



FAUNA *of* AUSTRALIA



5. NATURAL HISTORY OF THE ANURA

J. Dale Roberts

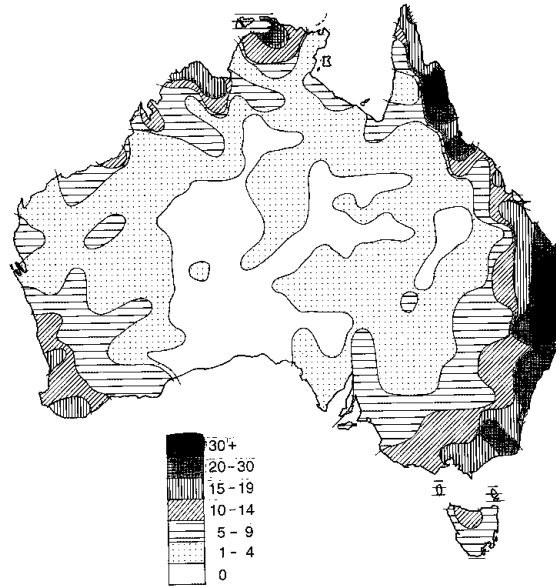


Figure 5.1 Species diversity plot for Australian frogs. The most detailed data available have been used for plotting distributions of all species. However, ranges for species that might cover half the continent, such as *Neobatrachus sutor*, may have significant gaps in remote areas. Therefore areas of zero diversity should be viewed critically, as frogs may occur there. (Updated from Brook 1983) [W. Mumford]

INTRODUCTION

The Australian frog fauna is diverse and widespread, although regional species richness may vary. Frogs are found in all parts of Australia, from the tops of the coldest, highest mountain ranges in the Australian Capital Territory and New South Wales to the most remote desert areas in inland Australia. For example, *Pseudophryne corroboree* (Pl. 2.5) occurs at elevations of greater than 1800 m in the Brindabella Range near Canberra (Osborne 1989), whereas the type locality for *Neobatrachus centralis* is on the arid Birdsville Track, 112 km east of Lake Eyre (Ledo & Tyler 1973). Areas of highest species diversity are in the tropics and around the wet continental margins, particularly on the east coast near the New South Wales—Queensland border and in far north Queensland, but even desert regions may support up to six species (Fig. 5.1; Pianka & Schall 1981).

This chapter reviews the biology and natural history of frogs with specific reference to Australian species. An excellent, detailed treatment of the biology of amphibians has been given recently by Duellman & Trueb (1986). A specific treatment of many aspects of the biology of Australian frogs is given by Tyler (1989a).

LIFE HISTORY

Reproductive Strategies

Breeding in frogs may be explosive, extending over one or a few nights per year, or be prolonged over weeks or months (Wells 1977). Prolonged and explosive breeding are the divergent ends of a continuum. Both extreme breeding strategies may be found in temperate and arid zone species in Australia.

In explosive breeders such as many *Neobatrachus* species, there may be up to 250 or more adults in a small pond (Roberts 1978). The operational sex ratio (OSR, defined as the number of fertilisable females to available males; Emlen and Oring 1978) is typically biased towards males. For example, in a single pond near Narembeen, Western Australia, observations on 17 amplexed pairs and 14 unpaired males of *Neobatrachus kunapalari* in a breeding chorus on one night after summer rain in January 1987 (Roberts pers. obs.), indicated an OSR of roughly 1:2. This is comparable with values for six north American and European species of *Rana* and *Bufo* (Arak 1983).

Prolonged breeders, such as *Rana*, *Hyla* and *Bufo*, have OSR values ranging from 1:5 to 1:31 (Arak 1983). In *Limnodynastes tasmaniensis* calls from up to twenty males per night in a single pond were recorded, though amplexed females or females moving through the breeding chorus were rare (Roberts pers. obs.). However, the breeding season for this species extends over several months during spring and into summer (Roberts 1993).

Prolonged breeding may be more common in the tropics. All of twenty one well-studied species in the Magela Creek system, Northern Territory, have an extended calling period but often a much more limited period for egg deposition (Tyler, Crook & Davies 1983a). *Pseudophryne occidentalis*, which is widespread in the arid zone of Western Australia, may call in summer after rain or in autumn (January to late June) (Main, Littlejohn & Lee 1959), while *Neobatrachus aquilonius*, from near Port Hedland, observed in 1983 and 1993, called for only one night after heavy rain (Roberts pers. obs.).

Prolonged breeders experience severe male-male competition for access to females, which may be reflected as males fighting or as strong vocal interactions (see Calls below). Such competition may be less severe or absent in explosive breeders.

Males of many prolonged breeders spend extended periods at breeding sites and some will probably mate more than once. Where a few males dominate many matings, highly skewed breeding success can occur (for example, Ryan 1983). The same dominance by certain individuals is not apparent in explosive breeders (for example, Howard 1988). No data reflecting male mating success are available for any Australian frog species. However, it is likely that these two extreme patterns of individual male success will be found in Australian frogs. Male mating success may be correlated with body size (for example, Ryan 1983, bigger males do better), calling rate (Howard 1988, faster callers do better) or number of nights attending a breeding chorus (for example, Godwin & Roble 1983) amongst other variables.

Woodruff (1976a) noted either multiple clutching by females in *Pseudophryne* species or that females spread egg laying (with a single male parent) over several nights. Humphries (1979) established that some species, for example, *Limnodynastes tasmaniensis*, may make multiple entries to breeding ponds in one season, but this was not the norm. Females bred twice in one breeding season in five species studied by Humphries. The second clutch was generally smaller than the first, but only 2 to 10% of females in these five species actually entered the breeding pond more than once in a single season.

