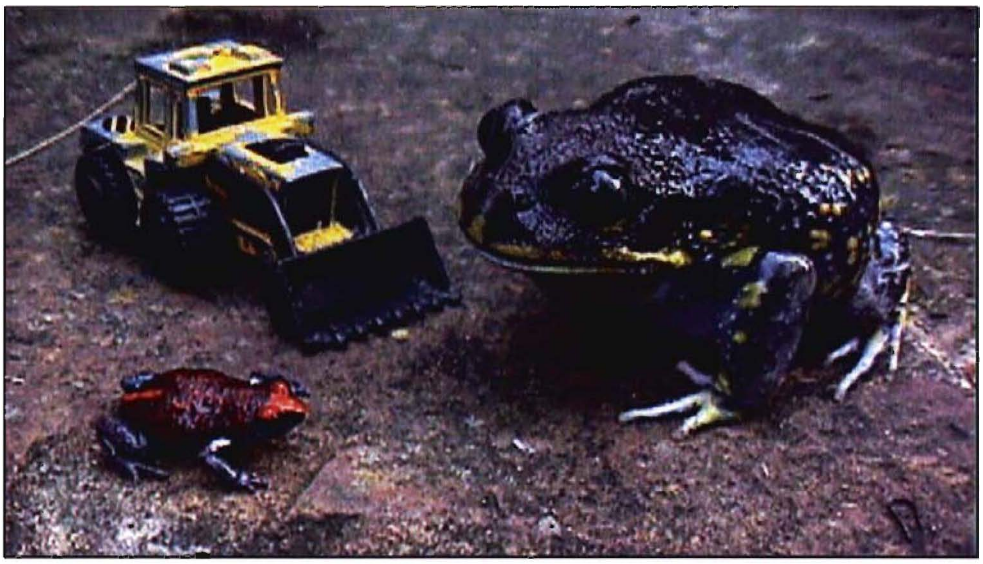
HABITAT REQUIREMENTS AND HABITAT USE OF THE RED-CROWNED TOADLET *PSEUDOPHRYNE AUSTRALIS* AND THE GIANT BURROWING FROG *HELEIOPORUS AUSTRALIACUS* IN THE SYDNEY BASIN



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CERTIFICATE OF AUTHORSHIP / ORIGINALITY

I certify that the work in this thesis has not previously been submitted for a degree nor has it been submitted as part of requirements for a degree except as fully acknowledged within the text.

I also certify that the thesis has been written by me. Any help that I have received in my research work and the preparation of the thesis itself has been acknowledged. In addition, I certify that all information sources and literature used are indicated in the thesis.

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Andrew Stauber

June 2006

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Some personal comments

This research program provided me with a unique opportunity to learn more about some of the animals I feel passionate about. Working on these threatened frogs, I learned that it is often difficult to reach conclusions due to low sample sizes. Nevertheless, it is my belief that conservation efforts for any threatened species can only be maximised if they are based on information of that particular species.

The threatened status of both frogs was more than once the catalyst for restrictions on experimental procedures and sample sizes imposed by the Animal Care and Ethics Committee. The numbers of animals encountered in the field were generally low because of both species' rarity, and the ongoing drought may also have interfered with sample sizes. I am strongly convinced however, that the numbers of animals identified and measured for this report are the highest ever recorded for both species.

Occasionally things do not work out the way they were planned. I had manufactured and installed 192 buckets and fencing in three replicated sandstone areas in a layout that would have allowed me to test for differences in abundance based on relative distance from a road, relative distance from a water course, and vegetation structure. Over six months, 1824 bucket nights yielded 10 individual *H. australiacus*. Shortly after trapping had started, an arson attack to a trapping site meant that 16 buckets had to be relocated to a new, unburnt site. After six months, 75% of all traps had become inoperable as a result of four different fires. Those fires spelt the end of that exercise.

It was not all doom and gloom. I acquired many new and useful skills and saw many wonderful things during all those days and nights in the bush. I also got the opportunity to learn the developmental stage at which *H. australiacus* tadpoles hatch from their eggs, a fact previously unknown (Anstis, 2002). My work also led to the first record of a snake parasite *Sphaerocephalus rotundicapilatus* in an amphibian (many thanks to Prof. Lesley Warner for identifying the organism).

I hope the work I put into this program will eventually be used to benefit both the "lively perky little frog" as well as the large one whose "rarity must apologise for its deformity" (a statement I disagree with; see Chapter 1, Sections 4 and 5).

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LIST OF ABBREVIATIONS

ACEC	Animal Care and Ethics Committee
AM	Australian Museum, Sydney
AMG	Australian Map Grid (always Zone 56 in this text)
Culvert	pipe or similar structure used to direct water under the track
E	Easting (AMG Reference)
GIS	Geographic Information System
IUCN	International Union for Conservation of Nature and Natural Resources
LMF	Digital Location Map of animals where they were First encountered
m	metre (unit of length)
Mitre drain	drain to conduct runoff from the shoulders of a track to a disposal area away from the road alignment
M-W	Mann-Whitney statistical test
N	Northing (AMG Reference)
n	Numbers, sample size
NPWS	NSW National Parks and Wildlife Service
NP	National Park
NR	Nature Reserve
NSW	New South Wales
Reserve System	protected lands including NP, NR, as well as SF
SE	Standard Error
SF	State Forest land
SF NSW	State Forests of New South Wales
Table drain	side drain of a track running adjacent to and parallel with the shoulders and forming part of the track formation
WA	Atlas of NSW Wildlife

ABSTRACT

Habitat requirements and habitat use for *Pseudophryne australis* and *Heleioporus australiacus* were investigated to aid management of these threatened frogs around Sydney, Australia. Much of the work focussed on roads, commonly encountered features in the habitat of both species.

The habitat requirements based on locality records of both frogs in the Sydney Basin were investigated at four spatial scales. Both species are habitat specialists. They showed a strong geological association with Hawkesbury Sandstone and occupy upper topographic areas with ephemeral watercourses of gentle gradients. Both frogs occur predominantly in areas of higher precipitation and milder temperature regimes compared to averages representative of the region. Leaf litter is an important feature of *P. australis* breeding sites, whereas *H australiacus* generally associate with crayfish burrows. Both species are dependent on natural vegetation with a complex structure.

H australiacus have a relatively long larval period (3 - 12 months) and breed in ephemeral pools, exposing their tadpoles to the risk of dying due to early pond drying. In the laboratory, tadpoles responded to decreasing water levels by shortening their larval periods and metamorphosing earlier than siblings held at constant water level. Despite this plastic response, a number of pools in the field failed to produce metamorphs due to early drying, an observation also made on *P. australis.* Regular monitoring of breeding sites revealed increased reproductive success away from roads for both species probably because of relatively longer hydroperiods.

Spatial distributions and associations with habitat features, and movement patterns of both frogs were further investigated using mark-recapture methods. Both species showed strong site fidelity. *P. australis* formed small aggregations and predominantly selected leaf litter piles despite their relatively low availability. Leaf litter piles in creeks moved over time and the animals moved with these piles. In contrast, *H australiacus* individuals formed no aggregations and showed no preference for any available structural vegetation type.

Locations of individuals were independent of relative distances to creeks and artificial drains, but males appeared to be more common near culverts. However, individuals were randomly distributed in space and nearest-neighbour distances were high relative to individual movement distances, suggesting minimal overlap between relatively large home ranges.

Radio-telemetry demonstrated that some *H australiacus* individuals burrow in the road environment. There they would be at risk of being dug up and possibly injured during road works.

The results are discussed in relation to the spatial requirements of both species and the protection of utilised habitat features. Management options are suggested to mitigate the impacts of road works. Differences in spatial dynamics of both frogs with overlapping habitats highlighted in this study require species-specific management approaches.

Chapter 1

GENERAL INTRODUCTION

The red-crowned toadlet *Pseudophryne australis* and the giant burrowing frog *Heleioporus australiacus* are two threatened frogs that predominantly occur around Sydney, where habitat loss through urbanisation potentially impacts negatively on their populations. The research presented here focuses on habitat requirements and habitat use of both frogs to aid in their management. This introductory Chapter puts into perspective amphibian declines and the importance of the identification and preservation of habitat for the conservation of species. Both frogs associate with roads through bushland, and for this reason, a section is devoted to a literature review of the general impacts of roads on flora and fauna. This is followed by the research questions and aims of this project. Literature reviews of both species are presented before a brief preview of Chapters 2 - 6.

1 Amphibian population declines

The global declines of many amphibian populations are perhaps one of the most puzzling and urgent environmental problems of the late 20th and early 21th centuries (Alford & Richards, 1999; Barinaga, 1990; Blaustein & Wake, 1990; Daszak *et al.*, 1999; Gubta, 1998; Halliday, 1998; Lannoo, 2005; Stuart *et al.*, 2004; see also http://www.globalamphibians.org and http://www.frogs.org). In 1989, scientists at the First World Congress of Herpetology came to realise that amphibian population declines were widespread (Barinaga, 1990). Fifteen years later, the International Union for Conservation of Nature and Natural Resources (IUCN) Global Amphibian Assessment (GAA) published a study which found that of the 5743 amphibian species surveyed worldwide, an alarming 43.2% were experiencing some form of population decrease (Stuart *et al.*, 2004). Globally 32.5% of amphibians (1856 species) are listed as threatened, a larger percentage than birds (12%; 1211 species) and mammals (23%; 1130 species). The report also stated that the world's most rapidly declining amphibian species are those of Australia and New Zealand, and the Neotropics (Stuart *et al.*, 2004).

Likely causes for the now well documented global declines in amphibians (Alford & Richards, 1999; Blaustein *et al.*, 1994a; Campbell, 1999; Drost & Fellers, 1996; Sarkar, 1996) include pathogenic fungi and viruses (Blaustein *et al.*, 1994b; Daszak *et al.*, 1999; Speare, 2000), increased ultra-violet exposure (Blaustein *et al.*, 1997; Kiesecker *et al.*, 2001) and climate change (Kiesecker *et al.*, 2001; Wake, 1991), all of which may affect frog numbers on a global scale, whereas habitat destruction and disturbance, including pollution, introduced predators and competitors, logging and acid rain (see also review in Alford & Richards, 1999; Wake, 1991), are some of the factors listed to affect species at regional scales. Habitat disturbance and destruction has been identified as a single causal factor in significant amphibian population declines (Alford & Richards, 1999; Wilbur as quoted by Barinaga, 1990; Delis *et al.*, 1996; Ehmann & Cogger, 1985; Hayes & Jennings, 1986; Hecnar & M'Closkey, 1996; Stuart *et al.*, 2004; Tyler, 1997). Indeed, habitat destruction is considered the principal cause of the decline in 42% of the 435 species listed by the IUCN as "rapidly declining" (Stuart *et al.*, 2004), and was identified as the major cause of amphibian losses by Blaustein *et al.* (1994b).

2 Habitat protection – an integral part of conservation biology

The threat of habitat destruction is not restricted to amphibians alone. Habitat destruction is considered responsible for the decline of many of the now extinct and threatened plant and animal species in Australia (Ehmann & Cogger, 1985; Leigh & Briggs, 1992; Possingham *et al.*, 1995; Recher & Lim, 1990; Schur, 1990; Sivertsen, 1994) and globally (Brooks *et al.*, 2002; Clark *et al.*, 1990; Fahrig, 2001; IUCN, 2003; Janzen, 1986; May, 1990; Noss & Cooperrider, 1994; Wilson, 1989). Elsewhere, habitat destruction is the greatest threat to plants and animals (1880 species surveyed) (Wilcove *et al.*, 1998).

Habitat destruction can be viewed as having two components: habitat loss and habitat fragmentation. Habitat loss results from the total destruction or removal of habitat cover, or any other modification or degradation of an extent that renders the place unusable to its inhabitant. Habitat fragmentation creates a greater number of smaller, isolated habitat patches (Fahrig, 1997). In either form, habitat destruction has an obvious effect: the disappearance of habitat from the landscape leads to the displacement, or even loss of organisms which in turn produces the decline of a single or multiple populations (Bender, Contreras & Fahrig, 1998; Bolger *et al.*, 1991; Fahrig & Merriam, 1985; Soulé *et al.*, 1992; Wiegand *et al.*, 2005). It is not surprising then that biodiversity conservation efforts all over the world are based on the protection of habitat, for both terrestrial and marine systems (Hambler, 2004; Haskell, 2003; Noss & Cooperrider, 1994; Primack, 2002). For species conservation based on habitat protection to be successful, sound knowledge of the organism's habitat requirements is essential (Aberg *et al.*, 2000; Harding *et al.*, 2001).

Habitat (Latin: it dwells) is the place (Begon *et al.*, 1996) or environment (Purves *et al*, 1995) where an organism lives. Some definitions limit the word habitat to only include natural (i.e. not made, caused by, or processed by humankind) homes or environments (e.g. Pearsall, 2002). Here I use the word habitat in a more general sense to include man-made structures and landscape features. The habitat is an organism's most important asset and should contain all the resources necessary for a population, or populations of organisms to persist. The ideal habitat to maximise individual fitness and population persistence supplies resources in sufficient quantities for growth and reproduction, including mates. It also has few predators, except those that afflict competitors (Bazzaz, 1991).

Information on an organism's habitat requirements is an integral component of conservation biology. It is used to identify and rank sites where individuals are more likely to occur (e.g., Aebischer *et al.*, 1993; Christie & Van Woudenberg, 1997; Ferrier *et al.*, 2002). Furthermore, habitat information is essential for the prediction or modelling of potential species' occurrence at places that have not been sampled, and helps in the assessment of changes in habitat area resulting from disturbances (Burgman & Lindenmayer, 1998; Carroll *et al.*, 1999; Edwards *et al.*, 1996; Ferrier, 1991; Guisan & Zimmermann, 2000; Neave & Norton, 1991). Knowledge of a species' habitat requirements has found application in conservation area planning (Lehmkuhl, 1984; Remmert, 1982; Semlitsch & Bodie, 2003) and habitat restoration efforts (e.g., Matthews & Pope, 1999). Information on the species – environment relationship is also critical for impact assessment, the design of management strategies, and the framing of conservation legislation (Burgman & Lindenmayer, 1998; Noss & Murphy, 1995). In addition, habitat information facilitates metapopulation analysis and the prediction of recolonisation patterns (Hanski & Gilpin, 1997).

Habitat protection is usually achieved collectively for multiple species or communities through reserve allocation (e.g., Kavanagh, 1991). However, because habitat requirements and habitat use differ among invertebrates (e.g., Postle *et al*, 1991), birds (e.g., Recher, 1991), mammals (Catling, 1991; Dickman, 1991), reptiles and amphibians (e.g., Newell & Goldingay, 2004), management decisions often need to be based on species-specific habitat information (e.g., Newell & Goldingay, 2004).

2.1 Habitat requirements and habitat use

For convenience, species – environment relationships can be split into several components. Here I deal with two fundamental components of this relationship, which I loosely refer to as habitat requirements and habitat use. The distinction is largely a matter of scale. The habitat requirements of a species are described by the set of values determined for presumably biologically meaningful variables obtained for the range of sites where the species is known to occur. Habitat use is related to the spatial requirements of individuals and populations and takes into consideration the movement patterns of individuals and the spatial arrangement of individuals within populations (White & Garrott, 1990). Information on habitat requirements therefore allows the identification and modelling of potential habitat (Hayward & McDonald, 1997; Lindenmayer *et al.*, 1995; McIntyre & Lavorel, 1994; Neave & Norton, 1991; Parris, 2002), whereas data on habitat use pertain to the spatial requirements of individuals and populations (Goldingay & Kavanagh, 1991; Kearns, 1997; Lehmkuhl, 1984; Matthews & Pope, 1999; Remmert, 1982; Spieler & Linsenmair, 1998; Squires *et al.*, 1993) and may include a temporal dimension where seasonal movements in a heterogenous environment are involved (e.g., Spieler & Linsenmair, 1998).

