite an abundance of potentially suitable nests from previous years, males constructed a small proportion (<10%) of new nests each year and new nests were more likely to be used as oviposition sites than older nests. Discriminant function analysis showed that moss nests used as oviposition sites were distinguishable from empty nests by their greater horizontal dimensions. Eggs deposited in wider nests are restricted to fewer layers, and a preference for wider nests may be adaptive because embryonic oxygenation is enhanced under such conditions. However, rather than demonstrating nest-site selection, the use of relatively large nests as oviposition sites may be an artifact of their occupancy by a breeding pair.

Introduction

In oviparous (egg-laying) species, characteristics of the nest site may have important implications for individual fitness. Most notably, the nest environment affects the viability of developing eggs (e.g. Howard 1978; Kluge 1981; Seymour *et al.* 1995; Packard 1999), and may influence hatchling phenotype in ways that are liable to affect juvenile fitness (e.g. Kaplan 1987, 1992; Shine and Harlow 1996; Janzen 2001). Because the production of the fittest phenotypes requires a consistent environmental context (Resetarits 1996), the ability of parents to discriminate between nest sites should be favoured by natural selection if the behaviour does not incur significant costs (Shine 1978; Petranka and Petranka 1981). Moreover, in some fossorial anuran amphibians, characters such as burrow dimensions and nest moisture affect the acoustic properties of male courtship calls, and hence may impact directly on male fitness by influencing mating success (Bailey and Roberts 1981; Penna and Solís 1999; Mitchell 2001).

For oviparous species with internal or delayed fertilisation, the selection of an oviposition site is usually solely the jurisdiction of the female (e.g. many invertebrates and reptiles). However, the eggs of most anuran amphibians are fertilised externally, and consequently nest-site selection by the female is partially dependent on behaviours of the male. Pairs may select a site together (e.g. *Litoria lesueuri*: Richards and Alford 1992), but more commonly in terrestrially breeding species, males choose the nest, defend it from rival males, and call to attract females. In such circumstances selection should favour males that choose quality nests, and females that use nest quality to discriminate between potential mates (Townsend 1989; Resetarits and Wilbur 1991; Mitchell 2001).

If development in the nest is protracted, then nest quality may bear strongly on female mating preferences. The Tasmanian moss frog (*Bryobatrachus nimbus*) (Rounsevell *et al.* 1994; see also Read *et al.* 2001) has the longest nidicolous (nest-dwelling) lifespan known for an anuran amphibian. Parental care is absent, and metamorphosis of larvae occurs in a terrestrial nest 11–13 months after oviposition. Each of the 4–16 eggs is furnished with sufficient energy (about 249 J: Mitchell and Seymour 2000) to develop endotrophically (without feeding).

Profoundly different embryonic and larval phenotypes arise when the incubation environment of *B. nimbus* is manipulated in the laboratory. For example, embryonic growth proceeds normally in wet conditions, but embryos are stunted, asymmetric and experience high mortality when developing under slightly drier conditions (Mitchell 2002). Incubation temperature has a dramatic effect on the timing of metamorphosis and the size of froglet yolk reserves (Mitchell and Seymour 2000). In this study, based on six years of field observations, I describe the patterns and processes of nest-site utilisation, and address two fundamental questions: are nests that are used as oviposition sites distinguishable from vacant nests, and what are the cause and extent of egg mortalities? Together, these data allow assessment of the relevance of nest quality to female choice of mates.

Materials and Methods

Study site and data collection

The study site was the type locality of *B. nimbus*: a poorly drained plateau of sub-alpine heath in the Hartz Mountains National Park in southern Tasmania. Moss frogs nest in discrete patches of bryophyte and lichen scattered amongst the heath, and nests are often under snow (Rounsevell *et al.* 1994; Mitchell and Seymour 2000), which makes fieldwork impractical during winter months. Consequently, fieldwork was concentrated over spring/summer breeding seasons. Approximately 80 visits were made to the site between October 1995 and January 2000, and on all occasions nests were located by careful searching of low-lying patches of moss, lichen, liverworts and lycopods. Nests were easily identified as frog-sized cavities with a compacted base, and sometimes contained jelly residue (indicating a recently metamorphosed clutch). Nest occupancy (male, breeding pair or clutch; Fig. 1) was noted, and the snout to vent length (SVL) of occupant frogs was measured to the nearest 0.1 mm with dial callipers. Clutch size was measured on the first inspection, and thereafter clutches were periodically re-examined (2–10 times per clutch). Any egg mortality was recorded.