In non-Australian frogs, reproductive patterns of females are very variable and may vary geographically within species. Females of *Hyla rosenbergi* from central America mature at one year old, deposit up to six different egg clutches at an average interval of 24.7 days, then do not return to the chorus the next year and presumably die (Kluge 1981). Patterns of maturation and egg deposition may be environment specific as Berven (1981) reported large differences in age at first egg clutch and first entry to breeding ponds for both male and female

wood frogs (*Rana sylvatica*) from lowland and montane sites in North America. This species has only a single clutch per year, but it is also an explosive breeder (Berven 1981).

Egg and Tadpole Survival

Mortality of amphibian eggs and tadpoles is often very high. Malone (1985) estimated from 0 to 95% survival from egg deposition to hatching for the direct developing *Phyllorhina frosti* (based on 77 egg masses from seven sites). Humphries (1979, Table 5.7) estimated a survival rate of 0 to 2.7% from egg to metamorphosis for seven species over two years. These data are comparable with studies on other continents (*cf.* Table 11.3, in Duellman & Trueb 1986). No other data on egg or tadpole survival are known for Australian frogs.

Duration of the tadpole stage is known for many species and ranges from 16 to 30 days in *Notaden nichollsi*, a species found in north-west desert areas (Main 1968). In temperate species, larval life-spans may be as long as 160 days (for example, *Limnodynastes dorsalis*; Main 1968) and up to 430 days for *Litoria moorei* (Roberts pers. obs.). Overwintering by tadpoles, resulting in very long larval life-spans, is known in several North American and European species (Duellman & Trueb 1986).

Population Size and Persistence

There are few detailed studies of population size or structure in Australian frogs. Humphries (1979) showed that the size of breeding populations was variable between species. For example, over one thousand individuals of *Limnodynastes tasmaniensis* bred in one year in a single pond of 20 m diameter, compared to only one or two individuals at the same site for *Limnodynastes dumerilii* and *Neobatrachus pictus*. Although these data give some indication of population sizes at breeding sites, there are few data which actually give a reliable estimate of density.

Frogs may be very common in some environments. Roberts (1985) estimated a minimum population density for *Arenophryne rotunda* of 277.6 frogs ha⁻¹ and summarised earlier data on several other Western Australian species. Ingram (1983) gave population estimates for *Rheobatrachus silus* (Pl. 2.7) of 1.11 frogs ha⁻¹ with considerable variation in density between adjacent pools and stretches of stream. Morton, Masters & Hobbs (1993) estimated 34–68 frogs ha⁻¹ for the burrowing species *Cyclorana maini*, *Neobatrachus* sp., *Notaden nichollsi* and *Uperoleia micromeles* in the spinifex grasslands of the Tanami Desert, Northern Territory.

There are no studies documenting long term fluctuations in population size. Some cover two to three seasons (for example, Main 1965a; Humphries 1979; Ingram 1983; Osborne 1989). These indicate apparent large fluctuations related to annual variations in rainfall (Humphries 1979), declines resulting from unknown causes (Ingram 1983; McDonald 1990), declines where severe drought may be a cause (Osborne 1989) or, for *Crinia insignifera*, apparent stability of the adult population size over three years (Main 1965a). However, it is important to distinguish attendance at a breeding site from death. In other words, if the population estimate is low because few frogs make it to the study pond because of low rainfall, is the population truly low? Will the frogs survive and breed next season or are they dead?

We do not understand the causes of fluctuations in population estimates or the ecological phenomena they reflect. Although Humphries (1979) reported low population densities for several species around a farm dam near Canberra, the same species have been reported to be extremely abundant at other sites that

have different ecological attributes. For example, *Neobatrachus pictus*, rare in Humphries's study, was extremely abundant in natural ponds in south-eastern South Australia (Roberts 1978). These differences relate to the specific habitat requirements of species like *N. pictus* which generally breeds in temporary, rather than permanent, ponds.

Age at first breeding is known for several Australian frog species. *Heleioporus eyrei* bred at age two years (Lee 1967). Some males of *Arenophryne rotunda* may breed at age one year, but most breeders were older (Roberts 1984), and Ingram (1983) reported that *Rheobatrachus silus* attained maturity at age two years. Humphries (1979) estimated that several hylid and myobatrachid species at his study site could mature as early as nine months, but that young frogs of all species studied could attend their first breeding congress at 18 to 20 months old. However, age estimates in the studies on *H. eyrei* and *A. rotunda* were based on body size and these may not correlate with chronological age (Humphries 1979; Platz & Lathrop 1993). There are no published data on Australian frogs relating known age animals to the presence of growth rings, such as have been reported for amphibians from other continents (for example, Kalb & Zug 1990). However, Lynch (1992, pers. comm.) has demonstrated the existence of growth rings in five species of West Australian frogs.

Longevity of Australian frogs is poorly known. Duellman and Trueb (1986, Table 11.2) summarised data on longevity of frogs. The range for 12 species (representing most frog families) was from 6 to 36 years. The only Australian species in their study, *Litoria caerulea*, lived for 16 years. However, most of these records were from captive animals and may not reflect longevity in the field.

Little is known of the persistence of populations at particular sites for any Australian species. In Humphries's (1979) study, the abundance of particular species varied radically from year to year, partly in relation to obvious, proximate factors like rainfall. The disappearance of several species in eastern Australia in recent years (Czechura & Ingram 1990; McDonald 1990) is cause for some concern, but it is still not clear whether this is a natural phenomenon or a consequence of human activities (Blaustein & Wake 1990). In Brazil, similar disappearances have been attributed to severe frosts (Heyer, Rand, daCruz & Peixoto 1988). Osborne (1989) has invoked drought as a cause for the decline of *Pseudophryne corroboree*. These 'disappearing species' may actually undergo radical fluctuations in population size, previously unknown simply because they have not been studied (Tyler 1991b).