Generally, the life history of frogs, including both *P. australis* and *H. australiacus* (but see species profiles on differences in egg deposition sites), is made up of an aquatic tadpole phase, followed by a terrestrial existence after metamorphosis (Duellman & Trueb, 1994). These species therefore require two distinctly different habitat types. The nature and quality of the aquatic habitat can determine the duration of the tadpole stage and the timing of metamorphosis. The tadpole stage may have a carry-over effect and influence fitness and reproductive success of individuals in the terrestrial life stages (e.g., Werner 1986). The quality of the terrestrial habitat is most likely to also have a direct influence on individual reproductive success. Most frogs therefore require access to both aquatic and terrestrial habitats of suitable qualities. This subject is extensively reviewed in Chapter 3.

2.2 Roads as habitat components and their effects on flora and fauna

Roads are permanent landscape features in terrestrial habitats and are ever increasing in number. The construction of roads inevitably changes habitats and leads to a whole array of negative effects on a variety of ecosystem attributes. Emerging evidence suggests that road construction can result in significant decreases in biodiversity at both the local and regional scale (Findlay & Bourdages, 2000) due to a combination of increased extinction rates and decreased recolonisation rates (Findlay & Houlahan, 1997). There are several mechanisms associated with roads that act negatively on biodiversity. These were reviewed by Andrews (1990), Bennett (1991) and Trombulak & Frissell (see also Goosem, 2004; 2000). A number of these mechanisms are briefly mentioned below.

Road construction can destroy habitat (Carr & Fahrig, 2001). This is also documented for *Pseudophryne australis* and *Heleioporus australiacus* in Chapter 5. Roads can act as barriers by restricting the movement of species between populations (Findlay & Bourdages, 2000; Merriam *et al.*, 1989; Vos & Chardon, 1998), negatively impacting gene flow among populations (Gibbs, 2001; Trombulak & Frissell, 2000). Roads also impose edge effects on adjacent habitat (Andrews, 1990; Bennett, 1991) and often fragment the landscape. Habitat fragmentation by roads has been shown to have negative effects on flora and fauna, including amphibians (Andrews, 1990; Bennett, 1991; Carr & Fahrig, 2001; Soulé *et al.*, 1992). Roads may facilitate the invasion of exotic species including competitors and predators (Cowie & Warner, 1993; Lonsdale & Lane, 1994) and allow increased human access (Young, 1994).

Roads also bring with them structural changes to the environment. Abiotic effects of road construction are changes to the hydrology of the local environment within and beyond the boundary of the road reserve. Such changes include impeded or increased supply to wetlands, wetland creation or drainage (Bennett, 1991; Carr & Fahrig, 2001; Trombulak & Frissell, 2000). Roads also increase erosion and sedimentation in waterways, sometimes impacting streams considerable distances from roads (Bennett, 1991; Carr & Fahrig, 2001; Harr & Nichols, 1993; Krause *et al.*, 2003; Trombulak & Frissell, 2000).

Traffic is a major cause of mortality in mammals (e.g., Groot & Hazebroek, 1996), birds (e.g., Dhindsa *et al.*, 1988), amphibians (Carr & Fahrig, 2001; Ehmann & Cogger, 1985; Fahrig *et al.*, 1995; Trombulak & Frissell, 2000) and reptiles (e.g. Ehmann & Cogger, 1985; Fowle, 1996). *H. australiacus* populations are known to be negatively affected by traffic (Mahony, 1994). Mortality increases with traffic volume (Fahrig *et al.*, 1995), and road density may be correlated with a decrease in biodiversity (Findlay & Houlahan, 1997). Findlay & Bourdages (1997) demonstrated that it may take decades after the construction of a road to detect the full extent of the effect on wetland biodiversity (see also Carr & Fahrig, 2001; Findlay & Bourdages, 2000). Roads also have the potential to alter animal behaviour and negatively affect reproductive success in birds (Trombulak & Frissell, 2000) and amphibians (Chapter 5).

While roads generally have a negative impact on flora and fauna, they may also provide resources to some flora and fauna, including basking sites for reptiles, breeding sites for amphibians (including *P. australis* and *H. australiacus*) and foraging opportunities for a range of vertebrates and invertebrates (Andrews, 1990; Bennett, 1991). Beneficiaries are weeds and feral animals, but also fauna from other habitats (Goosem, 2004).

3 Research questions and aims

Australia's alarming record of frog declines, (IUCN, 1996; Stuart *et al.*, 2004; Wake, 1991) prompted the establishment of the National Threatened Frogs Working Group (Campbell, 1999), and provided the impetus for Environment Australia to publish the Action Plan for Australian frogs (Tyler, 1997). The plan identified 27 Australian frogs at threat and a further 14 species that may be of concern but which were poorly understood. Two species of the latter group are the red-crowned toadlet *Pseudophryne australis* and the giant burrowing frog *Heleioporus australiacus*. Both species predominantly occur around Sydney, one of Australia's most densely populated regions (Australian Bureau of Statistics, 2002; State of the Environment Advisory Council, 1996). Sydney and its surrounds have been described as "among the most extensively and irrevocably altered landscapes in Australia" with around

94% of native vegetation cleared (Sivertsen, 1995). Both frogs have had declines reported in some populations (Gillespie & Hines, 1999; Mahony, 1996).

Urban expansion continues to encroach on the habitat of both frogs. Nevertheless, only limited information is available on the habitat requirements and habitat use of both species (details are given under the section *Species profiles* below). This situation presents difficulties to managers charged with the conservation of these species.

Furthermore, ecologists are interested in knowing how these frogs, and their habitat, are affected by encroaching urbanisation. Many ecological studies ignore the fact that anthropogenic factors or influences are present in the habitat of just about every species on Earth. This study does not. And even in the absence of urbanisation, wildlife biologists are keen to learn more on organisms and their interactions with others and their environment. As will be shown later, there are large gaps in our knowledge of these two truly remarkable frogs. Ecological research on species such as these not only serves us to better understand the organisms, but also to teach us what sets them apart from others.

The work presented here addresses the gaps in the knowledge of habitat related issues of both *P. australis* and *H. australiacus* in the Sydney Basin Bioregion (NSW National Parks and Wildlife Service, 2003). I asked the following three main questions for *P. australis* and *H. australiacus* separately:

1. How are the habitats of *P. australis* and *H. australiacus* best described?

2. How do *P. australis* and *H. australiacus* use their habitats?

3. Is track-side habitat beneficial to *P. australis* and *H. australiacus*?

The first question clearly relates to the frog's habitat requirements. The aim is to provide wildlife managers and ecologists with the information required to accurately model the distribution of both frogs. This will allow the identification of potential habitat where the species have not (yet) been observed, and will facilitate assessment of the overall impact of disturbances and habitat destruction on the species. The information can also be used in reserve design and habitat ranking. Furthermore, information gained on the habitat requirements of these species allows comparisons with those of other species, whether sympatric or allopatric, and is essential in understanding the complex nature of the spatial distribution of both related and unrelated organisms and their links to specific environments. A thorough understanding of a species' habitat requirements can also provide answers to other biological questions that may relate to wide-ranging topics including behaviour, morphology or breeding biology of the organism studied.

The second question addresses habitat use. It also investigates associations with a set of habitat features. The aim is to provide wildlife managers and ecologists with information they need to decide on the spatial requirements of populations, and to provide additional information that helps with the identification of likely sites of animal presence in the field. This information also pertains to habitat connectivity and potential migration paths. Wildlife biologists and population ecologists also will find the results of great interest. Links to habitat attributes as well as the spatial arrangement at the intra-specific level are identified. Such information provides interesting insights into interactions among individuals as well as links of individuals and populations to certain habitat features.

The third question relates to both species' associations with roads (details are given under the section *Species profiles* below). The aim is to determine the value of artificial road drainage structures including table drains and mitre drains to recruitment, and to evaluate potential impacts of road maintenance works. This aspect of the study focuses on the interface where frog habitat and human infrastructure, as well as ongoing human activity, meet. Frog presence on road sites obviously pose management problems, particularly those associated with the maintenance of these roads, but also the potential of traffic induced mortality. Ecologists also find interest in studying organisms that incorporate artificial habitat features into their natural habitat. Such studies allow assessment of the potential value of novel habitat features, their relative importance to the organism in question, and may contribute to a better understanding of the distributional limits imposed on this organism.

A table drain is the side drain of a track running adjacent to and parallel with the shoulders and forming part of the track formation. A mitre drain is a drain to conduct runoff from the shoulders of a track to a disposal area away from the road alignment. Culverts are pipes or similar structures used to direct water under the track (Department of Conservation and Land Management, 1994). From this point forward, roads are defined as roadways with a sealed surface, whereas roadways with an unsealed surface, such as dirt tracks, bush tracks or fire trails are termed tracks.

The research questions and their specific aims are further elaborated in Section 6 *A brief preview of the main chapters* below.

4 *Pseudophryne australis* species profile

4.1 Species description

Pseudophryne australis, the red-crowned toadlet, was the second myobatrachid frog to be described (Littlejohn *et al.*, 1993). Gray (1836) exhibited a specimen of what he called *Bombinator australis* at a meeting in London. The type locality was given as Swan River, Australia. Parker (1940) proposed the type locality as erroneous, a suggestion that has since been accepted (Cogger *et al.,* 1983; Moore, 1961). The species was described at least another three times and eventually placed in the genus *Pseudophryne* Fitzinger, 1843 (Cogger *et al.,*, 1983).

P. australis has been described historically as a "lively perky little frog" (Fletcher, 1889) with an "amusing turtle-like waddle" and that they "use a swimming bath much as a man might" (Ross, 1908). "In all their movements these funny little toads are most quaint and frequently most human "(Ross, 1908).

P. australis is a small and stocky frog with males and females measuring 18 – 28 mm and 25 – 30 mm respectively (snout – urostyle lengths), with larger specimens occurring at higher altitudes (Stauber, 1999). The back is dark and may be covered in red, orange or yellowish spots or patches. There is a prominent yellow, orange or red patch covering various amounts of the top of the head between eyelids and nares (nostrils). A stripe of the same colour usually covers the lower vertebral region. The dorsal skin may be smooth or covered in numerous warts. The legs are dark with white areas. The ventral side is black with bold white or peach coloured blotches (Cogger, 1994; Keferstein, 1868; Moore, 1961; Stauber, 1999).

4.2 Distribution

P. australis is only found within a radius of about 120 km around Sydney, NSW, and ranges from Pokolbin and Morisset (near Newcastle) in the north, to Mount Victoria in the west, and to Barren Grounds (near Nowra) in the south, but is excluded from the Cumberland Plains in western Sydney (Thumm & Mahony, 1996).

4.3 Habits

These frogs are nearly always underground, beneath vegetation, in leaf litter, in rock crevices, or under large stones and logs (Jacobson, 1963a; Moore, 1961; Ross, 1908). They were said to be gregarious (Jacobson, 1963a) and socially inclined (Harrison, 1922). The call of *P. australis* has been described as a harsh grating "creek" (Harrison, 1922), a nasal "ank – ank" or "ank" or a short metallic "erk" (Moore, 1961). See Thumm (2004) for call analyses.

The species typically breeds in ephemeral situations (Mahony, 1994; Thumm & Mahony, 1999) in shallow pools in low order streams and drains (Jacobson, 1963a; 1963b; Thumm & Mahony, 1999; Woodruff, 1978). Terrestrial nest sites (Jacobson, 1963a; Woodruff, 1978) are established in leaf litter piles and among vegetation in soaks (Harrison, 1922; Woodruff, 1978) or under stones (Fletcher, 1889).

Eggs are laid during or after rain (Harrison, 1922; Jacobson, 1963a). *P. australis* lay about 20, but up to 51 relatively large eggs (ovum diameter: 1.6 – 2.8 mm) (Harrison, 1922; Jacobson, 1963b; Thumm, 2004; Thumm & Mahony, 2005). Larvae remain in the eggs for a relatively long time (up to 119 days (Thumm & Mahony, 2002a)) and can suspend development, apparently indefinitely at immediate pre-hatching stage until the eggs are flooded (Jacobson, 1963b). This was described by Jacobson (1963b) as an unusual specialisation to the ephemeral nature of their breeding habitat. However, Thumm & Mahony (2002b) emphasized that desiccation of egg masses prior to hatching is a main cause of mortality in *P. australis* because essential follow-up rain frequently materializes too late.

Eggs have been found in any month of the year after rain (Harrison, 1922; Jacobson, 1963a). As eggs can remain in nests for prolonged periods confirmation was needed to establish whether *P. australis* indeed breeds throughout the year. Thumm (unpubl. data) confirmed that egg laying took place in every month by staging (ageing) the embryos in individual clutches found in the field. All year round breeding sets *P. australis* apart from all other *Pseudophryne* (Pengilley, 1973). Females are continuously iteroparous breeders and may produce egg clutches every 15 to 192 days (Thumm, 2004). This is thought to be a life history strategy in response to unpredictable rainfall and the limited availability of suitable nest sites (Thumm, 2004).

Four weeks after laying, *P. australis* hatched from flooded eggs (Jacobson, 1963a). However, detailed field and laboratory studies revealed that hatching times can vary greatly within and between clutches (15 to 119 days) (Thumm & Mahony, 2002a). The authors interpreted the variability as yet another bet-hedging strategy driven by unpredictable rainfall.

Flood waters that pass through the nest sites release the embryos from the egg capsules and sweep them into small ponds below (Barker *et al.*, 1995; Parker, 1940). Embryonic periods are highly variable (17-69 days; Thumm & Mahony, 2002a). The tadpoles hatch in a well developed state and are free feeding and free swimming (Jacobson, 1963a). They are bottom dwellers and appear to feed on sediment and algae (Anstis, 2002). The larval duration from hatching to metamorphosis is at least 39 days (Thumm & Mahony, 2006). Laboratory experiment showed that a higher proportion of tadpoles metamorphosed in response to pond drying compared to the treatment where water levels remained constant (Thumm & Mahony, 2006).

During the egg and tadpole stages, *P. australis* are adapted to a narrow range of environmental conditions, with a danger of desiccation (Jacobson, 1963b). During the terrestrial life stages, *P. australis* feed on cockroaches, ants (Rose, 1974), mites, pseudoscorpions, collembolans and termites up to 5 mm long (Webb, 1983).

P. australis are a long-lived species. Captive males and females reached more than nine years in age (Thumm & Mahony, 2002a). A female stilled layed eggs at age 13 years and 4 months (Thumm, pers. comm.).

No published information is available on potential predators. The striking colouration may afford some protection because it acts to disrupt the frog's outline and possibly is a Batesian mimicry system (Woodruff, 1978). The ventral patterns may also serve to startle potential predators (Tyler, 1976).

The skin secretions contain at least two classes of alkaloids, pumiliotoxin-B and pseudophrynamine (Daly *et al.*, 1990). The first is sequestered, the other biosynthesized (Smith *et al.*, 2002). The secretions produce behavioural stimulation in rat brains (Bagetta *et al.*, 1992) and muscle tissues of birds and mammals (Erspamer *et al.*, 1986), frogs (Erspamer & Severini, 1987) and leeches (Erspamer & Farrugia, 1986). These substances have a pre-synaptic neurogenic point of attack (Erspamer *et al.*, 1985) and induce heart rhythm disorders affecting systemic blood pressure (Erspamer *et al.*, 1989; Severini *et al.*, 1992). These studies were all of a physiological nature and the ecological role of the substances and their toxicity remain to be investigated. However, it is assumed that these secretions serve against predators.

4.4 Status and threats

In the 1960s Jacobson (1963a) revisited Harrison's (1922) bushland sites where the latter used to study *P. australis* and found that many had been cleared and settled over the previous 40 years. Many of the pools had been destroyed (Jacobson, 1963a). Elsewhere, Jacobson (1963a) also found that *P. australis* were absent from gutters that were concrete lined. In the mid-1990s Thumm & Mahony (1996) estimated that 20% of the former distribution area was no longer suitable for the species. Urban development was the major cause of habitat loss. A recent view expresses that pressure from human induced changes and interference are likely to increase and become more widespread, regardless of the conservation status of the frog's habitat (Lemckert *et al.*, 2001a).

Threats to the species include housing development and secondary effects associated with urbanisation (hydrological changes, pollution, etc.), bush rock removal, high frequency hazard reduction burning, the use of blue metal and spray bitumen to stabilise tracks and turbo-mowing (Thumm & Mahony, 1996; 1999). Upgrading works of tracks and roads have led to the destruction of sites (Thumm & Mahony, 1996).