Frequency of nest use

In total, 67 patches of *Dicranoloma* moss within 2 ha of breeding habitat were surveyed over four breeding seasons. Patches were selected at random in October 1995 (prior to the onset of the breeding season), and were tagged and drawn to detail their shape, dimensions, and the locations of any nests. Nest status (i.e. vacant or containing larvae from the 1994/95 breeding season) was recorded. Nests containing jelly residue were assumed to have contained clutches deposited in the 1993/94 breeding season. Patches were not searched again until March 1996 (when breeding activity had ceased, thus avoiding disturbance), and the occurrence of clutches and the location of new nests were recorded. Thereafter, the census was repeated in the late summer of 1997, 1998 and 1999. Patches were deliberately not examined in the interim, but photographs of patches were taken in 1998 to replace the 1995 drawings. Because some patches could not be relocated, the survey was reduced to 62 patches by the final year.

Survey of nest characters of occupied and vacant nests

The presence of large numbers of empty nests in moss patches was the catalyst for a survey aiming to identify the features of preferred oviposition sites. The survey, conducted in the 1998/1999 breeding season, was confined to 89 nests within two very similar and locally common mosses, *Dicranoloma robustum* and *D. billardieri*. Surveyed nests either contained a clutch in the previous breeding season ($n = 45$), or were vacant ($n = 44$). Vacant nests were selected on one or both of two criteria: a male *B. nimbus* had occupied the nest within the previous year, or the nest was the closest nest to a nest containing a clutch. Hence vacant

nests were potentially rejected as oviposition sites, and provided a relevant comparison to nests used as oviposition sites.

Six nest characters were measured: (1) nest depth (mm), (2) nest width and breadth (mm), (3) the elevation of the nest base above soil (mm), (4) distance to nearest edge of the moss patch (mm), (5) patch exposure (1–5), and (6) the water content of moss (% dry mass). Dial callipers accurate to 0.1 mm were used to measure nest depth (1), which was defined as the distance between the base of the nest and the moss surface. Similarly, nest diameters (2; Fig. 1c) were the widest horizontal span (a), and the span perpendicular to it (b). The horizontal area of a nest was then calculated as the area of an ellipse ($\pi \times a/2 \times b/2$). The elevation of the nest base above the soil (3) was measured by pushing a piece of 3-mm-diameter dowel through the nest until the dowel tip contacted the soil, and then sliding a plastic sleeve down the dowel to meet the nest base. The dowel was removed and the distance between the dowel end and the sleeve was measured with callipers. Moss-patch exposure (5) was scored as 5 if all sides were exposed (i.e. the patch experienced full sunlight), and 4, 3, 2 and 1 if shaded by heath on one, two, three or four side(s), respectively. Representative samples of moss (within 10–15 cm of each surveyed nest) were collected over 2.5 h in March 1999. Samples were immediately sealed inside a labelled snap-lock bag, and in the laboratory, sealed bags were weighed to the nearest milligram on a Mettler AE 163 analytical balance. Bags were then opened and oven-dried for two days at 70°C before being reweighed. The water content (6) of each moss sample could be calculated after subtracting the mean mass of empty bags from total masses.

Statistical analysis

Descriptive data are means \pm 95% CI, or expressed as percentages. Stepwise discriminant function analysis (Tabachnick and Fidell 1996) determined whether nests used as oviposition sites could be distinguished from vacant nests in terms of the nest variables measured, using the computer programme Statistica (Statsoft Inc. 1995).