ECOLOGY

Distribution and Habitat Use

Frogs occur in a vast array of habitats and make use of both natural and disturbed areas. For example, pit-trapping on rehabilitated, bauxite mine-sites near Jarrahdale, Western Australia, captured seven of nine frog species known from adjacent undisturbed, upland jarrah forest (Nichols & Bamford 1985). However, few of the species actually bred in the rehabilitated area. Breeding may occur in fast-flowing streams (for example, *Crinia riparia*, Littlejohn & Martin 1965), arid-zone ponds that may only last 10 to 14 days before they dry up (for example, species of *Cyclorana*, *Limnodynastes*, *Notaden* and *Neobatrachus*; Main 1968) or in permanent and temporary ponds and streams (for example, *Limnodynastes* and *Crinia* species in south-eastern and south-western Australia; Main 1965a, 1968). Many species use natural breeding sites,

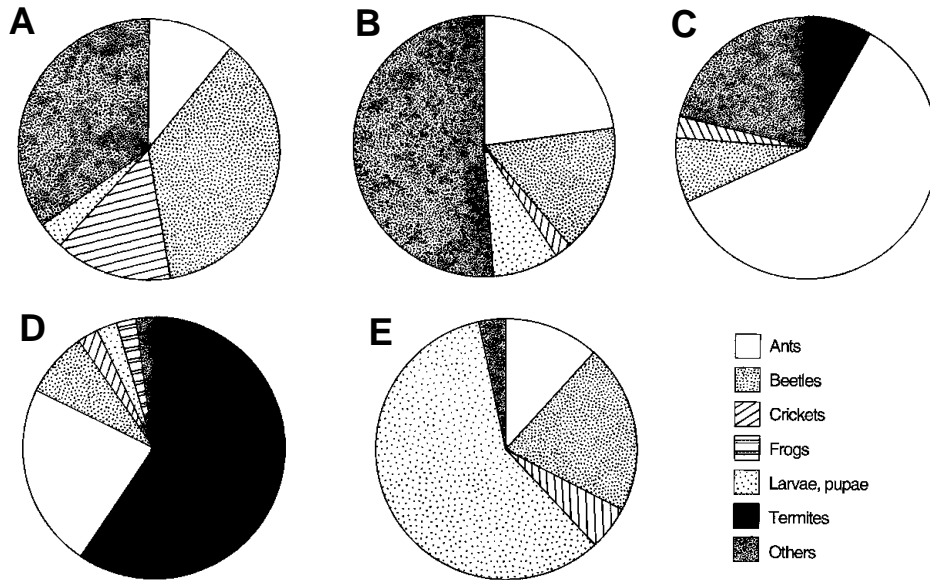


Figure 5.2 Diets of one introduced and four indigenous species from the Northern Territory. **A**, *Litoria pallida*; **B**, *L. rothii*; **C**, *L. rubella*; **D**, *Bufo marinus*; **E**, *Crinia* sp. (After Freeland & Kerin 1988) [D. Wahl]

but commonly frogs also breed in farm dams and in many other man-made structures that can hold water. Tyler (1991b) reported breeding by many northern Australian species in borrow-pits resulting from road construction.

Despite their propensity to lose water through the skin, frogs also survive well in arid areas. Several species of *Neobatrachus* and *Cyclorana* are able to burrow and form waterproof cocoons which reduce water losses to levels comparable to those of lizards (Lee & Mercer 1967; Chapter 4 this volume). These species can depress their metabolic rates when underground (van Beurden 1980; Flanigan, Withers & Guppy 1991). Such adaptations facilitate long-term survival in arid habitats. Van Beurden (1980) estimated that 10% of dormant *Cyclorana platycephala* could live for at least 5 years without feeding or emerging, and some could have survived longer.

Food

Among Australian frogs, the only known feeding specialist, *Myobatrachus gouldii*, feeds almost exclusively on termites (Calaby 1956). The remainder appear to be generalists. Freeland & Kerin (1988) reported seven diet classes: termites, ants, beetles, crickets, larvae-pupae, frogs and 'other', in their analysis of the food of *Litoria pallida*, *L. rothii*, *L. rubella*, *Bufo marinus* and a *Crinia* species from the Northern Territory. Five to seven of these prey groups were found in each of the five species. Similarly, the dietary items reported by Main (1968) for most species are very diverse, ranging from a variety of insects to land snails.

Generally, smaller frogs consume smaller prey. For example, *Crinia signifera* and *C. parinsignifera* in Victoria, eat mostly prey items weighing up to 29 mg and may actively avoid larger items, even though they are present in the habitat (MacNally 1983). However, large species also often eat surprisingly large numbers of small prey items. For example, *Heleioporus barycragus*, one of the largest Australian frogs (up to 86 mm snout-vent length), eats large numbers of ants and beetles (Lee 1967). By contrast, Lee (1967) found that the largest prey item, a centipede 9 cm long, was eaten by *H. eyrei* which has an average body length of about 55 mm.

Studies of the food of Australian frogs based on museum specimens may not necessarily represent diets at all times. For example, specimens of *Notaden nichollsi* collected after cyclonic rain are likely to have guts full of termites, as this is also a time when termites are particularly active. If this species had been collected after cool, winter rain the diet might be different (Main 1968).

Tadpoles feed either by actively foraging and scraping material off with the labial teeth and the beak or by trapping material in mucus secreted by the internal gills. The mucus traps bacteria, algae, zooplankton *etc.* from water flowing through the mouth and out over the gills. The mucus is then transferred into the oesophagus (Tyler 1989a). Most tadpoles are suspension feeders, consuming a combination of aquatic invertebrates, algae or other micro-organisms in the water column. However, tadpoles of some species are more predatory. The North American *Scaphiopus bombifrons* feeds on tadpoles of other species, and those of the Australian *Lechriodus fletcheri* (Pl. 2.10) may feed on tadpoles of its own species (Martin 1967b).