The species is listed as vulnerable in NSW (*Threatened Species Conservation Act 1995*) and also by the *International Union for Conservation of Nature and Natural Resources (IUCN)* (Lemckert *et al.*, 2001a).

4.5 Habitat information

The species was reported from Hawkesbury Sandstone (Fletcher, 1889; Harrison, 1922; Krefft, 1863). After Moore's (1961) suggestion, Woodruff (1978) recognised that no specimens had been collected in areas where shales of the Liverpool subgroup lie at the surface, nor in areas covered by Tertiary or Quaternary deposits. Information on broad habitat associations was collated and later expanded on by Thumm & Mahony (1996; 1999). They confirmed that *P. australis* occurs mostly on Hawkesbury Sandstone. A summary of published habitat statements (all about geology, the nature of water courses and shelters) and altitudinal range, landforms, soil and geology of 47 sites was included, with some information on vegetation (Thumm & Mahony, 1996). On sandstone, the species occurs within 100 m from ridge tops in temporary feeder creeks primarily below the first cliff line on the talus slope in open forest, woodland or heath (Thumm & Mahony, 1999). Ponds were five to 25 cm deep (Thumm & Mahony, 1999). This information is very useful for the broad delineation of potential habitat within the species' geographic range. It is expected that more detailed habitat information will increase the accuracy of habitat models.

4.6 Summary of additional published studies

Woodruff (1978) investigated possible hybridisation between *P. australis* and *P. bibronii* in a very narrow zone of sympatry. Phylogenetic relationships within *Pseudophryne* were investigated by Roberts & Maxson (1989). Stauber (1999) found significant intra-specific variation in both external morphology and allozyme frequencies. The subject of territoriality in the species was studied by Thumm (2004).

5 *Heleioporus australiacus* species profile

5.1 Species description

The genus *Heleioporus* is endemic to Australia and contains six species. *H. albopunctatus, H. barycragus, H. eyrie, H. inornatus* and *H. psammophilus* all occur in the south-west of Western Australia. *H. australiacus*, the giant burrowing frog, is the only *Heleioporus* that occurs in south-eastern Australia (Cogger, 1994). Lee (1967) investigated the taxonomy, ecology and evolution of this disjunctly distributed genus.

Shaw & Nodder (1795) originally described *H. australiacus* as *Rana australiaca* and added the following note:

> This animal certainly cannot be numbered amongst the most beautiful of its genus: it is a species, however, which has never before been described, and is more peculiarly interesting from the circumstance of its being a native of the distant region of New Holland, which has added so many zoological treasures to the cabinets of natural history. Its rarity must therefore apologize for its deformity.

This made the giant burrowing frog the first myobatrachid to be described (Littlejohn *et al.*, 1993). Some taxonomic confusion followed and after several name changes and parallel discoveries, the species was merged with *Heleioporus* Gray, 1841 and became known as *Heleioporus australiacus* (Moore, 1961). A more thorough species account describes the animal as large sized (see Table 1), with a toad-like body form. The pupil is vertical and tympanum distinct. The back colour is a deep chocolate brown or greyish brown, the sides lighter, and the venter and lower sides of arms and legs are bluish-white. Some individuals occasionally have pale yellow spots on their sides, around the cloaca and on the upper side of limbs. The back and sides are covered with numerous warts, each tipped with a tiny black spine (Lee, 1967; Moore, 1961).

The species is sexually dimorphic, with males attaining a larger body size and greater weight than females (Table 1) (A. Stauber, unpubl. data). In males only, the circumference of the forelimbs is greater than that of the hind legs (Lee, 1967). Males also have prominent cone-shaped nuptial spines on their fingers (Moore, 1961).

Table 1 Snout-urostyle lengths (SUL) and weights of live male and female *H. australiacus* measured in the field (mostly members of three populations) during the course of this study (refer to Chapter 4 for methods). Males are larger (ANOVA $F_{1,\ 165} = 5.55$; $P = 0.019$) and heavier (ANOVA $F_{1,\ 163} = 11.4$; $P < 0.001$) than females. * two males did not have their weights recorded.

	Males (n = 77*)	**Females** (n = 89)
Mean SUL ± SD (mm)	82.4 ± 9.9	79.3 ± 6.8
Min. SUL – max. SUL (mm)	49.1 – 101.2	58.9 – 95.3
Mean weight ± SD (g)	68.9 ± 21.6	59.4 ± 14.1
Min. weight – max. weight (g)	15.0 – 124.4	28.0 – 92.4

5.2 Distribution

The distribution of the giant burrowing frog *Heleioporus australiacus* is confined to the eastern slopes of the Great Dividing Range and coastal regions in eastern Australia and extends from Olney State Forest in the Watagan Mountains near Morisset, NSW, to Walhalla in the Central Highlands, VIC (Littlejohn & Martin, 1967).

5.3 Habits

H. australiacus is an efficient burrower and seeks refuge in burrows where it may aestivate for prolonged periods (Bentley *et al.*, 1958). The species appears to spend most of its life below the surface (Moore, 1957).

This cryptic species (Harrison, 1922) is not frequently observed above ground and the number of calling males at a single location rarely exceeds five (Daly, 1996a; Moore, 1961; Recsei, 1996). Males usually call from underground (Gillespie, 1990; Moore, 1961). Work on Western Australian *Heleioporus* demonstrated that burrow morphology can enhance the principal frequency component of a call and thus compensate for the lack of a vocal sac (Bailey & Roberts, 1981). The call is a soft owl-like “ou – ou – ou” (Moore, 1961)(my observations suggest that each call is made up of four distinct “ou” calls in very quick succession). Calls were described by Littlejohn & Martin (1967).

The species calls throughout the year but call activity peaks in late summer and autumn (Gillespie, 1990; Littlejohn & Martin, 1967; Moore, 1961; Recsei, 1996)(A. Stauber, unpubl. data). *H. australiacus* are considered autumn breeders (Fletcher, 1889; Harrison, 1922) but may also spawn in spring (A. Stauber, unpubl. data) and late summer (Daly, 1996a). They call predominantly during warm nights after periods of intense rain (Daly, 1996a). Breeding takes place in semi-permanent and permanent shallow creeks and occasionally dams (Gillespie, 1990; Littlejohn & Martin, 1967; Recsei, 1996)(A. Stauber, unpubl. data). The species may also breed in man-made gutters or drains (Daly, 1996a)(A. Stauber, unpubl. data).

Egg capsules measure 2.5 – 2.6 mm in diameter (Moore, 1961; Watson & Martin, 1973) and have been described as “huge” (Moore, 1961). Spawn, a foam raft with 698 – 1239 eggs, is deposited in concealed positions within creeks under organic debris and vegetation (Daly, 1996a; Watson & Martin, 1973), rocks (Harrison, 1922), or in crayfish burrows (Hoser, 1989). Western Australian *Heleioporus* spp. also ovideposit into their own constructed burrows (Lee, 1967), but I have found no evidence of this occurring in *H. australiacus*. In contrast to *H. australiacus*, the Western Australian species apparently lay their eggs out of water (Main, Littlejohn & Lee, 1959).

The duration of the embryonic phase is unknown. Tadpoles are benthic and graze on algae on rocks (Daly, 1996a; Lee, 1967). They may grow up to 75 mm in length (Moore, 1961) during the larval period of three to 11 months (Daly, 1996a)(see also Chapter 3). Tadpole descriptions have been published (Anstis, 2002; Watson & Martin, 1973).

At the terrestrial life stage, the species may be a generalist in terms of microhabitat (Lemckert *et al.*, 1998). Gillespie (1990) suggested that the species may be dependent on forest habitat and may be excluded from farmland. Adults appear to be wide-ranging and can be found considerable distances away from creeks and drains (Gillespie, 1990; Lemckert & Brassil, 2003; Lemckert *et al.*, 1998; Webb, 1991).

Analyses of gut contents and scats showed that *H. australiacus* eat cockroaches, ants, beetles, bugs, moths, grasshoppers, woodlice, spiders and scorpions, centipedes and millipedes (Littlejohn & Martin, 1967; Rose, 1974; Webb, 1983; Webb, 1987), some of which are up to 65 mm long and / or noxious (Webb, 1983).

H. australiacus can exude a white, sticky, perhaps poisonous (see Softly & Nairn, 1975) fluid when handled. It may also emit a loud, high-pitched distress call and inflate the body with straightened legs to maximise its size (Daly, 1996a; Towerton & Lemckert, 2001)(A. Stauber, unpubl. data). It is known that *Varanus varius* (lace monitor) and *Pseudechis porphyriacus* (red-bellied black snake) prey on *H. australiacus* (Towerton & Lemckert, 2001). Foxes (*Vulpes vulpes*) and cats (*Felis catus*) are potential predators (Lemckert *et al.*, 2001b).

5.4 Status and threats

Information on the abundance of *H. australiacus* indicates that the species is rare (Gillespie, 1990; Gillespie & Hines, 1999; Recsei, 1996; Webb, 1987). However, this species is also highly cryptic (Harrison, 1922) and is only rarely detected, usually on nights following heavy rains (Daly, 1996a; Gillespie, 1990). It is likely that *H. australiacus* has recently declined throughout the greater Sydney region (Recsei, 1996). Proposed causes of these postulated declines are fires of high frequency and / or intensity, forestry activities, grazing, track maintenance and traffic mortality, feral predators, urban runoff, as well as housing and other developments (Daly, 1996a; Mahony, 1994; Recsei, 1996). The potential impacts of these processes have not been tested; however, the patterns, nature and potential causes of declines were examined by Gillespie & Hero (1999). Several individuals have been unearthed at the base of trees during logging operations (Gillespie, 1996).

The species is listed as threatened in Victoria (*Flora and Fauna Guarantee Act 1988*), and vulnerable in NSW (*Threatened Species Conservation Act 1995*), at the Commonwealth level (*Environment Protection and Biodiversity Conservation Act 1999*) and also by the *International Union for Conservation of Nature and Natural Resources (IUCN)* (Lemckert *et al.*, 2001b).

5.5 Habitat information

Information on broad habitat associations was collated at various scales for several regions. Recsei (1996) reviewed published habitat statements. These are not repeated here but they generally provided information on the nature of water courses, vegetation structure, topography and or geology in each case based on one or a small number of sites where the animals had been observed by the various authors. In addition, the vegetation structure and floristics have been detailed for *H. australiacus* sites in Victoria (Gillespie, 1990). Habitat information including floristics and vegetation structure was also collected at several sites in the southern half of the species' range in NSW (Webb, 1981; 1991; 1993). Daly (1996a) provided very detailed information for *H. australiacus* sites in the Shoalhaven region (Nowra, NSW) ranging from floristics to breeding pool characteristics. Recsei (1996) added a summary of soil types and the altitudinal range of animal locations. Apart from general habitat statements and Recsei's (1996) additions, very little information is available on the habitat characteristics of sites occupied by *H. australiacus* in the northern half of its range, the Sydney Basin (NSW National Parks and Wildlife Service, 2003).

5.6 Brief summary of additional published studies

Radio-tracking studies were undertaken to investigate the movements of individuals in timber production forests (Lemckert & Brassil, 2003). The effects of logging on ground-dwelling vertebrates including *H. australiacus* was investigated by Webb (1991). Studies on hydration and dehydration rates demonstrated that *H. australiacus* can lose almost 38 % of body weight in water before death occurs (Bentley *et al.*, 1958). The ecological requirements of *H. australiacus* are poorly known (Gillespie & Hines, 1999).

6 A brief preview of the main chapters

Throughout this work, the research questions asked on page 9 are generally answered for each frog separately within the same Chapter. The methodologies chosen occasionally vary among species to suit the biology (e.g., differences in size, behaviour, etc.) of each frog. Comparisons between the species are generally avoided and are only made where it is ecologically relevant.

The main chapters 2 to 6 are written as freestanding, independent units and for this reason information is occasionally repeated. Cross referencing is used within the main chapters to avoid the repeat of key information outside the relevant chapter. These chapters are briefly previewed below.

It is appropriate to point out that the study period coincided with long and repeated episodes of very low rainfall. This unusually dry period may have had a significant influence on the data collected.

6.1 The Habitat requirements of *Pseudophryne australis* and *Heleioporus australiacus* (Chapter 2)

Chapter 2 relates to research question 1: How are the habitats of *Pseudophryne australis* and *Heleioporus australiacus* best described? The main objective of the work presented in this chapter was to collect quantitative information on a large number of habitat variables that may have an influence on the frogs' distribution. The aim was to identify the variables and their values that may be useful for the prediction of potential habitat for both species. I hypothesised that animal locations were not randomly distributed throughout the landscape within their ranges, but were linked to some specific, but unknown, environmental attributes of these sites.

Three different scale levels add different information on each scale, but also serve to indicate how well some analyses function as support for predictive modelling. Furthermore, the identification of habitat variables and the determination of their values that link these animals to their environment are an essential contribution to the ever, albeit slowly growing knowledge of the ecology of these two difficult to study species. Information on the habitat requirements of these species allows comparisons with the habitat requirements of other species, whether they co-exist or not. Such information is essential in understanding the complex nature of the spatial distribution of both related and unrelated organisms and their links to their specific environments. A thorough understanding of a species' habitat requirements also helps shed light on other biological questions including those concerned with animal behaviour, morphology or breeding biology and how they relate to the environment.

Because so many unanswered questions remain, the habitat requirements of *P. australis* and *H. australiacus* were investigated. The work concentrated on the Sydney Basin and was carried out at three different spatial scales. 1) On the broadest scale, six variables and climatic conditions were quantified for sites where frogs were present based on *Atlas of NSW Wildlife* records using GIS and printed maps. 2) On a finer scale, field visits to most areas collected details on 51 habitat variables, including slope and aspect which were also determined using GIS. 3) The third and most detailed analysis centred around the Broken Bay area (by road, approx. 80 km north of Sydney, NSW). The same 51 variables were analysed at sites of frog presence vs. absence using logistic regressions. Breeding pool characteristics for both species, and microhabitat details of burrowing locations of *H. australiacus* were determined separately.

This is one of very few studies of Australian amphibians that address conservation at a landscape scale (but see Parris, 2001) and may well be the most detailed quantitative analysis to date of the habitat requirements of any Australian frog.

6.2 Adaptive phenotypic plasticity in the larval period of *Heleioporus australiacus* (Chapter 3)

Chapter 3 is a contribution to the literature of ecological plasticity and adaptation. The aim of this chapter was to establish the larval duration of *Heleioporus australiacus* under several environmental conditions, and particularly to test whether *H. australiacus* is capable of a phenotypic response to habitat drying, by metamorphosing earlier. Such a response would be a beneficial adaptation to its habitat. Establishment of the larval period and the determination of a possible phenotypic response to pond drying relate to research question 1. The answers contribute to a more thorough understanding of this species' habitat requirements, and contribute to the discussion on the adaptive values of possible phenotypic plasticity. *Pseudophryne australis* was excluded from this experiment because Thumm & Mahony (2006) have already investigated phenotypic plasticity in larval duration in this species.

Chapter 3 contains an extensive review of phenotypic plasticity in frogs which is intended to provide all the necessary background information relevant to the subject. I also address the question: is phenotypic plasticity in the larval period of *H. australiacus* adaptive?

Heleioporus australiacus breed in ephemeral pools (Chapter 2). Their tadpoles run the risk of dying if the hydroperiod of the breeding pond is shorter than the time required to reach metamorphosis (Chapter 5). A laboratory experiment was set up to test the response of *H. australiacus* tadpoles from three populations to decreasing water levels. In addition, growth and development in the siblings of one population were monitored in the field.

Information on the larval duration and a possible response to pond drying is an integral part in the assessment of the overall value of artificial ephemeral breeding ponds (Chapter 5). Furthermore, such information allows for interesting comparisons with other frogs and their habitat relationships and contributes to the growing understanding globally of the adaptive values of phenotypic plasticity.

6.3 Habitat associations and movement patterns of *Pseudophryne australis* and *Heleioporus australiacus* (Chapter 4)

Chapter 4 comprises a comparative study of dispersion and dispersal relative to habitat in both frog species to address research question 2: How do *Pseudophryne australis* and *Heleioporus australiacus* use their habitat? The aim was to quantify spatial distributions as well as the movement patterns of these threatened frogs and to identify associations with certain habitat features. The knowledge gained will contribute to a better understanding of each species' basic biology, and to improve the planning for their conservation management.