Results

Characters of *B. nimbus* nests

Nests were located in ten species of low-lying vegetation nestled between taller heath (*Epacris serpyllifolia*, *Richea scoparia*) and pineapple grass (*Astelia alpina*). The mosses *Dicranoloma robustum* and *D. billardieri* were most commonly used as oviposition sites (81.7% of 290 clutches), followed by the edaphic lichens *Cladia retipora* and *C. sullivanii* (6.6%), a leafy liverwort, *Heteroscyphus billardieri* (6.2%), sphagnum moss, *Sphagnum australe* (2.8%) and a rhizoid moss *Breutelia pendula* (1.6%). Species used infrequently (<1% of clutches) were the lycopods *Lycopodiella diffusa* and *Lycopodium scariosum*, and the branching moss *Lepidozia ulothrix*. Nest vegetation appeared to be used in proportion to its abundance within the heath. Most nests were concealed beneath surface vegetation, but occasionally a fully hydrated clutch was visible before vegetation was searched. Nest vegetation was compacted in near the base of the nest and formed a solid wall (Fig. 1), but was progressively less rigid toward the surface, usually forming a goblet-shaped cavity of about 30 cm³. The average diameter of *Dicranoloma* nests was 3.24 ± 0.80 cm ($n = 89$). Nests in lichen were shallower depressions (1–2 cm deep; mean diameter 3.47 ± 0.27 cm, $n = 5$) in a sponge-like stratum of soil and lichen, underlying 3–10 cm of surface lichen.

Frequency of nest use

The annual surveys of *Dicranoloma* moss patches showed that nests were not created by an oviposition event, as many vacant nests were found to contain a clutch in later surveys. Patches contained 0–9 nests (mean 2.8 ± 0.5 nests) and patch size ranged between 113 and 1178 cm³ (mean 459 ± 65 cm³). The number of nests in a patch was positively correlated with its size ($r = 0.46$, $n = 64$, $P = 0.0002$). On average 7.3% of surveyed nests contained a clutch, but ratios differed from year to year (Table 1). Four survey patches contained two

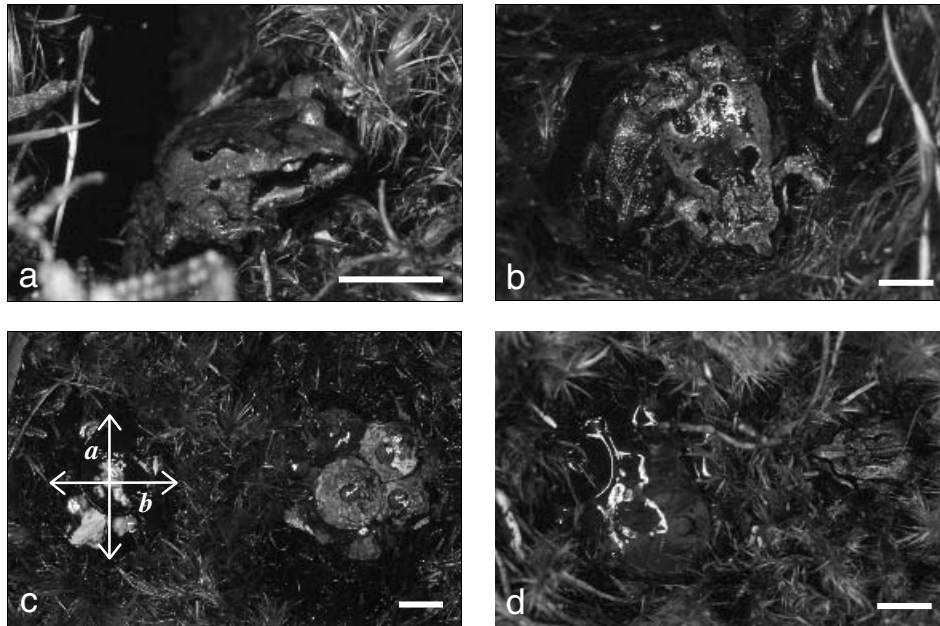


Fig. 1. Sequence of nest-site utilisation in *Bryobatrachus nimbus*. (a) a male occupying a moss nest; (b) a male attracts a female (right); (c) two egg masses deposited in adjacent nests, with nest dimensions *a* and *b* indicated on older mass at left (see Methods); (d) a male occupying a nest immediately adjacent to a mass of late-stage embryos. Scale bars are 10 mm.