Breeding Seasons

Temperate frog species usually have a well-defined breeding season, but tropical species may reproduce throughout the year. In south-western Australia different species can be found breeding all through the year. Autumn breeders include the five species of *Heleioporus*, *Geocrinia leai*, *Pseudophryne guentheri* and *P. occidentalis*. These species deposit eggs on land where they hatch later and adopt a conventional tadpole life-style when flooded by rising water levels in winter. Winter breeders include *Crinia georgiana*, *C. insignifera*, *C. pseudinsignifera*, *C. glauerti* and *Litoria adelaidensis*. In spring, species of the *Geocrinia rosea* complex and *Litoria moorei* and *L. cyclorhyncha* breed. After heavy rains in autumn or early winter, species of *Neobatrachus* will also call and breed for short periods. In summer, *Myobatrachus gouldii* and *Metacrinia nichollsi* call after rain. In addition, some species that occur within the area of reliable winter rainfall will also breed after summer rains (*Neobatrachus kunapalari* and *Pseudophryne occidentalis*; Main 1965a, 1968).

Similar seasonal patterns are evident in other parts of the country though breeding and calling is likely to be cued in some way to local seasonal rainfall. The predictability of winter rainfall is crucial to egg survival and later tadpole survival, even in autumn breeders like *Heleioporus*.

Most species in the arid zone are explosive breeders that respond whenever significant rain falls (Main *et al.* 1959; Main 1968). However, there may be some temperature constraints on breeding activity. For example, according to Main (1965a), *Neobatrachus centralis* only breeds at temperatures above 16°C.

Egg and Tadpole Ecology

Australian frogs show a wide range of egg depositional strategies (Table 5.1). These range from the conventional frog strategy of eggs deposited in water with a free-swimming tadpole (all known hylid species and many myobatrachids), through terrestrial egg deposition with an aquatic tadpole (many myobatrachids such as *Heleioporus* and *Pseudophryne*), to total withdrawal from water with a direct developing egg (that is, no tadpole stage; microhylids and some myobatrachids such as *Geocrinia* and *Myobatrachus*). The complete withdrawal from water, combined with obligate parental care undertaken by the genera *Rheobatrachus* and *Assa* represents the ultimate depositional strategy for frogs. The diversity of egg depositional strategies is wide in myobatrachids, but only the conventional frog strategy is known certainly for hylids (Table 5.1). However, even if the eggs are deposited on land and there is a greater or lesser period of development out of water, in no case is this development independent

of water. Without either free water, or water in the surrounding soil, eggs will desiccate. No known frog anywhere in the world has evolved mechanisms that allow egg survival independent of external sources of water.

Ten reproductive modes are recognised here for Australian frogs (Table 5.1), compared to the eight recognised by Tyler (1985b). Modes I to X of Table 5.1 represent increasing removal of part of the development process from free-standing water. Thus I have recognised divisions based on the foamy or non-foamy form of the egg mass, and the site of egg deposition. The difference between eggs deposited in a burrow or amongst vegetation rather than buried underground represents the difference between easy and no access to free-standing water for the tadpole. Forms in which the egg hatches during development and the tadpole moves into water, or must persist in a locally moist microhabitat, are distinguished from those in which the egg is deposited in a locally moist microhabitat and all development takes place inside the egg capsule. Two categories relate to different forms of obligate parental care.

However, the modes do not represent a simple phylogenetic development with mode II derived from mode I and so on. Foamy egg masses in *Heleioporus* and other members of the subfamily Limnodynastinae may not represent an homologous form as *Heleioporus* lack the flanges on the first two fingers of females of other foam nesting species (*cf.* Roberts & Seymour 1989). A foamy egg mass may protect eggs from predators and desiccation, and reduce internal temperature by reflecting heat. It may also allow development of eggs on land, giving tadpoles an advantage when they enter ponds, or hold eggs at the water surface in well-oxygenated water.

Terrestrial egg deposition has probably evolved independently in each of the genera in mode III. None of these genera are closely related (Farris, Kluge & Mickevich 1982; Maxson 1992). Mode V may have evolved from the form in mode III, but it is less certain that mode VIII evolved from mode III, despite the close relationship between *Pseudophryne* and *Myobatrachus*, *Metacrinia* and *Arenophryne* (Roberts 1984; Maxson & Roberts 1985; Roberts & Maxson 1989). Highly-derived breeding biologies have apparently evolved independently in many Australian frog genera, although in their analyses of relationships of Australian frogs both Heyer & Liem (1976) and Farris *et al.* (1982) treated direct development as an homologous character in all genera of myobatrachids.

Eggs of many Australian species which are not direct developers can survive in moist terrestrial environments. Martin (1967a) reported survival for up to 118 days for eggs of *Geocrinia victoriana*. Shorter survival periods are known for eggs of *Heleioporus* and *Pseudophryne* species held out of water (Main 1965a; Lee 1967). During this period the developing embryo grows and survives on nutrients stored in the egg yolk. Eggs of these species hatch when flooded by rising water levels.

BEHAVIOUR

Basking

Though frogs are usually active at night (for example, Tyler *et al.* 1983a), several Australian species are active during the day. *Taudactylus diurnus* from south-east Queensland takes its specific name from its exclusively diurnal activity pattern (Straughan & Lee 1966). Johnson (1971a) showed that body temperatures of *T. diurnus* were generally higher than ambient air temperatures (greatest differences were 5.5°C for adults and 8.0°C for juveniles), suggesting

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Table 5.1 Reproductive modes in Australian frogs. References are given for species where unusual reproductive modes are indicated, or only certain species in a genus have a particular egg mass form. Otherwise data are taken from Table 1 of Tyler (1985).