Seven *P. australis* breeding sites and three *H. australiacus* populations were regularly monitored in the field. Animals were marked for identification and had locality details recorded. Nearest-neighbour distances between individuals were calculated to investigate the spatial pattern of individuals within populations. Where animals show a clustered distribution, habitat selection or even preference may be indicated. For this reason, the habitat characteristics were investigated more closely at the locations of such clusters. Habitat associations were also investigated independently of the locations where clusters form. The distances moved by individuals of both species were used to provide information on site fidelity. The combination of movement distances and nearest-neighbour distances are essential to the determination of the spatial requirements of populations. The results are discussed in relation to the spatial use by both species and how utilised habitat features can be protected.

6.4 *Pseudophryne australis, Heleioporus australiacus* and the track environment: do natural and artificial track-side breeding sites allow equal reproductive success (Chapter 5)?

Chapter 5 specifically relates to the track-side habitat utilised by both frogs and is therefore linked research question 3: Is the road habitat beneficial to *Pseudophryne australis* and *Heleioporus australiacus*? Ecologists and managers alike are interested in knowing whether tracks provide habitat enhancement or ecological traps for these species.

Even within the reserve system there are numerous tracks and roads, the majority of which are placed in the topographical region inhabited by both frogs. It is therefore not surprising that these species often associate with tracks, roads, and their drainage structures. Such roads, tracks and their drainage system in particular are subject to frequent maintenance operations (Austroads, 2001; Department of Conservation and Land Management, 1994) which may pose a risk to both frog species. The complex relationships between these frogs and the artificial track habitat are poorly understood.

In this chapter, hydroperiod, or pond duration, was used as an indirect measure to assess and compare the reproductive success of track and non-track breeding sites. The aim was to determine whether artificial track breeding sites allow equal reproductive success compared to natural breeding sites away from tracks. Twenty-eight *P. australis* and eleven *H. australiacus* artificial track-side breeding sites (track sites) and natural breeding sites located away from tracks (non-track sites) were monitored to determine the hydroperiod and other physical characteristics of these sites. Hydroperiods were compared among track and non-track sites and related to the larval requirements of both frogs. Records were also made of sites which held tadpoles to determine whether they produced metamorphs. Impacts related to traffic and road works were also assessed. Management options are suggested to mitigate the impacts associated with the operation and maintenance of track sites, taking into consideration the species' ecologies and life histories.

6.5 *Heleioporus australiacus* movement and habitat use in the track environment (Chapter 6)

Chapter 6 also relates to research question 3. *Heleioporus australiacus* is a burrowing species that frequently associates with tracks. Based on previous observations, I hypothesised that at least some individuals occasionally burrow in the track environment.

In this chapter I describe how five individuals known to utilise track habitat were tracked weekly for up to three months using radio-telemetry. I investigated primarily whether this frog burrows in the track environment, where it may be exposed to potential injuries due to track maintenance works. Burrowing depths and weekly distances moved between burrows were also analysed. Home ranges of two individuals were also estimated. Such values have never been reported previously for this species and add considerably to our understanding of the basic biology of this frog and its spatial requirements.

This chapter reports observations on dispersal behaviour with respect to tracks by this frog. These observations build on our current knowledge of the species and are undoubtedly of great interest to ecologists and managers alike. A number of recommendations have been made to minimise potential negative impacts of track maintenance operations on population persistence.

Finally, the key findings are summarised in Chapter 7.

Chapter 2

THE HABITAT REQUIREMENTS OF *PSEUDOPHRYNE AUSTRALIS* AND *HELEIOPORUS AUSTRALIACUS*

Abstract

The habitat requirements of *Pseudophryne australis* and *Heleioporus australiacus* in the Sydney Basin were investigated at four different spatial scales. 1) On the broadest scale, six variables and climatic conditions were quantified for sites where frogs were present based on *Atlas of NSW Wildlife* records using GIS and printed maps. 2) On a finer scale, field visits were conducted to most areas in order to collected details on 51 habitat variables, including slope and aspect which were also determined using GIS. 3) The third and most detailed analysis centred around the Broken Bay area (by road, approx. 80 km north of Sydney, NSW). The same 51 variables were analysed at sites of frog presence vs. absence using logistic regressions. 4) Breeding pool characteristics for both species, and microhabitat details of burrowing locations of *H. australiacus* were determined separately.

Both species showed a very strong association with Hawkesbury Sandstone and were generally found in the elevated parts of the topography where watercourses are ephemeral and at sites with gradients of no more than 10 degrees. *P. australis* breeding sites are ephemeral and usually located near cliffs. *H. australiacus* breeding pools are ephemeral, semi-permanent or permanent. BIOCLIM modelling revealed that both frogs favour areas of higher precipitation and generally milder temperature regimes compared to average values for the Sydney Basin.

Soils at breeding sites were poorly structured and supported open forest, woodlands and heaths. *H. australiacus* sites may also be in wet sclerophyll forests in gullies. Breeding sites were weed free. The probability of *P. australis* breeding sites occurring increases with increasing amounts of leaf litter. *H. australiacus* breeding sites were generally associated with crayfish burrows. Both species were absent from cleared open land and may be dependent on natural vegetation with a multilayered and floristically diverse structure.

The habitat occupied by both *P. australis* and *H. australiacus* is unusual in that only one other frog, the wide-ranging *Crinia signifera*, is known to utilise it. Each of the three frogs has its own reproductive adaptations that allow it to persist in its own way in marginal environments away from permanent water courses.

1 Introduction

Habitat choice is an important component of the life history of animals (MacArthur, 1972). Information on an organism's spatial distribution is an integral component of ecological and conservation research (Aberg *et al.*, 2000; Harding *et al.*, 2001), has application in habitat restoration efforts (e.g., Matthews & Pope, 1999) and allows the identification and ranking of sites where individuals are more likely to occur (e.g., Aebischer *et al.*, 1993). An understanding of a species' habitat requirements is therefore an essential tool in conservation biology because it can be used to predict that organism's distribution in places which have not been sampled and help in the assessment of changes in habitat area resulting from disturbances (Burgman & Lindenmayer, 1998). Furthermore, knowledge about the species – environment relationship is critical for impact assessment, the design of management strategies and the framing of conservation legislation (Burgman & Lindenmayer, 1998; Noss & Murphy, 1995).

Can habitat be used as a predictor of species occurrence? As examples given by Burgman & Lindenmayer (1998), Australian forest birds (MacNally, 1989), plant species in Western Australian sand heaths and mallee communities (Burgman, 1989), and rare Eucalypt species (Proper & Austin, 1990), occur in low numbers not because of limited tolerances to environmental conditions, but because the habitat they required is rare in the landscape. The presence of suitable habitat may be one of several conditions of a species' existence at a site, but the presence of such habitat clearly does not mean that the taxon will be present there. Modelling of environmental conditions can be helpful in predicting species occurrences by identifying additional habitat. Good habitat models should be able to predict species presence in previously unsampled areas as was demonstrated for the greater glider *Petauroides volans* (Lindenmayer *et al.*, 1994; 1995). Other habitat models have been constructed from extensive data sets for frogs (e.g., Parris, 2001; 2002), but their predictive powers still need to be tested in the field.

Does habitat protection directly lead to species' protection? Habitat loss is considered responsible for the decline of many of the now extinct and threatened species in Australia (Leigh & Briggs, 1992; Possingham *et al.*, 1995; Recher & Lim, 1990; Schur, 1990; Sivertsen, 1994) and globally (Brooks *et al.*, 2002; Clark *et al.*, 1990; Fahrig, 2001; IUCN, 2003; Janzen, 1986; May, 1990; Wilson, 1989). In the United States of America, habitat loss, at least in the terrestrial environment, is overwhelmingly the greatest threat to plants and animals (1880 species surveyed) (Wilcove *et al.*, 1998). It is for this reason that conservation efforts are often based on reserving land for the protection of species, communities and ecosystems. Burgman & Lindenmayer (1998) provide a historical overview of habitat protection in Australia.

However, habitat protection is often not sufficient for the long term survival of a species. This has been illustrated by the example of the endangered Australian western swamp tortoise *Pseudemydura umbrina* (Kuchling *et al.*, 1992). Furthermore, at least eight frog species from the Wet Tropics bioregion of northern Queensland and four from the Snowy Mountains (NSW and VIC) have undergone declines since the late 1980s, despite being in protected reserves (McDonald & Alford, 1999; Osborne *et al.*, 1999).

Habitat loss and degradation is considered a major threat to *P. australis* (Thumm & Mahony, 1999) and *H. australiacus* (Gillespie & Hines, 1999; Recsei, 1996). In this Chapter I identify habitat variables which correlate to the distribution of *P. australis* and *H. australiacus* and determine their values. Notes on general aspects of *P. australis* habitat have previously been published and were summarised by Thumm (1996). More detailed habitat studies on that species were also undertaken (Thumm, 1997a; Thumm & Mahony, 1999). Recsei (1996) provided a general account and a literature review of habitat requirements for *H. australiacus*. General information was added by Gillespie (1996), and Daly (1996a) undertook a detailed study of *H. australiacus* habitat in the Shoalhaven region.

Comprehensive surveys across the Sydney Basin Bioregion (NSW National Parks and Wildlife Service, 2003) were undertaken and the data analysed to add to this knowledge. In this study, the Sydney Basin Bioregion is defined as the area south of the Hunter River, east of the western edge of the Blue Mountains (e.g., Mt. Victoria), and north of the Shoalhaven

River. This area covers all known *P. australis* localities, and the portion of *H. australiacus* distribution where the species is most abundant (Barker *et al.*, 1995). The Sydney Basin has one of Australia's highest human population densities (State of the Environment Advisory Council, 1996), which keeps increasing (Australian Bureau of Statistics, 2002), and includes vast urban areas as well as reserves (e.g., national parks, state forests, etc.). Analyses were undertaken at various scales investigating the relationships between presence or presence-absence data and numerous habitat variables to identify the characteristics of the habitat and the core habitat of both frogs.

Core habitat is defined as the habitat which is covered by locality records for which the values of individual variables fall within the 10 – 90% level, and exclude outliers (Lindenmayer *et al.*, 1991). By no means does this imply that the remainder of the habitat utilised by a species is unimportant (see Buchanan *et al.*, 1998).

The main objective of the work presented in this chapter was to collect quantitative information on a large number of habitat variables that may have an influence on the frogs' distribution. The aim was to identify the variables and their values that may be useful for the prediction of potential habitat for both species. I hypothesised that animal locations were not randomly distributed throughout the landscape within their ranges, but were linked to some specific, but unknown, environmental attributes of these sites. Three different scale levels add different information on each scale, but also serve to indicate how well some analyses function as support for predictive modelling. Furthermore, the identification of habitat variables and the determination of their values that link these animals to their environment are an essential contribution to the ever, albeit slowly growing knowledge of the ecology of these two difficult to study species. Information on the habitat requirements of these species allows comparisons with the habitat requirements of other species, whether they co-exist or not. Such information is essential in understanding the complex nature of the spatial distribution of both related and unrelated organisms and their links to their specific environments. A thorough understanding of a species' habitat requirements also helps shed light on other biological questions including those concerned with animal behaviour, morphology or breeding biology and how they relate to the environment.

This is one of very few studies of Australian amphibians that address conservation at a landscape scale (but see Parris, 2001) and may well be the most detailed quantitative analysis to date of the habitat requirements of any Australian frog.

2 Materials and methods

The habitat analyses were carried out separately for each species. Protocols were generally the same for both species. Differences are detailed where appropriate. Locality data are given in metres using Australian Map Grid data (AMG) in Zone 56.

Habitat variables were collected and analysed at various scales. This approach made full use of all known animal locations, covering the full distribution ranges of both species (excluding the southern *H. australiacus*), while at the same time allowing for logistical constraints related to travelling distances and access. Note that the areas covered are the full known distribution range for *P. australis*, and the full known distribution range north of the Shoalhaven River (AMG 254000 - 294000E, 6139000N) for *H. australiacus*. Most *H. australiacus* records are concentrated in that region (Barker *et al.*, 1995). *H. australiacus* south of the Shoalhaven were primarily excluded because this research is focused on the Sydney Basin Bioregion. Another important reason is the possibility that *H. australiacus* may be made up of two disjunct populations (Gillespie, 1990) that may be taxonomically distinct (Daly, 1996a). Apart from an area near Jervis Bay (AMG 294000E, 6125000N), there are no known records between the Sydney Basin and Eden–Bombala in south-eastern NSW (a latitudinal distance of approx 300 km from the southern limits of the Sydney Basin). The taxonomic status of both populations is currently being investigated (M. Mahony & S. Donnellan pers. comm.). The southern animals are the subject of concurrent ecological research through the University of Newcastle (M. Mahony, pers. comm.).

2.1 Locality data

Unless indicated otherwise, the locations were determined from the *Atlas of NSW Wildlife* (WA) (extraction date 13/4/2003). This database includes records from the Australian Museum (AM) and State Forests of NSW (SF NSW) and from a wide range of professional and amateur contributors. Pre 1980 records were excluded to eliminate several historical locations which have since been turned into suburbs and to allow habitat analyses based on the current known distributions of both species.

Table 2 Topographic map sheets (1:25000) covering the distribution of *P. australis* (*P.a.*) and *H. australiacus* (*H.a.*) in the Sydney Basin. The presence of a species on a particular map sheet is indicated by a tick. References: (Central Mapping Authority of New South Wales, 1982; 1982-1989; 1988-1989; Land Information Centre, 1975-1978; 1982-1989; 2000; Land and Property Information, 2000).

	Map sheet	*P.a.*	*H.a.*		Map sheet	*P.a.*	*H.a.*
1	Mount Pomany	✓		27	Cowan	✓	✓
2	Monundilla	✓	✓	28	Broken Bay	✓	✓
3	Parnell		✓	29	Katoomba	✓	✓
4	Coricudgy	✓	✓	30	Springwood	✓	✓
5	Kindarun	✓	✓	31	Riverstone	✓	✓
6	Howes Valley	✓		32	Hornsby	✓	✓
7	Putty	✓		33	Mona Vale	✓	✓
8	Gospers Mountain	✓		34	Jamison	✓	✓
9	Murrays Run	✓		35	Penrith	✓	
10	Morisset	✓	✓	36	Parramatta River	✓	
11	Ben Bullen	✓		37	Sydney Heads	✓	✓
12	Six Brothers		✓	38	Bimlow	✓	✓
13	Kulnura	✓	✓	39	Warragamba	✓	
14	Rock Hill	✓		40	Liverpool	✓	
15	Colo Heights	✓		41	Campbelltown	✓	✓
16	St Albans	✓	✓	42	Port Hacking	✓	✓
17	Mangrove	✓		43	Appin	✓	✓
18	Wyong	✓	✓	44	Otford	✓	✓
19	Wollangambe	✓		45	Bargo	✓	✓
20	Mountain Lagoon		✓	46	Bulli	✓	✓
21	Lower Portland	✓	✓	47	Avon River	✓	✓
22	Gunderman	✓	✓	48	Wollongong	✓	✓
23	Gosford	✓	✓	49	Robertson		✓
24	Mt Wilson	✓		50	Kangaroo Valley	✓	✓
25	Kurrajong	✓		51	Burrier		✓
26	Wilberforce	✓		52	Berry		✓

The WA records were modified as follows. One database was created for each species. All duplicate entries within a database were reduced to a single record. In addition, two *P. australis* records (AMG 344000E, 6285900N; 346774E, 6289277N) and one *H. australiacus* record (AMG 342500E, 6290400N) were removed because of doubtful accuracy after discussion with other field biologists. One *P. australis* record (AMG 352750E, 6338000N) was removed as an erroneous entry (M. Mahony, pers. comm.). The coordinates of one *H. australiacus* record were changed to bring it into line with the accompanying locality description (Binya Close, Hornsby Heights, a site I confirmed in the field).