Table 1. Frequency of oviposition in old nests, new nests and all nests over six breeding seasons

Breeding season	% of nests containing a clutch (no. of nests)			No. of moss patches
	Old	New	Total	
1993/94			7.8 (140)	67
1994/95			11.4 (140)	67
1995/96	3.6 (140)	10.7 (28)	4.8 (168)	64
1996/97	6.5 (170)	50.0 (6)	8.0 (176)	65
1997/98	5.3 (171)	22.7 (22)	7.3 (193)	65
1998/99	4.5 (179)	6.3 (16)	4.6 (195)	62
Mean	4.9 (165)	22.4 (18)	7.3 (183)	

clutches in a single season, while a patch of *Heteroscyphus* liverwort (that was not part of the survey) contained nine clutches over three successive breeding seasons.

Small numbers of new nests appeared in *Dicranoloma* patches each year, and these were more likely to be used as oviposition sites than pre-existing nests ($\chi^2_{0.05,1} = 27.8$, $P < 0.001$, based on mean frequencies in Table 1). Four survey patches contained nests that were used twice in five breeding seasons; in one of these nests, froglets were observed on the nest wall on 17 November, and a fresh clutch appeared in the nest one week later.

On average, 2.3 males were located in moss nests for every 100 nests examined (Table 2). This estimate reflects daytime occupancy rates, for nests were not searched at night. In total 109 males were resident in nests, including one case where three males were found in neighbouring nests within a small patch (10 × 15 cm) of *Dicranoloma* moss. A

Table 2. Frequency of nest occupancy by males, and frequency of clutches with embryonic mortality during surveys of moss nests over five breeding seasons

	Breeding season					Sum	Mean
	1995/96	1996/97	1997/98	1998/99	1999/2000		
Estimated number of nests examined ^A	420	717	1393	1818			
Number of males found ^B	9	0	34	44	22	109	
% Nests containing males	2.14		2.44	2.42			2.33
Total number of clutches found	20	57	101	84	28	290	
% Clutches with embryonic mortality	20.0	22.8	49.5	41.7	25.0		31.8

^AThe estimate was based on the assumption that the total number of clutches located each breeding season was proportional to the number of clutches located in survey nests over the same period (Table 1). Fieldwork ended in January 2000, before breeding activity ceased; hence estimates were not available for the final season.

^BExcludes males found in lichen, and males found near to a moss nest. No males were located in 1996/1997 when fieldwork was limited to the end of the breeding season in March 1997.

Table 3. Mean values of nest parameters of vacant nests and those used as oviposition sites, and their canonical loadings (correlation with the discriminant function)

Variable	Nest group mean ($\pm 95\%$ CI)		Standardised correlation of variable with the discriminant function ^A
	Vacant ($n = 42$)	Containing clutch ($n = 43$)	
Horizontal area (cm ²)	7.4 \pm 0.7	9.2 \pm 0.7	0.928
Elevation above soil (cm)	5.0 \pm 7.3	5.5 \pm 6.0	0.380
Moss moisture content (% dry weight)	164 \pm 26	160 \pm 25	-0.342
Moss patch exposure (0–5)	2.1 \pm 0.3	2.2 \pm 0.3	
Distance of nest to edge of patch (cm)	5.1 \pm 0.6	5.2 \pm 0.6	
Nest depth (cm)	4.9 \pm 0.4	4.8 \pm 0.3	
Nest volume (cm ³)	28.3 \pm 3.2	32.7 \pm 3.4	

^AThree predictor variables were sufficient to distinguish between vacant and occupied nests.

further 10 males were located outside nests, usually on the edge of a moss patch, or else crawling on its surface. Four males were found under a rock slab. Of the 109 males in moss nests, 12 were paired with a female, 4 sat on the surface of a fresh clutch, and 17 were in the same vegetation patch as a fresh clutch. The mean diameter of a nest containing a breeding pair was 3.43 ± 0.24 cm ($n = 9$); nest diameters were not noticeably altered once a clutch had been deposited.