Mode	Eggs	Larvae	Family	Genus
I	in water, non-foamy egg mass	in water	Hylidae Myobatrachidae	<i>Cyclorana</i> , <i>Litoria</i> , <i>Nyctimystes</i> , <i>Crinia</i> , <i>Limnodynastes tasmaniensis</i> (southern call race ¹), <i>Neobatrachus</i> , <i>Notaden</i> , <i>Pseudophryne douglasi</i> ² , <i>Taudactylus</i> , <i>Uperoleia</i>
			Ranidae	<i>Rana</i>
II	in water, foamy egg mass	in water	Myobatrachidae	<i>Adelotus</i> , <i>Heleioporus australiacus</i> ³ , <i>Lechriodus</i> , <i>Limnodynastes</i> , <i>Megistolotis</i>
III	on land, in burrow or amongst vegetation above water	in water	Hylidae (?) Myobatrachidae	possibly <i>Litoria longirostris</i> ⁴ <i>Geocrinia</i> (except <i>G. rosea</i> group ⁵), <i>Mixophyes</i> , <i>Pseudophryne</i>
IV	foamy egg mass on land, in burrow.	in water	Myobatrachidae	<i>Heleioporus</i>
V	on land, in depression, hatches from capsule	direct development, no feeding stage	Myobatrachidae	<i>Geocrinia rosea</i> group ⁵
VI	foamy egg mass, on land, in depression or nest	direct development, no feeding stage	Myobatrachidae	<i>Kyarranus</i> , <i>Philoria</i>
VII	on land, in depression or nest	direct development, no feeding stage	Microhylidae	<i>Cophixalus</i> , <i>Sphenophryne</i>
VIII	deep under soil surface (up to 1.2 m), intracapsular development	direct development, no feeding stage	Myobatrachidae	<i>Arenophryne</i> , <i>Myobatrachus</i> , possibly <i>Metacrinia</i>
IX	on land, male carries developing larvae in inguinal pouches	direct development, no feeding stage	Myobatrachidae	<i>Assa</i>
X	on land, female carries developing larvae in stomach	direct development, no feeding stage	Myobatrachidae	<i>Rheobatrachus</i>

¹ Roberts & Seymour 1989; ² Main 1965; ³ Watson & Martin 1973; ⁴ Tyler & Davies 1977; ⁵ Roberts, Wardell-Johnson & Barendse 1990.

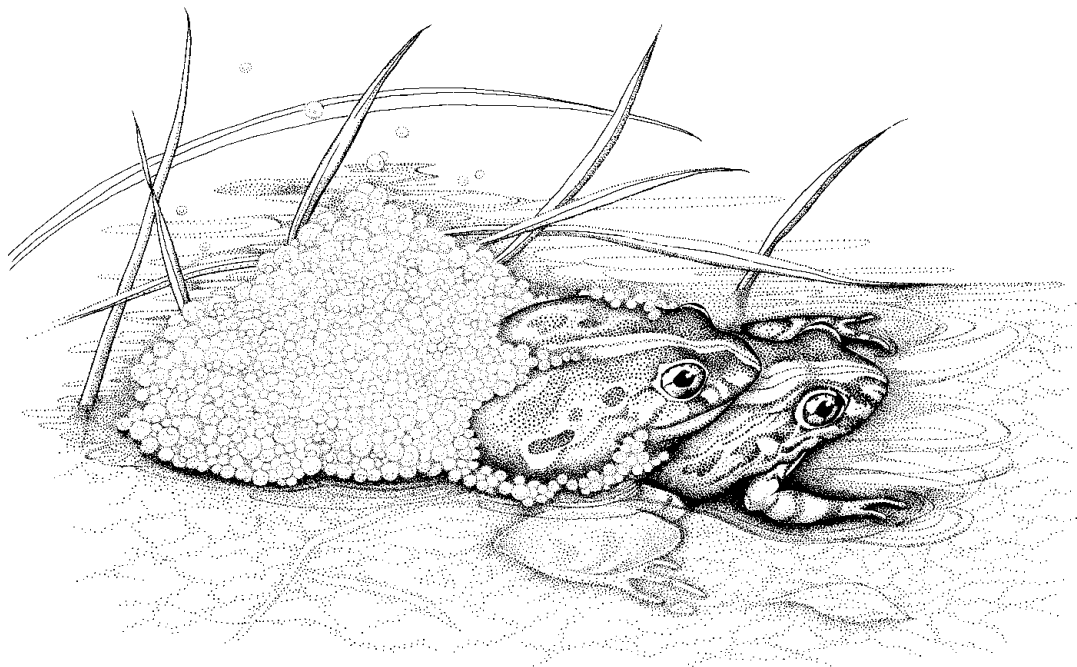


Figure 5.3 Amplexed pair of *Limnodynastes ornatus* depositing foam nest. Eggs are mixed up in the foam or are in a jelly layer at the water surface 9

that there is active thermoregulation. However, the mechanism is not clear as eleven nocturnally active species also showed body temperatures higher than ambient (Johnson 1971b).

Tyler *et al.* (1983a) reported diurnal basking in *Cyclorana australis* and *Litoria dahlia* from the Northern Territory. Field body temperature in both these species was very similar to those of their local environment. Field studies on other continents have shown that many frog species may maintain body temperatures above the ambient temperature by actively moving between different thermal micro-climates. Basking forms part of this process and is particularly common in species from high mountain habitats (see summary in Hutchison and Dupré 1992).

BREEDING BEHAVIOUR

The basic breeding system of frogs involves adults pairing, external fertilisation of eggs which develop in water and hatch into a tadpole, followed by metamorphosis into a small frog. However, this basic summary hides much of the complexity and diversity in breeding systems.

In most frogs, pairing of males and females is initiated by the male's call (see section on Calls below) which has a crucial function in attracting females. Once together the male and female amplex with the male on the back of the female. Eggs are released from the cloaca of the female and typically are fertilised externally by sperm released simultaneously by the male.

A few frogs have internal fertilisation. For example, sperm is transferred by a specialised intromittent organ in *Ascaphus truei* from the north-west coast of the United States of America. Internal fertilisation may occur in *Eleutherodactylus coqui*, as sperm have been found in the female reproductive tract and fertile eggs can be deposited without male involvement (Townsend, Stewart, Pough & Brussard 1981). The American genus *Eleutherodactylus* and the West African genus *Nectophrynoides* achieve internal fertilisation by apposition of the cloaca of males and females. Though internal fertilisation may occur in Australian frogs, it has not been demonstrated.