Clusters of records were then identified using GIS software ArcView 3.2's (Environmental Systems Research Institute, Inc.) buffer tool. Clusters were manually thinned out so that the minimum distance between records was greater than 500m to eliminate possible erroneous duplicate entries due to grid conversions, and to somewhat reduce over-representation of certain areas. Records to be deleted were selected primarily to minimise data loss and secondarily by coin flipping. The remaining numbers of locality records were 332 for *P. australis*, and 145 for *H. australiacus* covering a total of 52 1:25000 topographic map sheets (Table 2).

NSW National Parks and Wildlife Service licensing conditions prohibit the reporting of exact WA locations. Details are only stated here for erroneous entries. I suggest researchers contact the service for precise locality data. This limitation makes replication of my work more difficult.

2.2 Habitat scaling and variables analysed

The following subsections define the various scales of the habitat analyses and the variables measured and analysed at each scaling level. The scaling is a hierarchical arrangement where the broader levels cover a larger area with reduced habitat information as opposed to medium and fine levels which cover relatively smaller areas, but with much more habitat information collected. The amount of habitat information increases from broad scale to medium scale by the addition of more habitat variables.

2.2.1 Extra-broad scale habitat analyses

All known locations as defined above within the Sydney Basin Bioregion were covered at the extra-broad scale. Habitat descriptions at this level were based on information available from maps, geographic information system (GIS) files and BIOCLIM (Busby, 1991; Nix, 1986).

2.2.1.1 Extra-broad scale data collected

Details of physical factors, geology and climate data analysed are given in Table 3.

Table 3 Factors analysed at the extra-broad scale level. Given for each factor (with units in parentheses) are the method of data extraction, explanatory notes and the source of the data with references.

Variable	**Method**	**Data source / Explanatory notes**	**Source / References**
Geology	Manual plotting on printed maps		(NSW Dept. of Mines, 1966; 1969)
Elevation (m)	GIS	Digital elevation model (25m grid)	NSW NPWS
Height above valley floor (m)	Manual / GIS (Valley floor: highest point below site where terrain flattens out)	10m Contour lines derived from digital elevation model (25m grid)	
Height above lowest point within 1km (m)	Manual / GIS (Lowest point: lowest point below site within 1km radius)	10m Contour lines derived from digital elevation model (25m grid)	
Height below ridge or knoll (m)	Manual / GIS	10m Contour lines derived from digital elevation model (25m grid)	
Aspect (°)	GIS	Digital elevation model (25m grid)	NSW NPWS
Slope (°)	GIS	Digital elevation model (25m grid)	NSW NPWS
Climate	BIOCLIM	35 modelled climatic variables extracted, based on atlas (WA) locality and altitude data	(Busby, 1991; Nix, 1986)

2.2.1.2 Extra-broad scale data analysis

Extra-broad scale data were summarised to fully describe the whole range of values of the habitat variables measured, effectively summarising the environmental conditions the animals experience in the field throughout their geographic ranges within the area covered by this study. Where practical and appropriate, the conditions were compared to the full range of values available to the animals for certain variables within the Sydney Basin. These were geology, elevation and climate.

Such comparisons assume that animals do not occur in places for which no WA records exist. However, non-presence in the WA records certainly does not constitute an absence value because of the obvious difficulties associated with the collection and verification of such data. I recognise these limitations and justify comparisons by exploring only general patterns of appropriate variables at the broad-scale level, which have a lower resolution than the general sampling resolution of the WA. For example, if a species has never been recorded on a particular reasonably widespread geological type which is accessible to researchers at least in some places (and was presumably sampled during several fauna surveys, either formal or informal), then it seems unlikely that that geological type offers suitable habitat for the species in question.

Elevation, aspect and slope GIS files were generated from a 25 m grid Digital Elevation Model (DEM) supplied by NSW NPWS, using ArcView Spatial Analyst (Environmental Systems Research Institute, Inc.). Unfortunately, metadata were not available for the DEM, hence it is unknown how the DEM was originally constructed. DEM-derived 10 m contours however very closely followed the contour lines of the corresponding topographic map sheets and for this reason it was assumed that the DEM was based on contours of the 1:25000 topographic map series (references in Table 2). Relative positions of locality records in the topography were calculated as a percentage above the valley floor (a somewhat subjective evaluation of the highest point downstream of the locality record where the terrain flattens out) as well as above the lowest point downstream within 1 km (an objective measure). The 100% mark was taken as the highest point (ridge or knoll) above the locality record or the highest point within 1 km radius where the mountain top was located further away. Site records were grouped into 8 widely accepted 45° aspect sectors labelled by their median values (North, North-East, etc.). Slope was calculated in degrees (°).

Climatic factors including rainfall, temperature and solar radiation regimes typically set constraints to the broad distribution of most taxa (Jarvis & McNaughton, 1986; Woodward, 1987a). Bioclimatic modelling is based on this ecological principle and finds its application in predicting potential limits to the broad distribution of species (Nix, 1986). BIOCLIM (Nix, 1986) within the ANUCLIM 5.0 (Houlder *et al.*, 1999) package was used to estimate the climate at each locality using 35 climatic indices, producing bioclimatic species profiles. Climate data were derived from continent-wide surfaces of monthly mean minimum and maximum temperatures, rainfall, radiation with rainfall, and evaporation. Interpolation was set to weekly intervals. The input consisted of eastings, northings and elevation. Bioclimatic species profiles for both frogs were defined by pooling index estimates from all locations.

BIOCLIM was also run using the settings above to estimate the full climatic range that occurs within the Sydney Basin, based on a 5 km gridded DEM with 10 m contour intervals (AMGs: 230000 – 400000 m East or the coast line where the latter number is over the ocean; 6130000 – 6390000 m North). The bioclimatic profiles were compared to predict areas of similar climate within the Sydney Basin. BIOMAP (Houlder *et al.*, 1999) within ANUCLIM was supplied with those to produce maps on which each grid cell was assigned a value for its suitability as potential habitat based on climatic parameters. For each bioclimatic parameter, BIOMAP compares the value in a given location with the statistical distribution of that same parameter in the species profile to see if it falls within one of the statistical spans (here: 10th to 90th percentile – the core habitat; and the full range). For a given statistical span, all the parameters must pass for the point to be assigned the corresponding value.

Logistic regressions are particularly suited to habitat analyses based on presence / absence data and have been widely applied (Burgman & Lindenmayer, 1998; Osborne & Tigar, 1992; Parris, 2001; Peeters & Gardeniers, 1998). Recently termed the resource selection probability function (Boyce & McDonald, 1999), this approach yields outcomes directly interpretable as probabilities or alternatively as ratios of odds of occurrence as a function of any number of environmental variables. Binary logistic regressions were applied separately for each frog species to test the relationship between presence / absence and each climatic variable using Minitab 13.2 (Minitab Inc. 2000). Highly skewed variables as revealed by frequency histograms were transformed (natural log or exponential) prior to analyses. Significance levels were set at 0.01 because of the large number of required tests (reducing the likelihood of a type 1 error occurring). Separate analyses were carried out on each climatic variable resulting in the quadratic function that describes the relationship between this variable, x, and the probability of occurrence, $p(x)$ (Jongman *et al.*, 1997):

$$\log\left[\frac{p(x)}{1-p(x)}\right] = \beta_0 + \beta_1 x + \beta_2 x^2 \qquad \text{Equation 1}$$

where β_0, β_1 and β_2 are regression coefficients. One tailed z-tests were used to determine whether β_2 was significantly less than zero. The quadratic function with a coefficient $\beta_2 < 0$ results in a Gaussian logit curve with a unique optimum value, u, of the variable which is calculated:

$$u = \left[\frac{-\beta_1}{2\beta_2}\right] \qquad \text{Equation 2}$$

When $\beta_2 = 0$, there is a logistic increase ($\beta_1 > 0$) or decrease ($\beta_1 < 0$) in the probability of occurrence with an increase in the climatic variable. There is no relationship between the variable and species occurrence when both β_1 and β_2 equal zero (Jongman *et al.*, 1997). Optimum habitat values are reported as u (Equation 2) for Gaussian logit curves, maximum values for positive logistic curves and minima for negative logistic curves. Multiple logistic regressions were not carried out because of the high level of inter-correlation among variables.

To evaluate the relative position of animal locations in relation to the range of climates in the Sydney Basin, a correlation matrix principal components analysis (SPSS) was used reducing the 35 highly inter-correlated BIOCLIM variables to a smaller number. Principal components covering the whole Sydney Basin were then plotted for each species.

2.2.2 Broad scale habitat analyses

Broad scale and finer sampling scale habitat analyses were based on data collected in the field. Locations were systematically selected. For each of the two species, two sites were chosen within each area covered by a 1:25000 topographic map sheet (references in Table

2). Ideally, sites were well spaced within each map sheet, but also in relation to those on adjacent sheets to provide a reasonably uniform geographical coverage. The landmass of the map sheets *Broken Bay, Mona Vale, Otford* and *Sydney Heads* cover less than 50% of the total map coverage, and thus contributed only a single record to the broad scale analyses. Map sheet *Wollangambe* contained a single tight cluster of *P. australis* records and thus contributed only one site for the broad scale analyses. Some map sheets contained only single records. These sites were included where possible. The only *H. australiacus* locality on the *Riverstone* map sheet was excluded because this record came from near the foundations of a house in a garden (Emerton & Burgin, 1997) in the middle of a suburb with no natural vegetation within 1 km. The only *H. australiacus* record on *Sydney Heads* provided very little habitat information because land use had changed to parklands.

Some sites were not considered for field analyses. Certain map sheet coverages had to be excluded due to site remoteness (Wollemi wilderness) or access restrictions (Holsworthy Army Base, Sydney Catchment Authority land). These are shown as shaded rectangles in Figure 1. Field data were collected for 50 *P. australis* sites, and 36 *H. australiacus* sites.

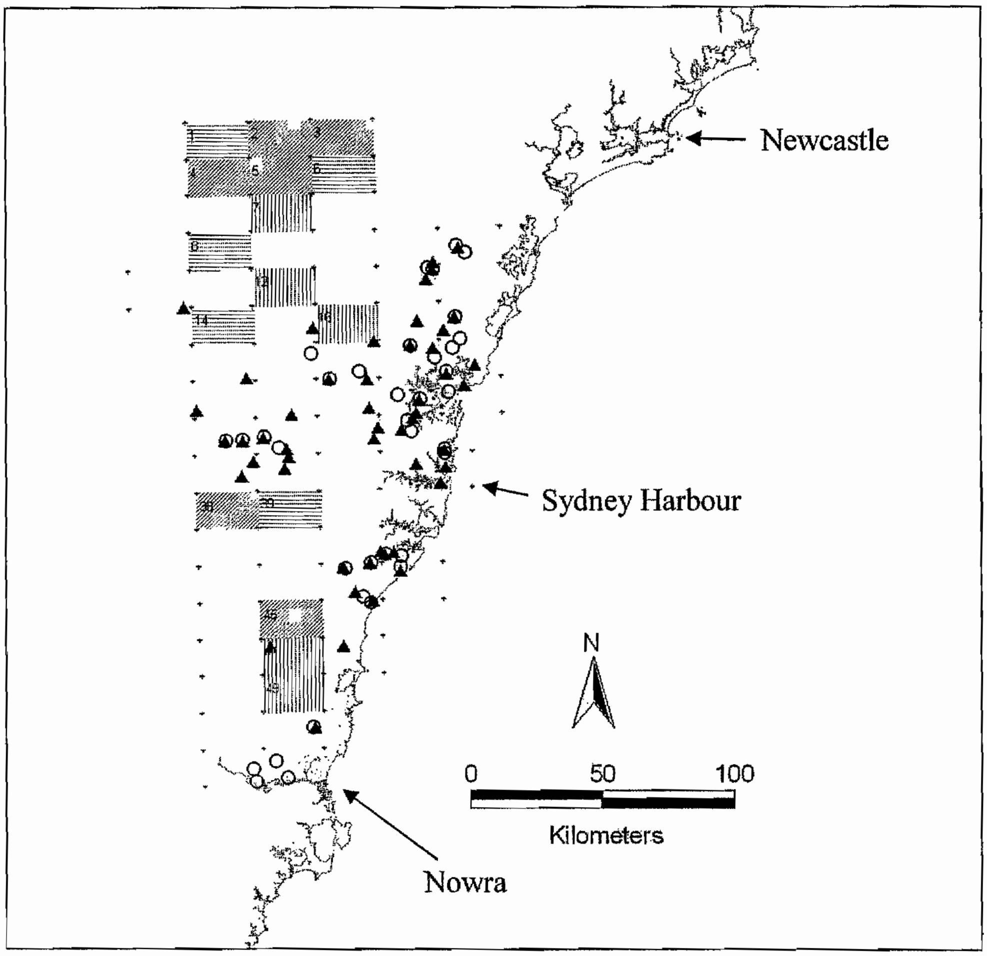

Figure 1 Locations of *P. australis* (triangles) and *H. australiacus* (circles) field sites visited for broad-scale habitat analyses. The shaded rectangles indicate map sheet coverages (grid) not visited that contain records of *P. australis* (horizontal shading), *H. australiacus* (vertical shading) or both species (diagonal shading). A number in the top left corner refers to the map sheet name listed in Table 2.

2.2.2.1 Data collected

WA records are of variable accuracy and precision. In most areas specific sites were identified in the field drawing on available information, personal knowledge, and in many cases also on the intuition and reasoning of experts. Details of environmental variables analysed are given in Table 11. Where likely breeding sites could not be located, the following information on physical factors and vegetation was collected in the general area: The presence / absence and distance to cliffs within 200m above or below the site, and whether the terrain flattens out relative to up-slope gradients, as well as details on landscape morphology (Adair *et al.*, 1994) and shape (simple – little or no curvature; convex – outward curvature like a headland; concave – inward curvature like a valley head; or amphitheatre – a concave shape of at least 180°).

Sydney Basin vegetation was characterised into broad communities based on published species compositions (Benson, 1986; 1992; Benson & Howell, 1994; Buchanan, 1980; Buchanan & Humphries, 1980; Burrough *et al.*, 1977; Keith, 1994; Keith & Benson, 1988; LeBrocque & Buckney, 1994; McRae, 1990; Outhred *et al.*, 1985; Thomas & Benson, 1985a; 1985b). These were condensed to 117 communities. While carrying out the field work, it was soon realised that there is considerable geographic variation in vegetation communities across the region and overlap between communities in which the frogs occur. Broad scale data analyses at the species level of flora were therefore considered uninformative and are not reported here. Instead, structural vegetation types were classified within a 100m radius defined by growth form and crown separation of woody plants (Walker & Hopkins, 1998).

Where breeding sites (places where moisture is likely to accumulate, at least during rainfall events; i.e. generally drainage lines) could be identified, further information was collected on vegetation, geology, soil, disturbances, biota and other breeding site characteristics. The area covered was defined as within a circle of 10 m radius, with the central point being a likely breeding site.

Vegetation was assessed by percentage cover (Walker & Hopkins, 1998) and species diversity for the ground storey, shrub layer, top storey and combined cover. Mean heights of the three layers were also classified, and a species list was compiled of three or four dominating species for each layer. Vegetation associations were named following Groves (1994). Aspect was determined (°) with a handheld SILVA™ compass (Type 7NL) and slope was measured (°) with a SUUNTO™ PM-5 optical reading clinometer following the method and classifications of Speight (1998).

Percent coverage at ground level was estimated for leaf litter, logs, bush rock and bare ground. A ruggedness index was developed for the ground surface (even or smooth; stubble; sticks; cobble; as ploughed with a moldboard plough (Steinmetz, 1982)).

The presence of laterite and clay lens (where this was possible) was recorded and the soil analysed for texture and structure from both the surface and 10 cm below close to the edge of a likely breeding site following McDonald & Isbell (1998). “Medium clay” and “medium heavy clay” were combined into one class because I was unable to distinguish between the two using this method. The assessed disturbances were earthworks, fire, road / track surfacing, slashing, traffic intensity and erosion intensity. These assessments were kept simple and used classifications that could be answered consistently in the field (see classifications in Results).

Weed degradation was classified (none, light, moderate, heavy, based on coverage of all strata combined) and the number of different types of likely shelters available to the animals noted. Breeding sites were further described by type (Pond: water body not associated with a water course; - creek; - table drain; - artificial drain: a man-made channel that is not a table drain or a mitre drain; - soak: a place that is kept damp for prolonged periods by seeping or dripping water; - mitre drain; - depression; - pool in creek), and permanence of water course and its origin, and whether crayfish or their burrows were present.