Do nests used as oviposition sites differ from vacant nests?

A stepwise discriminant function analysis was performed using six nest variables as predictors of membership of two nest groups: vacant nests, and those containing clutches. Predictors were nest depth and horizontal area, elevation of the nest above the soil, distance to the nearest edge of a moss patch, moss patch exposure, and moss water content. Of the 89 surveyed nests, four were identified as multivariate outliers and were deleted. The outliers were evenly distributed between the two nest groups (clutch and vacant), and were either very elevated, deep or wet nests. For the remaining cases, nest elevation, distance of the nest to the patch edge, and moss water content were log- or square-root-transformed to satisfy normality. All variables satisfied homogeneity of variance criteria.

A significant difference ($F_{3,81} = 6.003$, $P = 0.001$) was detected between vacant and occupied nests, based on only three predictor variables: the horizontal area of the nest, nest elevation, and the water content of the moss. The canonical loading of predictors (their correlation with the discriminant function) suggested that the best predictor for distinguishing between the nest groups was the horizontal area of the nest (loading of 0.93) (Table 3), while nest elevation was the second most discriminatory variable (loading of 0.38). The mean horizontal area of nests used as oviposition sites was greater (9.2 cm²) than that of vacant nests (7.4 cm²) (Table 3).

Frequency and causes of clutch mortality

Embryonic mortality was recorded in 31.8% of clutches (Table 2), but was not usually severe – on average, 2–3 eggs died ($33.8 \pm 2.3\%$ of a clutch), and dead embryos were most often at the nest margins. The cause of embryonic mortality was unknown in 88 clutches, while in seven cases eggs had clearly desiccated, and predation was recorded in 10 clutches. Eggs that had been preyed upon were characterised by opaque yolk-coloured clouds in the centre of each egg that were similar to the aftermath of planarian predation of Western

Australian *Geocrinia* embryos (N. J. Mitchell, personal observation). Planarians were observed in an egg mass once, and dipteran larvae were seen burrowing through egg jelly in three clutches. Several fresh clutches had pale cream eggs about 1 mm in diameter scattered on their surface, possibly those of a mollusc.

Mortality of 1–2 larvae was observed twice (they appeared chewed and yolk was extruded from the body wall), while six clutches of larvae disappeared entirely between inspections in March and November. While it is possible that metamorphosis was complete and froglets had left the nest (cf. Mitchell and Seymour 2000), larvae may have been consumed by harvestmen (Opiliones: *Triaenonychidae*), which were conspicuously associated with jelly-coated nests (indicating the recent presence of *B. nimbus* larvae). Other potential predators co-habiting moss patches were numerous species of leech and spider, and the mountain skink (*Niveoscincus orocryptus*).

Discussion

Moss frogs utilised an array of bryophytes and lichens for nest construction, but apparently did not nest in soil depressions. Envelopment of the globular *B. nimbus* egg mass within a vegetative matrix presumably enhances egg viability, as eggs are provided with a moist environment and are afforded some protection from freezing and predators. Additionally, the oxygen produced by photosynthesising moss is critical to the viability of embryos developing at the base of the mass (Mitchell and Seymour, in press). At least two other Australian myobatrachines, *Kyarranus* (= *Philoria*) *sphagnicolus*, and *Philoria frosti*, routinely construct nest chambers in moss, but the base of the nest is a water-filled depression (de Bavay 1993; Malone 1985). *Philoria* are foam-nesters, and hence air pockets within the egg mass may free eggs of an association with a photosynthetic substrate.