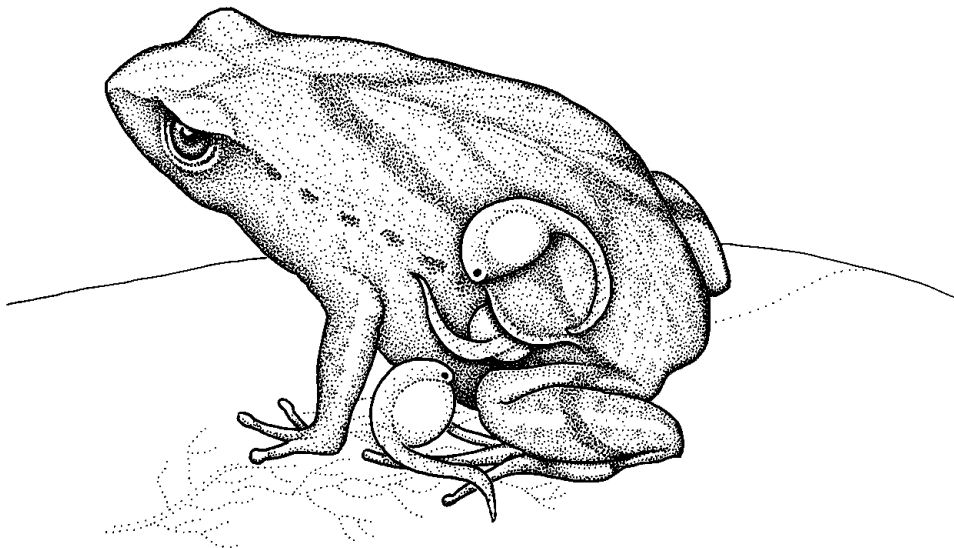


Figure 5.4 Hatched tadpoles entering the inguinal pouches of a male *Assa darlingtoni*. Eggs are deposited on land, hatch and then develop in the inguinal pouch for about 49 days. (After photo by H. Ehmann/NPIAW)

[T. Wright]

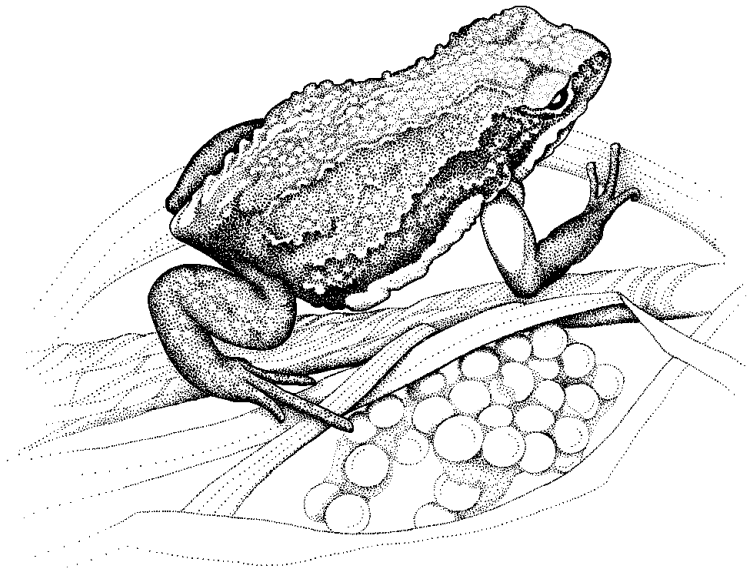


Figure 5.5 Male *Pseudophryne major* are commonly associated with eggs, but these eggs can develop without the male present. (After photo by M. Trenerry/NPIAW) [T. Wright]

There are several Australian species with direct development and in at least one case, *Arenophryne rotunda*, males and females stay associated for up to five months before egg deposition, suggesting that male involvement at that time is important (Roberts 1984).

Parental care by males is known in *Cophixalus parkeri* (a microhylid from New Guinea) and the presence of adults, usually males, enhances egg survival (Fig. 9.4; Simon 1983). Male parental care may be important in Australian *Cophixalus* though it has not been documented. Male parental care is well developed in *Assa* where males carry the developing young in inguinal pouches (Fig. 5.4; Straughan & Main 1966). In the genus *Pseudophryne*, males are commonly associated with eggs but these eggs can develop without the male present (Fig. 5.5; Woodruff 1977). As Woodruff noted, the association of eggs and males may not be a form of parental care, but rather continued use of a successful calling site by males. Gastric brooding is a bizarre and unique form of parental care, where developing eggs are carried in the stomachs of females of the genus *Rheobatrachus* from Queensland (Fig. 5.6; Tyler 1989a).

Calls

The functions of calls of frogs are now well known (for example, Wells 1977), with calls serving several different purposes. A detailed bibliography on calls of Australian frogs is given by Tyler (1989a, Table 4).

Advertisement calls are those that are usually heard. They are produced almost exclusively by males, and generally serve the equally important roles of attracting females and indicating the caller's location to other males. Species that call at the same site at the same time nearly always have very distinct calls. This distinction means that females are unlikely to approach males of the wrong species and there is therefore a reduced risk of hybridisation. The distinct calls of sympatric species has led to the discrimination of many Australian frog species that are morphologically similar, as discussed by Main (1968) for *Crinia*.

Advertisement call structures in myobatrachids range from simple short clicks, such as those of the southern call race of *Limnodynastes tasmaniensis*, *Geocrinia rosea* and *G. lutea* (Littlejohn & Roberts 1975; Roberts, Wardell-Johnson & Barendse 1990), through pulse trains and tones with fundamental and harmonic frequencies (for example, *Neobatrachus* and *Heleioporus* species respectively; Littlejohn & Main 1959) to rapid pulse trains with a complex harmonic structure, such as those of many *Cyclorana* species. The calls of hylid species show a similar diversity, but with more emphasis on pulse trains with high pulse repetition rates, and in some instances, complex harmonic structures. Detailed descriptions of hylid calls are not as readily available as for myobatrachid frogs, but there are data for various *Litoria* species and for a number of *Cyclorana* species (Tyler 1989a).