2.2.2.2 *Broad scale data analysis*

Data were summarised, generally by calculating relative frequencies of occurrences of a particular classification for each variable measured. Chi-square goodness of fit tests were calculated where appropriate against equal expected frequencies. Comparisons of presence vs. absence sites were not attempted because of the lack of comparable information for absence sites.

2.2.3 *Medium scale habitat analyses*

Several as yet unregistered sites were added to the WA records for medium scale habitat analyses. These are sites I discovered while working in the field. The medium scale study area is contained within the *Broken Bay* 1:25000 topographic map and the boundaries of Brisbane Water and Bouddi NPs. In addition, the area westward to Mullet Creek within the

Cowan 1:25000 topographic map was included. Twelve sites were chosen for each of *P. australis* track sites (from 43), *P. australis* non-track sites (from 25) and *H. australiacus* sites (from 28). Individual records in each set were assigned a number and randomly generated numbers were then used to choose subsets.

Fourteen confirmed absence sites were also included. These were chosen as follows. A 500m grid based on AMGs was superimposed onto a map of the study area. The intersections indicated potential study sites. After the exclusion of known presence-sites, 133 locations remained. Fifteen locations were randomly chosen as outlined above. The most likely breeding site for each species within 100m from the identified location was permanently marked and surveyed for frogs (calls for *P. australis* and tadpoles for *H. australiacus)*. Access paths were also marked by use of secateurs and with reflective tags to facilitate access at night. Each site was surveyed three times (Autumn 03, Spring 03, Spring 04) during weather conditions appropriate for frog calling activity. Several control sites (where animals were known to be present) were used to decide on the suitability of sampling sessions. The absence of any records (including pre 1980 WA records) and the absence of tadpoles for *H. australiacus*, or calling *P. australis* males were taken as a confirmation of respective absence. For each species, single localities provided new records of occurrence.

2.2.3.1 Medium scale data collected

The same information was collected as for broad scale analyses (Table 11), including absence sites. In addition, soil classifications of the area (Chapman & Murphy, 1989) were included.

2.2.3.2 Medium scale data analysis

Habitat data were subjected to chi-square tests and logistic regression analysis as detailed earlier.

P. australis track and non-track sites were compared to absence sites separately. Because none of the absence sites were near tracks, certain variables related to the presence of tracks were excluded from the track / absence site comparisons: the presence of laterite, % bare ground, some disturbances (earthworks, surfacing, slashing, traffic) and site character (e.g., creek, table drain, etc).

2.2.4 *Fine scale habitat analyses*

Breeding pool characteristics were obtained as part of the hydroperiod study (Chapter 5), and habitat details of *H. australiacus* burrowing locations were recorded during radio-tracking work (Chapter 6). Refer to these Chapters for methodological details. The pool characteristics presented in this Chapter are based on combined values of track and non-track breeding sites.

3 Results

3.1 Extra-broad scale habitat analyses

Locality records of *P. australis* and *H. australiacus* used for the extra-broad scale study are represented in Figure 2.

3.1.1 *Geological association*

Table 4 Number of locality records for *P. australis* and *H. australiacus* within each of the geological formations of the Sydney Basin. *H. australiacus* data are original, all other values were obtained from Thumm & Mahony (1999) to facilitate comparisons. *Seven *H. australiacus* records (Shoalhaven Group – Megalong Conglomerates) from the Shoalhaven region were excluded from this analysis because they fall outside of the area mapped by Thumm & Mahony (1999).

Species			***P. australis***		***H. australiacus***	
Geological Formation	**Area (km^2)**	**% of total**	**Number of localities**	**% of total**	**Number of localities**	**% of total**
Sydney Basin	26478	100	141	100	138*	100
Quaternary Sands and Volcanics	2863	10.8	2	1.4	1	0.7
Wianamatta Shale	2843	10.7	2	1.4	2	1.5
Hawkesbury Sandstone	7045	26.6	125	88.7	123	89.1
Narrabeen Group Sandstones	11144	42.1	11	7.8	12	8.7
Coal Measures	2583	9.8	1	0.7	0	0

Both species occur predominantly on Hawkesbury Sandstone and to a much lesser degree on the Narrabeen Group of sandstones, both of Triassic origin (Table 4) (NSW Dept. of Mines, 1966). Hawkesbury Sandstone derived soils are shallow (< 50 cm deep), highly permeable and of low fertility. They include Lithosols, Earthy Sands, Yellow Earths, Yellow and Red Podzolic Soils and Siliceous Sands. Narrabeen Group soils on sandstone are 30 – 200 cm deep and include Lithosols, Siliceous Sands and Yellow Podzolic Soils (Chapman & Murphy, 1989).

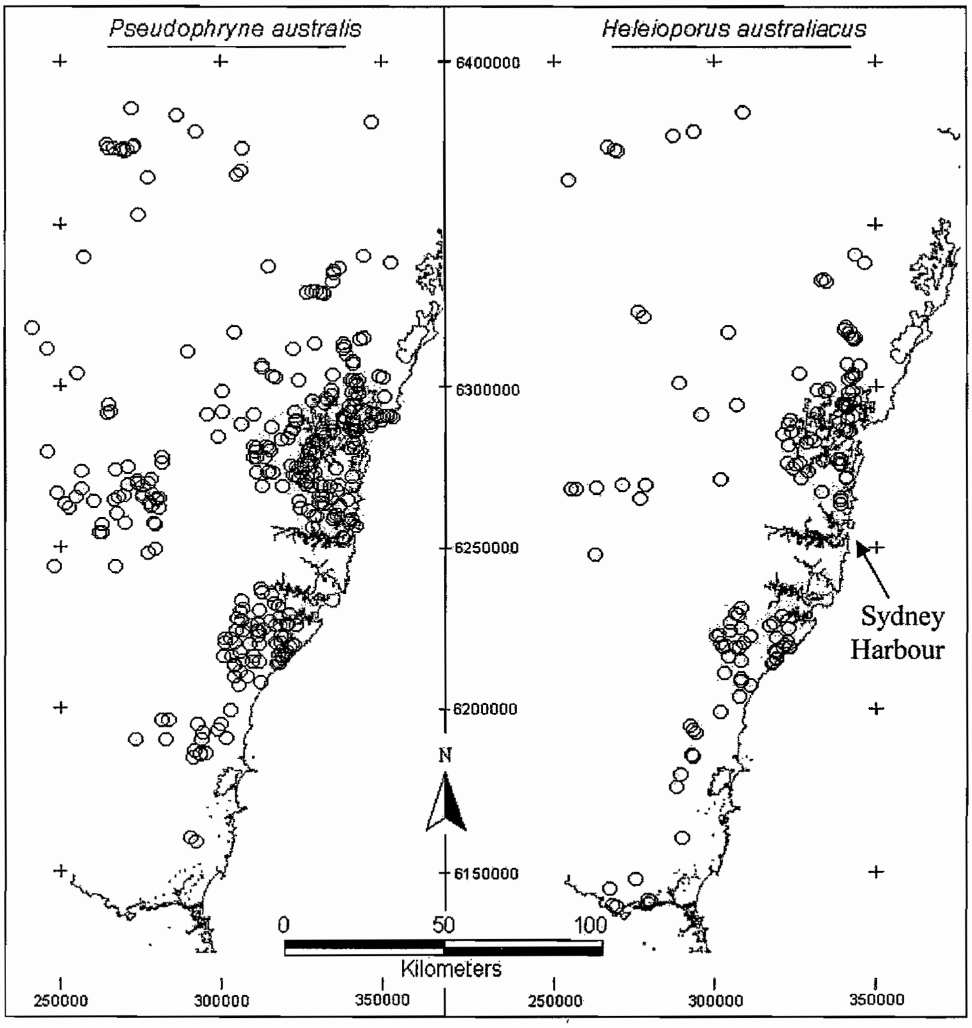

Figure 2 Distribution of *P. australis* and *H. australiacus* locality records within the Sydney Basin. The grey line represents the coast line. Each shown site contributed to the extra-broad scale habitat analyses. The AMG grid is indicated.

3.1.2 Elevation

Both frogs are absent from the highest areas, which cover only a small proportion of the Sydney Basin (Table 5).

Table 5 Summary statistics of altitude for *P. australis* and *H. australiacus* locations in the Sydney Basin. The horizontal plane area of unutilised high altitude area was calculated at the 10 m contour above the maximum elevation for each species and taken as a percentage of the total area within AMGs 6400000-6100000 N; 223000-400000 E; and the coast line.

Species	***P. australis***	***H. australiacus***
Mean elevation (SE)	236 (11.2) m	242 (15.5) m
Elevation range	10 – 1020 m	20 – 1000 m
Maximum elevation within distribution range	1360 m	1360 m
Percentage of unutilised high altitude area (horizontal plane area) within Sydney Basin	1.89%	2.23%

3.1.3 Relative position in topography

P. australis and *H. australiacus* sites are located in the upper parts of the topography (Figure 3 and Figure 4). The methods by which the lowest point was defined did not strongly influence the results (Table 6).

Table 6 Summary statistics of *P. australis* and *H. australiacus* locations based on their relative positions in the topography. Relative positions are expressed as a percentage above the lowest point (0%), where the 100% mark is the nearest ridge top or knoll above the site, or the highest point above the site within 1 km where the top is located more than 1 km away. The lowest point is either the valley floor below, or the lowest point below within 1 km.

Species	***P. australis***		***H. australiacus***	
Lowest point	Valley floor	Within 1 km	Valley floor	Within 1 km
Mean (SE)	63.9 (1.3)%	62.7 (1.3)%	67.6 (1.8)%	65.6 (1.7)%
Median	68.4%	66.7%	69.2%	68.2%
Mode	66.7%	50.0%	100%	100%
Sites within 1 km from top	77.1%		66.9%	

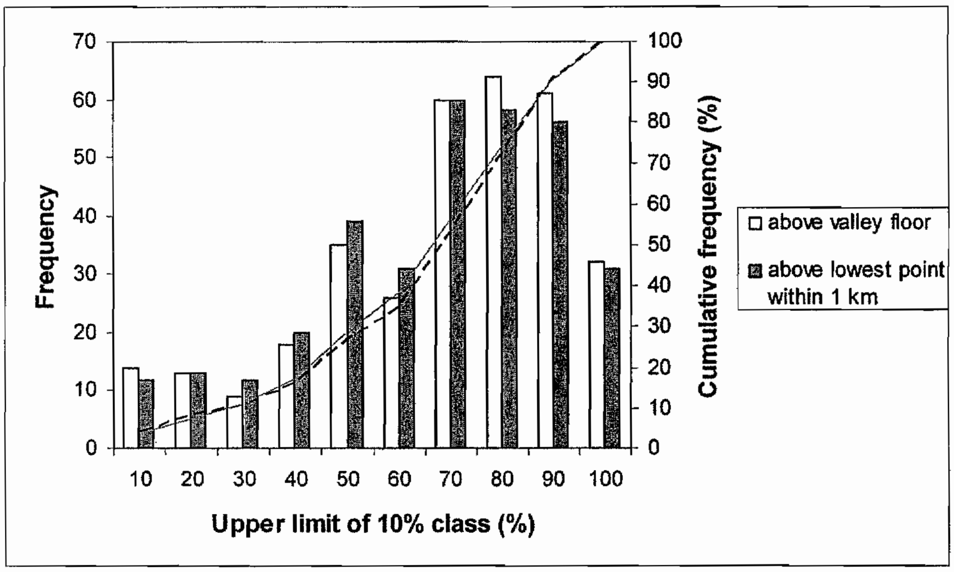

Figure 3 Frequency distribution of *P. australis* locations based on their relative positions in the topography. The curves (the dashed line corresponds to the white bars, the grey line corresponds to the grey bars) correspond to bars) indicate cumulative frequency values. The 10% class includes all records that are between zero to 10% above the valley floor or lowest point; 100% indicates that the location is on the mountain top.

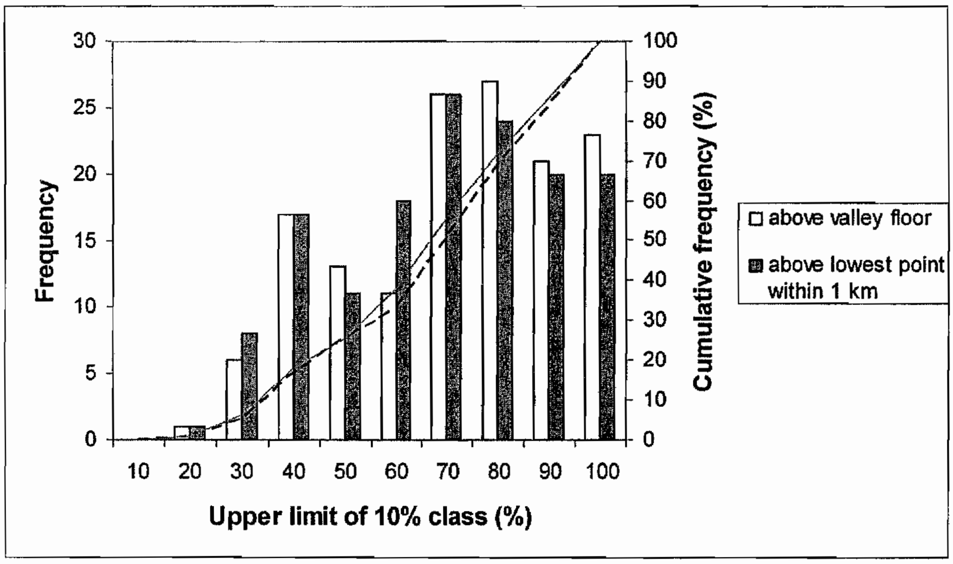

Figure 4 Frequency distribution of *H. australiacus* locations based on their relative positions in the topography. The curves (the dashed line corresponds to the white bars, the grey line corresponds to the grey bars) indicate cumulative frequency values. The 10% class includes all records that are between zero to 10% above the valley floor or lowest point; 100% indicates that the location is on the mountain top.

3.1.4 Aspect

P. australis ($\chi^2_{(7)} = 7.95$; P = 0.34) and *H. australiacus* ($\chi^2_{(7)} = 3.91$; P = 0.79) (Table 7) showed no significant preference for any particular aspect segment.

Table 7 Frequencies of *P. australis* and *H. australiacus* locations assigned to 45^0 aspect segments. Data were derived from a 25 m grid GIS file.

Aspect segment	***P. australis***	***H. australiacus***
N	40	14
NE	38	22
E	47	20
SE	38	19
S	32	14
SW	37	17
W	47	17
NW	53	22
Total	332	145

3.1.5 Slope

Both *P. australis* and *H. australiacus* sites were located where slopes were gentle (i.e., 6 – 11°) (Table 8). Flat areas and steep sections were not inhabited.

Table 8 Summary statistics of *P. australis* and *H. australiacus* locations based on slope of the terrain. Data were derived from a 25 m grid GIS file.

Species	***P. australis***	***H. australiacus***
Mean (SE)	11.4 (0.4)°	10.4 (0.7)°
Median	10°	8°
Mode	9°	6°
Range	1 - 34^0	1 - 37^0

3.1.6 Climatic variables

Bioclimatic species profiles and optimum climatic values are shown in Table 9. Optimum climatic values differed by more than 1 SD from the mean of the bioclimatic species profile in the following ways. For *P. australis*, temperature seasonality and radiation of the driest quarter were higher, minimum temperature of the coldest period, mean temperature of the wettest quarter, mean temperature of the driest quarter, and precipitation seasonality were lower. For *H. australiacus,* temperature seasonality and mean moisture index of the warmest quarter were higher, whereas mean temperature of the wettest quarter, mean temperature of the driest quarter, and precipitation of the driest period were lower. Core habitat and range as predicted by BIOCLIM are shown for *P. australis* (Figure 5) and *H. australiacus* (Figure 6). The predicted core habitat is restricted to a relatively narrow strip between 0 and 47 km from the coast for *P. australis*, and between 5 and 40 km from the coast for *H. australiacus*. A relatively large area to the south-west of Sydney does not fit the bioclimatic profile of either species. This region experiences less rainfall than the areas where each species occurs.