Vacant nests of *B. nimbus* were abundant at the study locality; on average, less than 8% of *Dicranoloma* nests contained clutches each breeding season (Table 1). Annual surveys revealed that most nests persisted for at least 5 years, relatively few nests were constructed each year, and that both old and new nests were used as oviposition sites. However, newly formed nests were more likely to be used as oviposition sites than older nests. Nests were not formed by the oviposition event (cf. Richards and Alford 1992), and the frequent occupation of vacant nests by males implicated males as the nest constructors.

Nesting strategies of males

The frequency of re-use of an oviposition site was low (<2% of nests) within the four-year survey period, but is relatively high in other anurans whose nest sites are less abundant (e.g. Kluge 1981; Kam *et al.* 1998). Male *H. rosenbergi* engaged in nest construction do not usually call, so re-occupation of an old nest both saves energy and allows earlier entry into the chorus (Kluge 1981). However, in this study new nests were more likely to be used as oviposition sites, possibly because more males resided in new nests. The occurrence of multiple clutches in a single moss patch and the frequent observation of a male near to a clutch suggest that successful males either constructed new nests, or occupied vacant nests adjacent to their clutch (e.g. Fig. 1d).

Discriminant function analysis showed that nests used as oviposition sites could be reliably distinguished from vacant nests, largely due to their greater horizontal surface area (Table 3). This result can be interpreted in one of two ways. First, male frogs select and/or shape the nest, females assess nest breadth before oviposition, and prefer to mate with males in wider nests. An analogous preference was found in female *Chirixalus eiffingeri* in

Taiwan: females preferred to oviposit on the walls of wider bamboo stems, and their eggs were more successful at such sites (Kam *et al.* 1998). Second, the larger horizontal dimensions of nests used as oviposition sites may have been an artifact of their occupation by a male–female pair (e.g. Fig. 1*b*). Gravid female *B. nimbus* are appreciably larger than males (female SVL = 3.04 ± 0.07 cm, $n = 12$; male SVL = 2.30 ± 0.04 cm, $n = 117$; N. J. Mitchell, unpublished data), and hence a pair manoeuvring within a nest may compact the vegetation and widen the nest base prior to the oviposition event. Unfortunately, given the cryptic behaviour of *B. nimbus*, it is not possible to distinguish between these alternative scenarios.

The variation in nest dimensions observed in this study was not correlated with the size of the male occupant (data not presented); similarly, correlations between nest size and male size have not been found in other studies (Kluge 1981; Kam *et al.* 1998). Nest size may, however, be influenced by the nature of the nest substrate. For example, nests of *Hyla rosenbergi* in Costa Rica were twice the size of those in Panama, yet male size was similar in both populations; Costa Rican nests were built in dense grass, which compacted to form an immovable barrier, while nests in Panama were constructed in soft mud (Kluge 1981). In the present study, lichen nests were broader than those in mosses, suggesting that the dimensions of nests were constrained by the density of nesting material.

How might nest site selection influence egg viability?

Experimental manipulation of nest dimensions would provide an ideal method to assess the adaptive value of a breeding pair preferring (or producing) a relatively broad oviposition site. Embryonic *B. nimbus* are particularly susceptible to hypoxia due to substantial diffusion distances posed by the unusually thick jelly capsule, and analytical models of spherical egg masses have demonstrated that a late-stage embryo centred amid a normal-sized mass experiences anoxia above 5°C (Mitchell and Seymour, in press). Field temperatures of *B. nimbus* egg masses are typically warmer at embryonic stages (10–16°C in midsummer: Mitchell and Seymour 2000), hence mortalities are more likely to occur in narrower nests that promote deeper egg stacks. In contrast, oviposition in relatively wide nests restricts eggs to fewer layers (usually 1–2) and so enhances embryonic oxygenation (Mitchell and Seymour, in press).