One notable feature of the calls of Australian frogs is the absence of significant frequency modulation, a common feature in the calls of central and South American frogs (Fig. 5.7; Duellman & Trueb 1986).

Territorial calls are used by males at close range to deter other males from a potential calling site. In many species, these calls are quite different from the advertisement call, but may be derived from it in a graded series of steps. As the level of interaction between two males increases, the form of the call alters, for example, by the addition of notes, or elongation of the call as occurs in *Crinia georgiana* (Ayre, Coster, Bailey & Roberts 1984). In *Geocrinia laevis*, for example, the territorial and female attraction functions are functionally uncoupled, with an introductory call used in male-male interactions and a repeated note used for female attraction (Littlejohn & Harrison 1985). A similar biphasic call occurs in *Eleutherodactylus coqui* from Puerto Rico. In this species behavioural studies have established that males and females respond differently to the 'co' and 'qui' components of male call (Narins & Capranica 1976, 1978). Investigations of neural anatomy confirmed that these are obligate responses by males and females: males hear and respond better to the 'co' component, and females better to the 'qui' component of coqui calls (Narins & Capranica 1980).

Release calls are well known in *Bufo* species (for example, Brown & Littlejohn 1972) and may be produced by frogs of either sex. Their function is to indicate to amplexing males that the frog amplexed is either a spent female or another



Figure 5.6 Oral birth in the gastric-brooding frog *Rheobatrachus silus*. (After photos by M. Tyler/ANT, R.W.G Jenkins/NPIAW) [T. Wright]

male. They have not been reported in Australian native species, perhaps because they have not been looked for. Such calls may occur in explosive breeders where males persist in calling for two or more nights and spent females are active at the same calling sites (for example, *Neobatrachus* species).

Alarm calls are well known in many Australian species and may be produced by frogs of either sex. For example, *Litoria moorei* commonly scream when attacked by domestic cats. However, it is not clear how effective these calls are in deterring predators. Heel, Hugo & Watts (1985) investigated the impact of the alarm scream of *Heleioporus eyrei*, on feeding activity of the bandicoot *Isoodon obesulus*, and found that simultaneous presentation of alarm calls and food items had no impact on the feeding of this known predator of *H. eyrei*.

Calling may also occur in other contexts in which its function is unknown. Martin (1969) reported calling by male *Limnodynastes dumerilii* in underground burrows. It is also important to note that it is not easy to arbitrarily categorise a function for any particular call. For example, Roberts (1978) reported amplexus

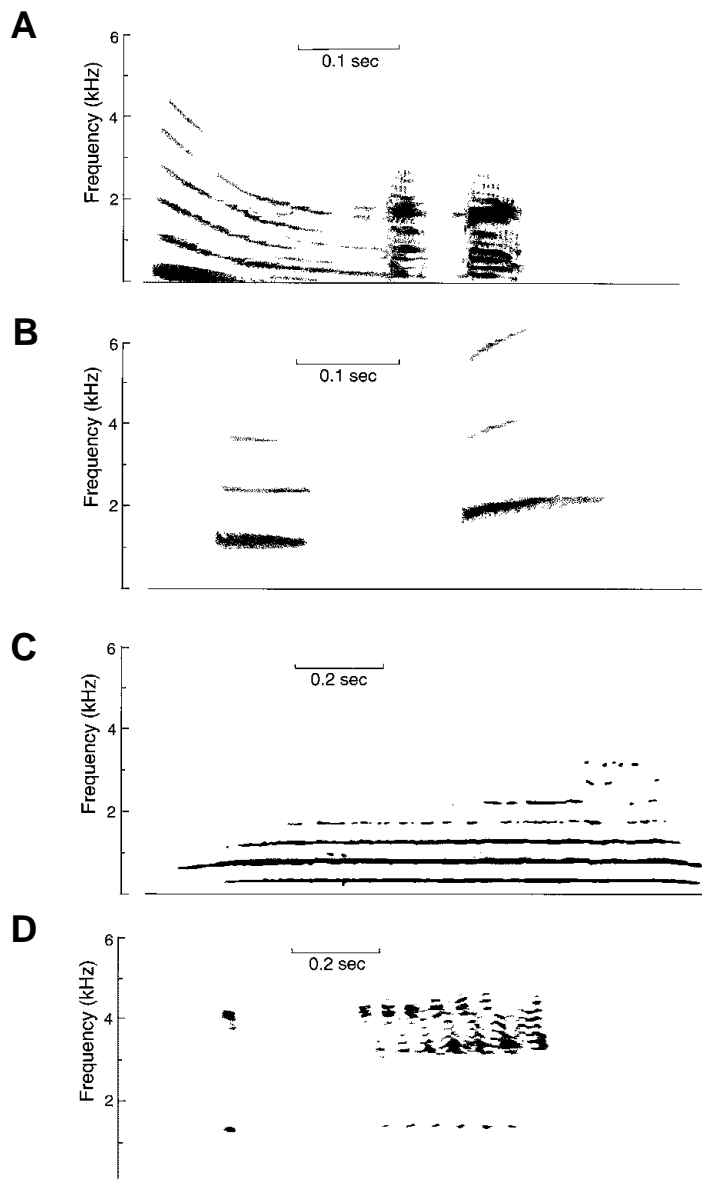


Figure 5.7 Sound spectrograms of call structure in two South American and two Australian frogs. **A**, *Physalaemus pustulosus*; **B**, *Eleutherodactylus coqui*; **C**, *Heleioporus eyrei*; **D**, *Litoria pallida*. (A, B from Duellman & Trueb 1983; C from Littlejohn & Main 1959; D from Davies, Martin & Watson 1983) [W. Mumford]

in *Neobatrachus pictus* before males called and before either frog in the pair entered the pond. Calls in this species may have a major function in male-male interactions where males are actively trying to displace other males from amplexus with females (cf. Davies & Halliday 1979).