Multivariate analyses also revealed that animal locations did not centre around localities that featured mean climatic values. However in context of all 35 variables, the combined influence of individual climatic variables on the species' geographic distributions were somewhat different. Core habitat of both species is shown as a cluster in positive territory for both PC1 and PC2 (Figure 7, Figure 8). The first principal component describes a gradient of increasing precipitation and moisture index; and decreasing radiation, temperature range and temperature maximum. The second component reflects a gradient of increasing minimum and mean temperatures. PC3 describes seasonality gradients, where that for precipitation increases, and those for radiation and moisture index decrease. PC4 represents decreasing isothermality (mean diurnal temperature range / annual temperature range) (Table 10).

Table 9 The bioclimatic envelopes of *P. australis* and *H. australiacus* in the Sydney Basin predicted by BIOCLIM. Logistic regression model types (g: Gaussian; -: negative logistic; +: positive logistic; ns: not significant) were used to determine optimum climatic values (u for Gaussian curves). Significance level was set at 0.01. Variables which were transformed for logistic regressions are indicated as: *natural logarithm; ^exponential. Abbreviations used: Opt.: optimum value; Temp. = temperature, CV = coefficient of variation, Qtr. = quarter, MI = Moisture Index. CV is the standard deviation of the weekly estimates expressed as a percentage of the annual mean of those estimates.

	P. australis					*H. australiacus*				
Variable	**Mean (SD)**	**Range**	**10 - 90%**	**Model**	**Opt.**	**Mean (SD)**	**Range**	**10 - 90%**	**Model**	**Opt.**
1. Annual Mean Temp. (^{0}C)	15.8 (1.17)	11.2 - 17.4	13.9 - 16.8	ns	-	15.7 (1.05)	11.7 - 17	14.1 - 16.7	ns	-
2. Mean Diurnal Range (^{0}C)	10.8 (1.04)	9.0 - 13.4	9.6 - 12.5	ns	-	10.5 (0.87)	9.0 - 12.9	9.4 - 11.9	g	11.0
3. Isothermality (2/7)	0.48 (0.01)	0.44 - 0.50	0.47 - 0.50	ns	-	0.48 (0.01)	0.46 - 0.51	0.47 - 0.49	ns	-
4. Temp. Seasonality (CV) ^	1.4 (0.11)	1.23 - 1.68	1.28 - 1.61	g	1.57	1.37 (0.1)	1.22 - 1.66	1.27 - 1.56	g	1.49
5. Max. Temp. of Warmest Period (^{0}C)	26.3 (1.11)	22.7 - 29.6	25.0 – 28.0	ns	-	26.0 (1.01)	23.5 - 29.2	24.7 - 27.1	ns	-
6. Min. Temp. of Coldest Period (^{0}C)	4.0 (1.46)	0.4 - 6.5	1.4 - 5.6	-	0.4	4.3 (1.24)	0.0 - 6.3	2.5 - 5.6	ns	-
7. Temp. Annual Range(5-6) (^{0}C)	22.3 (1.91)	19.1 - 26.7	20.1 - 25.4	g	23.7	21.7 (1.61)	19.1 - 25.9	19.9 - 24.5	g	22.9
8. Mean Temp. Of Wettest Qtr. (^{0}C)	20.0 (1.02)	16.2 - 22.7	18.5 - 21.2	g	18.6	19.6 (1.32)	13.0 - 22.1	18.3 – 21.0	g	17.5
9. Mean Temp. of Driest Qtr. (^{0}C)	11.6 (1.5)	6.4 - 14.6	9.2 – 13.0	-	6.4	11.7 (1.32)	6.6 - 13.5	9.8 - 12.8	-	6.6
10. Mean Temp. of Warmest Qtr. (^{0}C)	20.7 (0.99)	16.6 - 22.8	19.2 - 21.7	ns	-	20.5 (0.92)	17.3 - 22.4	19.4 - 21.5	ns	-
11. Mean Temp. of Coldest Qtr. (^{0}C)	10.4 (1.4)	5.5 - 12.3	8.2 - 11.7	ns	-	10.5 (1.24)	5.7 – 12.0	8.6 - 11.7	ns	-
12. Annual Precipitation (mm)	1156 (179.1)	759 - 1957	900 - 1352	g	1074	1215 (179.5)	726 - 1872	932 - 1434	g	1110
13. Precipitation of Wettest Period (mm)	33 (5.1)	23 - 58	27 - 40	g	35	35 (5.3)	22 - 55	28 - 42	g	36
14. Precipitation of Driest Period (mm)	12 (4.53)	0 - 20	2 - 15	g	8	13 (3.72)	0 - 19	10 - 15	g	9
15. Precipitation Seasonality (CV)	28 (3.21)	22 - 37	24 - 34	-	22	27 (2.62)	20 - 37	24 - 31	ns	-
16. Precipitation of Wettest Qtr. (mm) *	390 (57.9)	260 - 648	310 - 458	g	390	406 (59.92)	257 - 619	316 - 476	g	417
17. Precipitation of Driest Qtr. (mm) *	192 (31.21)	124 - 316	146 - 229	g	170	202 (29.02)	118 - 303	160 - 236	g	176
18. Precipitation of Warmest Qtr. (mm)	361 (48.76)	260 - 571	297 - 421	g	383	373 (50.39)	257 - 547	301 - 434	g	389
19. Precipitation of Coldest Qtr. (mm) *	249 (50.48)	142 - 440	173 - 310	g	205	266 (47.35)	134 - 419	193 - 318	g	220

Table 99 continued.

	P. australis					*H. australiacus*				
Variable	**Mean (SD)**	**Range**	**10 - 90%**	**Model**	**Opt.**	**Mean (SD)**	**Range**	**10 - 90%**	**Model**	**Opt.**
20. Annual Mean Radiation (MJ m^{-2})	16.4 (0.42)	14.8 - 17.5	15.9 - 16.9	g	16.7	16.3 (0.44)	14.9 - 17.6	15.7 - 16.8	g	16.5
21. Highest Period Radiation (MJ m^{-2})	24.3 (0.5)	22.8 - 25.3	23.6 - 24.9	g	23.9	24.1 (0.51)	22.9 - 25.3	23.4 - 24.8	ns	-
22. Lowest Period Radiation (MJ m^{-2})	8 (0.31)	7 - 9	7.6 - 8.4	g	8.2	8 (0.37)	7 - 9	7.4 - 8.4	g	8.1
23. Radiation Seasonality (CV) *	34 (1.03)	31 - 36	32 - 35	g	33	34 (1.22)	31 - 37	32 - 35	g	34
24. Radiation of Wettest Qtr. (MJ m^{-2})	18.5 (1.49)	15.9 - 23.3	16.7 - 20.2	g	19.2	17.9 (1.87)	9.6 - 23.3	16 - 19.7	g	17.5
25. Radiation of Driest Qtr. (MJ m^{-2})	13.7 (0.44)	12.4 - 16.2	13.1 - 14.2	g	15.0	13.6 (0.48)	12.3 - 14.5	12.8 - 14.1	ns	-
26. Radiation of Warmest Qtr. (MJ m^{-2})	21.4 (0.62)	19.4 - 23.3	20.7 - 22.3	g	21.5	21.3 (0.63)	19.6 - 23.3	20.5 - 22.2	g	21.4
27. Radiation of Coldest Qtr. (MJ m^{-2})	10.1 (0.25)	9.3 - 10.9	9.8 - 10.4	g	10.2	10 (0.29)	8.9 - 10.9	9.7 - 10.4	10.1	
28. Annual Mean MI	0.81 (0.08)	0.54 - 0.98	0.68 - 0.89	ns	-	0.83 (0.08)	0.51 - 0.97	0.7 - 0.91	ns	-
29. Highest Period MI ^	0.98 (0.04)	0.8 - 1	0.94 – 1.0	ns	-	0.99 (0.04)	0.74 – 1.0	0.96 – 1.0	ns	-
30. Lowest Period MI	0.46 (0.07)	0.33 - 0.85	0.37 - 0.54	g	0.50	0.47 (0.08)	0.33 - 0.79	0.37 - 0.57	g	0.51
31. MI Seasonality(CV)	21 (3.93)	5 - 30	16 - 26	g	19	20 (4.38)	7 - 29	16 - 27	g	18
32. Mean MI of High Qtr ^.	0.97 (0.06)	0.72 - 1	0.9 – 1.0	ns	-	0.98 (0.05)	0.67 - 1	0.95 – 1.0	ns	-
33. Mean MI of Low Qtr.	0.57 (0.09)	0.37 - 0.91	0.45 - 0.67	ns	-	0.58 (0.09)	0.38 - 0.87	0.45 - 0.70	g	0.61
34. Mean MI of Warm Qtr.	0.63 (0.08)	0.44 - 0.92	0.52 - 0.72	g	0.70	0.64 (0.08)	0.43 - 0.88	0.51 - 0.74	+	0.88
35. Mean MI of Coldest Qtr.	0.97 (0.06)	0.72 - 1	0.89 – 1.0	ns	-	0.98 (0.05)	0.67 - 1	0.94 – 1.0	ns	-

Table 10 Factor loadings, Eigenvalues and variance statistics for the first four principal components of climatic variables across the Sydney Basin. Loadings with an absolute value < 0.5 are not shown.

Variable	**PC1**	**PC2**	**PC3**	**PC4**
1. Annual Mean Temp. (^{0}C)		0.965		
2. Mean Diurnal Range (^{0}C)	-0.829			
3. Isothermality (2/7)		0.611		-0.511
4. Temp. Seasonality (CV)	-0.663	-0.591		
5. Max. Temp. of Warmest Period (^{0}C)	-0.750	0.577		
6. Min. Temp. of Coldest Period (^{0}C)		0.860		
7. Temp. Annual Range(5-6) (^{0}C)	-0.786			
8. Mean Temp. Of Wettest Qtr. (^{0}C)	-0.543	0.693		
9. Mean Temp. of Driest Qtr. (^{0}C)		0.953		
10. Mean Temp. of Warmest Qtr. (^{0}C)		0.905		
11. Mean Temp. of Coldest Qtr. (^{0}C)		0.956		
12. Annual Precipitation (mm)	0.970			
13. Precipitation of Wettest Period (mm)	0.890			
14. Precipitation of Driest Period (mm)	0.785			
15. Precipitation Seasonality (CV)		0.524	0.669	
16. Precipitation of Wettest Qtr. (mm)	0.913			
17. Precipitation of Driest Qtr. (mm)	0.927			
18. Precipitation of Warmest Qtr. (mm)	0.878			
19. Precipitation of Coldest Qtr. (mm)	0.922			
20. Annual Mean Radiation (MJ m^{-2})	-0.941			
21. Highest Period Radiation (MJ m^{-2})	-0.832			
22. Lowest Period Radiation (MJ m^{-2})	-0.677			
23. Radiation Seasonality (CV)			-0.702	
24. Radiation of Wettest Qtr. (MJ m^{-2})	-0.778			
25. Radiation of Driest Qtr. (MJ m^{-2})		0.562		
26. Radiation of Warmest Qtr. (MJ m^{-2})	-0.933			
27. Radiation of Coldest Qtr. (MJ m^{-2})	-0.590	0.511		
28. Annual Mean MI	0.970			
29. Highest Period MI	0.883			
30. Lowest Period MI	0.847			
31. MI Seasonality(CV)	-0.566		-0.750	
32. Mean MI of High Qtr.	0.902			
33. Mean MI of Low Qtr.	0.869			
34. Mean MI of Warm Qtr.	0.868			
35. Mean MI of Coldest Qtr.	0.912			
Eigenvalue	18.7	7.61	4.07	1.81
% variance	53.4	21.7	11.6	5.16
Cumulative % variance	53.4	75.1	86.8	91.9

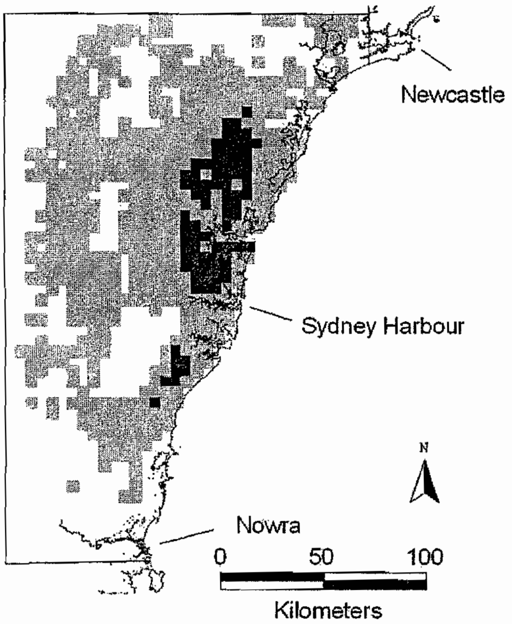

Figure 5 *P. australis* core habitat (dark shading) and range (grey shading) as predicted by BIOCLIM. Pixel side length is approximately 5 km. The extent of the analysis was confined to the area outlined by the rectangle and coast line.

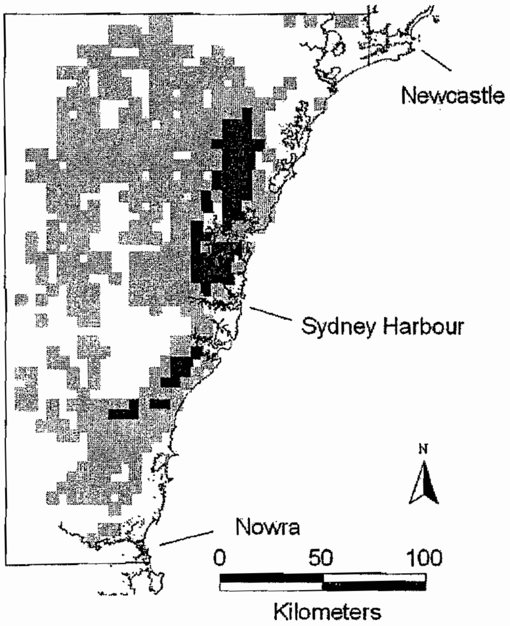

Figure 6 *H. australiacus* core habitat (dark shading) and range (grey shading) as predicted by BIOCLIM. Pixel side length is approximately 5 km. The extent of the analysis was confined to the area outlined by the rectangle and coast line.

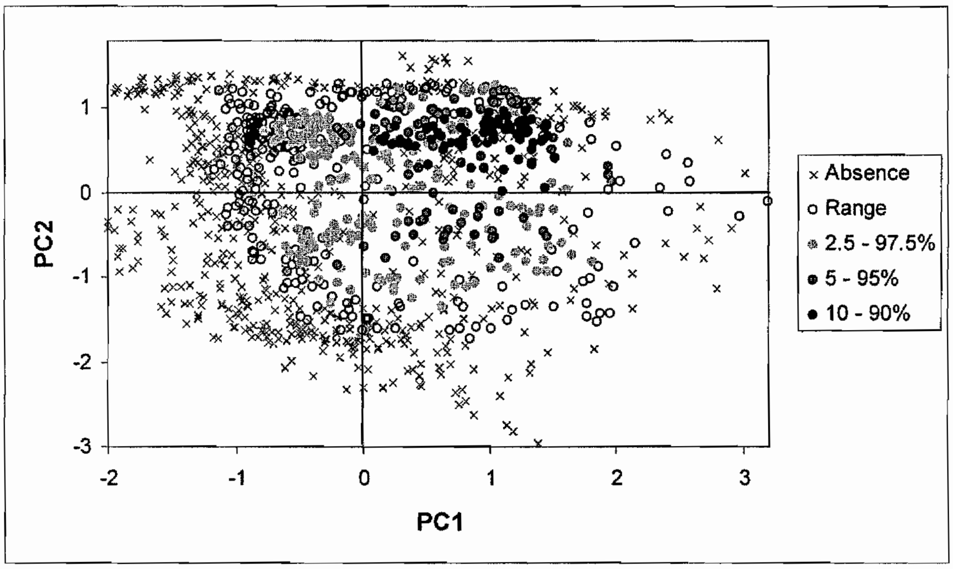

Figure 7 First two principal components of bioclimatic variables for the Sydney Basin and likelihood of occurrence of *P. australis* as predicted by BIOCLIM. Filled black circles show predicted core habitat.