Egg viability is also influenced by nest water potential. Because amphibian eggs freely exchange water with their surroundings, the water potential of embryos and larvae depends upon the water vapour permeability of the nest vegetation, and local variables such as soil drainage and solar radiation. Incubation of eggs at low substrate water potentials produces smaller hatchlings with higher frequencies of developmental abnormalities (Seymour *et al.* 1991; Mitchell 2002), and hence oviposition in relatively wet moss should favour normal embryonic development. Moreover, hydrated moss photosynthesises at greater rates than does dry moss (Proctor 1981) and hence wetter nests should produce more oxygen when the metabolic demands of embryos increase proportionally with daytime temperatures. However, there was no apparent difference in the water potential of selected and vacant nest sites (Table 3); water contents of moss was 20–382% in used nests, and 44–382% in vacant nests (data not presented). Continuous measures of moss water potential would provide more meaningful comparisons of the hydrous states of used and vacant nest sites.

Causes of egg mortality

Some mortality of embryos occurred in one-third of *B. nimbus* clutches, and in cases of complete mortality the clutch may not have been fertilised (Fig. 2). Comparable data for

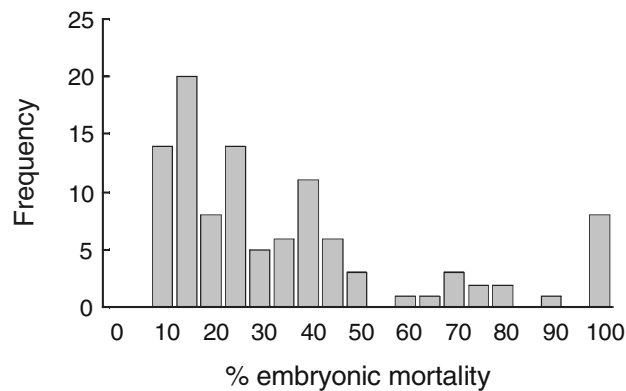


Fig. 2. Frequency of embryonic mortality of *Bryobatrachus nimbus* in natural nests ($n = 104$). Clutches where no embryonic mortality was recorded ($n = 185$) are excluded. Clutches with 100% embryonic mortality may not have been fertilised.

other myobatrachids are 0–10.7% mortality in *Pseudophryne* spp. (Woodruff 1976), 74% mortality in *Philoria frosti* (Malone 1985), and 26% mortality in *Kyarranus* (= *Philoria*) *loveridgei* (Seymour *et al.* 1995). In the first two studies, clutch desiccation was heavily implicated; similarly, desiccation accounted for some mortality of *B. nimbus* embryos at the margins of the egg mass. A few mortalities that occurred in very early embryonic stages were possibly due to developmental irregularities associated with cleavage of large eggs (Elinson 1987). Predators presumably caused the remaining mortalities: burrowing invertebrates killed embryos by ingesting yolk, while harvestmen (opilionids) and spiders may have preyed upon larvae that became temporarily exposed when jelly dehydrated in dry weather. However, a crust of dried jelly sometimes forms a seal around undisturbed egg masses, and in addition to reducing egg desiccation, it may also restrict the entry of smaller predators (Mitchell 2002).

Confounding issues in nest-site selection by females

This study provides important baseline information on the dynamics of nest-site utilisation in *B. nimbus*, and details how environmentally induced variation in fitness of the offspring may arise through nest-site selection. Given the large energetic investment per egg, female *B. nimbus* should be particularly discerning in mate choice (*sensu* Trivers 1972), and characters of nest sites of males may well be important selection criteria. However, demonstration of a female preference for a nest character is confounded by the fact that her choice of oviposition site will be influenced by the magnitude of the male's call advertisement (e.g. Kluge 1981; Mitchell 2001). Females can only choose between nests that are advertised, and preference for nest characters can only be demonstrated when other factors subject to selection (e.g. male size and call effort) are held constant.

Further, some studies suggest that males select nests using different criteria from females (Resetarits and Wilbur 1991). Males of the leptodactylid frog *Eupsophus emiliopugini* call from burrows that are also oviposition sites, and many males match the resonant frequency of their burrow to that of their call (Penna and Solís 1996, 1999). Because call frequency co-varies with burrow depth, male fitness may be enhanced in certain nests for reasons unrelated to egg viability. The potential for conflict in nest preferences between the sexes provides an intriguing avenue for future investigation.

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