Call Interactions

Variation in call structure as a result of competition with other males of the same species, or a different species, ensures that a male's signal is transmitted free of acoustic interference. Male *Crinia georgiana* vary the number of quacks per call when stimulated by an artificial stimulus similar to the call of a conspecific (Ayre *et al.* 1984). The basic call of *C. georgiana* is a single quack, like the sound of a duck (Main 1965a). Males increase the number of quacks per call to match the output of their neighbour. Adjacent males of this species, and many others, also alternate their calls. These variations in call and calling strategies are probably a response to the intense male-male competition in many species with prolonged breeding seasons.

Interspecific interactions may also occur. Littlejohn & Martin (1969) demonstrated that calling by *Pseudophryne semimarmorata* was inhibited when males of *Geocrinia victoriana* called at the same sites. In this instance, male *P. semimarmorata* called faster when the other species stopped calling.

Evolution of Calls

The evolution of call structures in frogs is not understood. Some species exhibit little change in call structure over long time periods, whilst others do not. Within the myobatrachids there are some striking examples of slow rates of call structure evolution. The call of *Arenophryne rotunda* is almost identical to the call of *Pseudophryne bibroni* (Roberts 1984), despite an estimated more than ten million years of separate evolution of these two genera (Maxson & Roberts 1985). However, this similarity might also be a result of convergence rather than stability in the form of the call.

The southern call race of *Limnodynastes tasmaniensis* has a single click call, but the closely related northern and western call races have amplitude modulated, multiple note calls (Littlejohn & Roberts 1975; Roberts 1993). These three call races have probably evolved within the last one to two million years (Roberts & Maxson 1986). In some cases interactions with related species are a likely cause of call structure variation. The calls of *Litoria ewingii* and *L. verreauxii* are almost identical where these two species are allopatric with respect to each other, but their calls diverge when the two occur together in central and eastern Victoria (Littlejohn 1965). Likely causes may be interaction between the two species and selection against hybrids, for example, by reinforcement or reproductive character displacement (Butlin 1987), or an acoustic interaction without hybridisation, as discussed above (Littlejohn & Martin 1969).

Mute males have been reported several times in Australian species, but none have been substantiated. Even species which use visual displays, foot, hand or complex body movements, to communicate in noisy environments like the splash zones of cascades and waterfalls have been found to call (Winter & McDonald 1986; Richards & James 1992). Main *et al.* (1959) reported no call for *Myobatrachus gouldii*. However, Roberts (1981) described the call of this species and showed that it called on only one or two nights per year and at times that were totally unexpected given patterns of egg development. Without the chance field observations of calling by *M. gouldii*, made by Baynes (pers. comm.) while he was catching bats, this species still might be classified as mute.

ECONOMIC SIGNIFICANCE

Conservation problems

Some Australian frog species are protected under general fauna protection legislation of the States, whilst others are protected by relevant local fauna authorities. For example, in Western Australia, *Geocrinia alba* and *G. vitellina* are listed as ‘fauna that is likely to become extinct, or is rare’, because *G. vitellina* has a very restricted distribution (less than 20 ha of suitable breeding habitat) and *G. alba* is threatened by land clearance (Wardell-Johnson & Roberts 1991).

Declining numbers of some species pose special conservation problems. Despite protection, both by legislation and their occurrence in National Parks, *Rheobatrachus* and *Taudactylus* species seem to have declined to the point of extinction (McDonald 1990). However, this may, or may not, be a natural phenomenon, as noted above.

The destruction of natural water courses and swamps by control of river systems and land drainage has undoubtedly affected the distribution of many species. Similarly, the widespread occurrence of land and water salination may have caused the local demise of many species (for example, Main 1990). However, there is no evidence of the loss of a significant portion of the known fauna, as has occurred with Australian birds and mammals. This may be a consequence of the poor knowledge of the Australian frog fauna until relatively recently; the loss of species with restricted ranges may well have gone unnoticed.

There is no clear evidence that interactions of native frog species with the introduced *Bufo marinus* (Pl. 1.2) have had any detrimental effects. Recent work in the Northern Territory, where *B. marinus* has arrived recently, suggested that the invader generally eats different food items and may not interact directly with native frog species (Fig. 5.2; Freeland & Kerin 1988), though these data are from a single sampling at one time of the year. Tyler (1989a) reported that *Bufo marinus* may have had an impact on other faunal components though the direct evidence is not strong.

Economic Values

No Australian frog species have been specifically exploited by European man as a food item, though many species have been used by indigenous Australians (for example, Peile 1978). The skins of many Australian species have been investigated for the presence of pharmacologically active compounds (Erspamer, Falconieri, Erspamer, Mazzanti & Endean 1984). Caerulein, in widespread use for a number of medical diagnostic procedures (Erspamer & Melchiorri 1983), was initially derived from the skin of *Litoria caerulea*, but is now manufactured artificially (Tyler 1976b). *Bufo marinus* was in widespread use as a pregnancy testing device before the advent of specific hormone analyses (Tyler 1989a).

Introduced Frogs

Only one frog species, the cane toad *Bufo marinus*, has been introduced into this country. As detailed in Chapter 11, *B. marinus* was first introduced to control insect pests in sugar cane, and is now widespread in Queensland and spreading rapidly into the Northern Territory and New South Wales. *Bufo marinus* has had a minor role in education, as items for dissection and other areas of biological research (Tyler 1989a).

Australian frogs have been introduced to several other countries. *Litoria aurea* and *L. ewingii* occur in New Zealand. *Litoria aurea* has also been introduced to Vanuatu (Tyler 1979b).