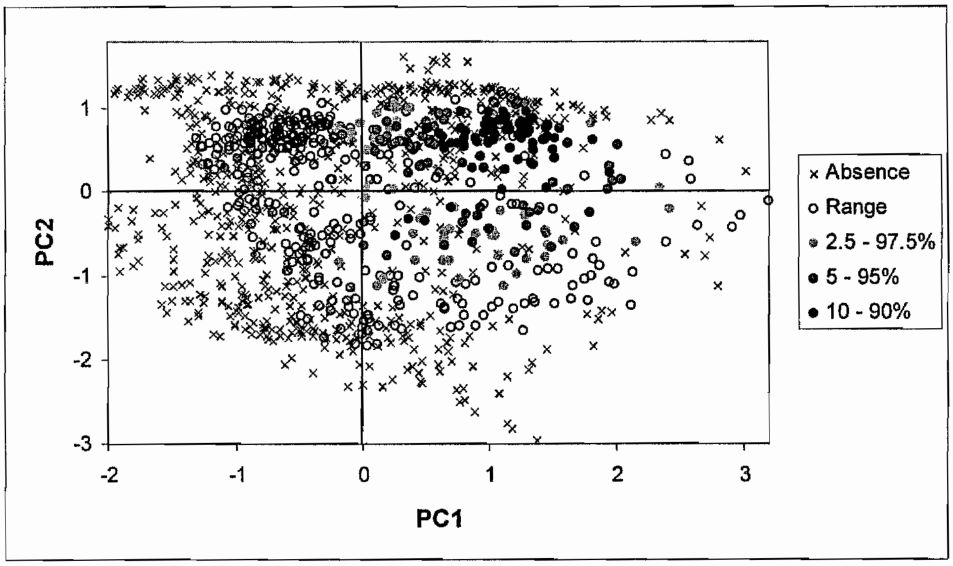

Figure 8 First two principal components of bioclimatic variables for the Sydney Basin and likelihood of occurrence of *H. australiacus* as predicted by BIOCLIM. Filled black circles show predicted core habitat.

3.2 Broad scale habitat analyses

Full results of the broad scale habitat descriptions are given in Table 11. Following is first a description of the habitat of *P. australis* and then of the habitat of *H. australiacus*, based on the informative habitat variables. *P. australis* field sites were based on locations where I had observed or heard frogs (40%) and WA records (60%). Field sites for *H. australiacus* were based on locations where I had observed or heard frogs (12%), seen tadpoles (12%), or WA records (76%).

3.2.1 The habitat of Pseudophryne australis

P. australis breeding sites were frequently (68%) found within 200 m of cliffs ($\chi_{(1)} = 6.5$; $P = 0.01$)(core habitat: 200 m above cliffs to 147 m below cliffs), on the upper slope or mid slope, but never in gullies or flats. *P. australis* were absent from closed forests. The vegetation structure of their habitat was predominantly open forest, but also included woodland, open woodland and heath types. Ground storey cover was generally greater than 25% with a mean height of 0.3 to 0.6 m and a diversity classification of 5 to 19 species. The shrub layer covered 5 to 50% at a mean height of 2 to 3 m, with 5 to 19 species present. Top storey coverage was predominantly 25 to 75% and never exceeded 75%. Top storey height for the core habitat was 10 to 30 m with 1 to 4 tree species present. Coverage with all three layers combined ranged from 50 to more than 75%.

There was no association with any particular aspect segment ($\chi_{(7)} = 7.7$; $P = 0.36$). The slope of core habitat did not exceed 10°. Leaf litter covered 5 to 50%, and if logs were present, these were few and covered less than 5%. Rocks were found on 54.2% of all sites, and where present, cover was sparse (<5%). Bare ground was rare, but where present, 5 to 25% coverage was most common. Roughness of the ground was described as "stubble", sometimes as "even" or "with sticks". Laterite was generally absent. Surface soil texture was loamy sand, sand and clayey sand. No clays were identified in the soil samples, however some sites were near a clay lens. Surface soil structure was usually apedal, or weakly pedal to a lesser extent. Soil texture 10 cm below the surface was generally loamy sand or clayey sand with an apedal or weakly pedal structure. Again no clay was found.

Seventeen percent of sites were man-made structures such as table drains. Half of these were regularly maintained. More than half the sites had experienced fire within three years prior to data collection. Only two sites were associated with surfaced roads (quartz gravel, and bitumen). Recent slashing and visible signs of traffic disturbances were generally not detected at the visited sites. Erosion of breeding sites was rated between "negligible" to "slight". No sites were found where erosion was "intense". Weeds were very rarely present, and then only sparsely so. Animals were generally located under leaves, rocks or grass. Sites contained many sheltering places both as dense low vegetation and lots of leaf litter piles.

Crayfish were usually absent and no fish were recorded. Breeding sites were generally associated with creeks (stream order <1, i.e. not mapped on the 1:25000 topographic map series) and to a lesser extent natural gutters, artificial drains (incl. mitre drains, table drains), soaks and depressions. Water courses originated mostly in reserves. All watercourses and breeding pools were ephemeral with soil, rocks and pebbles making up the substrate and sides.

3.2.2 The habitat of Heleioporus australiacus

H. australiacus breeding sites were not usually associated with cliffs. *H. australiacus* habitat was found predominantly on the upper slope, but also on mid slope and on flat ridges. The species also utilises gullies. Their habitat occurs in closed forest, open forest, woodland and various heath types. Ground storey cover was generally greater than 50% with a mean height of 0.3 to 0.6 m and a diversity classification of 5 to 19 species. The shrub layer covered 5 to 50% at a mean height of 2 to 3 m, with 5 to 19 species present. Top storey coverage was predominantly 5 to 75% and never exceeded 75%. Top storey height for the core habitat was 3 to 31 m with 1 to 4 species present. Coverage with all three layers combined exceeded 75%.

There was no association with any particular aspect segment ($\chi_{(7)} = 5.1$; $P = 0.65$). The slope of core habitat did not exceed 8°. Leaf litter covered 5 to 25%, and if logs were present, these were few and covered less than 5%. Rocks were found on 61.8% of all sites, and where present, rock cover was sparse (<5%). Bare ground was also rare, but where present, 5 to 25% coverage was most common. Roughness of the ground was described as "stubble" and “sticks”, sometimes as “even”. Laterite was generally absent. Surface soil texture was sand, loamy sand, clayey sand and sandy loam. No clays were identified in the soil samples; however some sites were near a clay lens. Surface soil structure was usually apedal, some were weakly pedal. Soil texture 10 cm below the surface was generally loamy sand or clayey sand, sandy loam or clay loam with an apedal or weakly pedal structure. Again no clay was found.

Fifteen percent of sites were man-made structures such as small dams. More than half the sites were burnt within three years prior to data collection. Erosion of breeding sites was rated “slight”. No sites were found where erosion was “intense”. Weeds were extremely rarely present, and then only sparsely so.

Crayfish were usually present and fish were always absent. Breeding sites were generally associated with pools and in creeks, and to a lesser extent creeks, table drains and soaks. Water courses originated mostly in reserves and were ephemeral (exception: two spring-fed dams). Breeding pools were ephemeral, semi-permanent or permanent with soil or rock shelves making up the substrate and sides.

Table 11 Details of broad scale descriptions of *P. australis* and *H. australiacus* habitat based on field collected data. Sample sizes are in (). Vegetation structure was classified following Walker & Hopkins (1998). Percentages represent proportions of animal locations that correspond to each habitat variable's categories.

Species **Habitat variable**		***Pseudophryne australis***	***Heleioporus australiacus***
Cliffs within 200m	none	32% (50)	60% (35)
	above site	34%	20%
	at site	10%	8.6%
	below site	24%	11.4%
above 1st cliff downslope?	not applicable	32% (50)	60% (35)
	no	46%	28.6%
	yes	22%	11.4%
Terrain	flattens out	56% (50)	45.5% (33)
	doesn't flatten	44%	54.5%
Morphological type	Flat ridge	6% (50)	11.4% (35)
	Ridge	2%	0%
	Upper slope	74%	45.7%
	Mid slope	16%	28.6%
	Lower slope	2%	2.9%
	Flat	0%	2.9%
	Open gully	0%	2.9%
	Closed gully	0%	5.7%
Landscape shape	simple	62% (50)	45.7% (35)
	convex	2%	0%
	concave	28%	45.7%
	amphitheatre	8%	8.6%
Vegetation structure	closed forest	0% (50)	8.6% (35)
	open forest	70%	40%
	woodland	18%	25.7%
	open woodland	8%	8.6%
	isolated trees with heath understorey	2%	2.9%
	open mallee shrubland	2%	0%
	closed heath	0%	2.9%
	open heath	0%	2.9%
	isolated heath shrubs	0%	2.9%
	isolated heath shrub clumps	0%	5.7%
Ground storey cover	<5%, many individuals	6.3% (48)	6.1% (33)
	5-25%	10.4%	6.1%
	25-50%	20.8%	6.1%
	50-75%	33.3%	33.3%
	>75%	29.2%	48.5%

Table 11 cont. **Species** **Habitat variable**		***Pseudophryne australis***	***Heleioporus australiacus***
Ground storey mean height	0.0 m	0% (48)	0% (33)
	0.3m	58.3%	60.6%
	0.6m	41.7%	39.4%
Ground storey diversity (number of species)	1-4	4.2% (48)	3% (33)
	5-9	35.4%	51.5%
	10-19	47.9%	42.4%
	20-34	12.5%	3%
Shrub layer cover	none	2% (49)	0% (33)
	<5%, few individuals	2%	3%
	<5%, many individuals	14.3%	15.2%
	5-25%	30.6%	42.4%
	25-50%	38.8%	30.3%
	50-75%	10.2%	3%
	>75%	2%	6.1%
Shrub layer mean height	none	2% (49)	0% (33)
	1m	2%	0%
	2-3m	79.6%	72.7%
	>3m	16.3%	27.3%
Shrub layer diversity	none	2% (49)	0% (33)
	1-4	10.2%	15.2%
	5-9	46.9%	51.5%
	10-19	40.8%	33.3%
Top storey cover	none	0% (49)	11.8% (34)
	<5%, few ind.	6.1%	8.8%
	<5%, many individuals	0%	8.8%
	5-25%	14.3%	17.6%
	25-50%	55.1%	32.4%
	50-75%	24.5%	20.6%
	>75%	0%	0%
Top storey maximum height	Range	6 – 35 m (49)	2 – 50 m (34)
	Core habitat	10 – 30 m	3 – 31 m
Top storey diversity	1-4	69.4% (49)	70% (30)
	5-9	28.6%	30%
	10-19	2%	0%
Combined cover	25-50%	0% (49)	2.9% (34)
	50-75%	34.7%	20.6%
	>75%	65.3%	76.5%
Aspect segment	N	20.8% (48)	6.1% (33)
	NE	14%	12.1%
	E	16%	24.2%
	SE	12%	9.1%
	S	8%	12.1%
	SW	4%	12.1%
	W	14%	12.1%
	NW	8%	12.1%

Table 11 cont. **Species** **Habitat variable**		***Pseudophryne australis***	***Heleioporus australiacus***
Slope	Mean (Range)	6.2°(0-15°) (48°)	4.8°(0-11°) (34°)
	Core habitat	3-10°	2-8°
Ground cover leaf litter	none	2.1% (48)	23.5% (34)
	<5%, few individuals	2.1%	5.9%
	<5%, many individuals	6.3%	8.8%
	5-25%	45.8%	35.3%
	25-50%	33.3%	17.6%
	50-75%	6.3%	0%
	>75%	4.2%	8.8%
Ground cover logs	none	16.7% (48)	23.5% (34)
	<5%, few individuals	45.8%	38.2%
	<5%, many individuals	37.5%	35.3%
	5-25%	0%	2.9%
Ground cover rock	none	45.8% (48)	38.2% (34)
	<5%, few individuals	20.8%	26.5%
	<5%, many individuals	25%	29.4%
	5-25%	6.3%	5.9%
	25-50%	2.1%	0%
Bare ground	none	68.8% (48)	61.8% (34)
	<5%, few individuals	6.3%	11.8%
	<5%, many individuals	2.1%	8.8%
	5-25%	20.8%	11.8%
	25-50%	2.1%	0%
	50-75%	0%	5.9%
Ruggedness	even	16.7% (48)	11.8% (34)
	stubble	47.9%	47.1%
	sticks	29.2%	41.2%
	cobble	6.3%	0%
	as ploughed	0%	0%
Laterite	absent	91.8% (49)	91.2% (34)
	on site	8.2%	8.8%
Soil texture surface	sand	28.6% (49)	41.2% (34)
	loamy sand	40.8%	20.6%
	clayey sand	20.4%	11.8%
	sandy loam	4.1%	11.8%
	sandy clay loam	4.1%	2.9%
	clay loam	2%	8.8%
	silty clay loam	0%	2.9%

Table 11 cont. **Species** **Habitat variable**		***Pseudophryne australis***	***Heleioporus australiacus***
Soil structure surface	apedal	65.3% (49)	57.6% (33)
	pedal - weak	34.7%	39.4%
	pedal - strong	0%	3%
Soil texture 10cm below surface	sand	4.2% (48)	5.9% (34)
	loamy sand	50%	35.3%
	clayey sand	29.2%	26.5%
	sandy loam	4.2%	11.8%
	sandy clay loam	6.3%	5.9%
	clay loam	6.3%	11.8%
	silty clay loam	0%	2.9%
Soil structure 10cm below surface	apedal	45.8% (48)	44.1% (34)
	pedal - weak	45.8%	50%
	pedal - strong	8.3%	5.9%
Earthworks	none	83.3% (48)	85.3% (34)
	yes	8.3%	14.7%
	maintained	8.3%	0%
Time since Fire	> 3 years	45.8% (48)	47.1% (34)
	< 3 years	54.2%	52.9%
Surfacing	none	95.8% (48)	100% (34)
	yes	4.2%	0%
	maintained	0%	0%
Slashing	not recently	97.9% (48)	100% (34)
	recently	2.1%	0%
Traffic intensity	negligible	93.8% (48)	100% (34)
	slight	2.1%	0%
	moderate	4.2%	0%
	intense	0%	0%
Erosion intensity	negligible	41.7% (48)	29.4% (34)
	slight	56.3%	61.8%
	moderate	2.1%	8.8%
	intense	0%	0%
Weed degradation	none	87.5% (48)	94.1% (34)
	light	8.3%	5.9%
	moderate	4.2%	0%
	heavy	0%	0%
Observation sites	in open	0% (20)	75% (8)
	in burrow	0%	12.5%
	under rock	10%	0%
	under leaves	85%	12.5%
	under grass	5%	0%
Rock shelter (number of rocks)	none	39.6% (48)	38.2% (34)
	<5	16.7%	23.5%
	5-10	22.9%	20.6%
	>10	20.8%	17.6%

Table 11 cont. **Species** **Habitat variable**		***Pseudophryne australis***	***Heleioporus australiacus***
Low vegetation (number of clumps)	none	2.1% (48)	2.9% (34)
	<5	8.3%	20.6%
	5-10	25%	8.8%
	>10	64.6%	67.6%
Leaf litter piles (number of piles)	none	0% (48)	14.7% (34)
	<5	12.5%	35.3%
	5-10	37.5%	26.5%
	>10	50%	23.5%
Cray fish	present	10.4% (48)	70% (30)
	absent	89.6%	30%
Fish	absent	100%	100%
Permanence of water course	ephemeral	100% (48)	94% (34)
	permanent	0%	6%
Permanence of water body (pool)	permanent	0% (48)	20.6% (34)
	semi-permanent	0%	35.3%
	ephemeral	100%	44.1%
Character	pool	0% (48)	5.9% (32)
	creek	68.8%	26.5%
	table drain	8.3%	2.9%
	artificial drain	4.2%	0%
	soak	8.3%	2.9%
	mitre drain	2.1%	0%
	depression	8.3%	2.9%
	pool in creek	0%	58.8%
Culvert within 10m	none	81.3% (48)	85.3% (34)
	present (pipe)	6.3%	14.7%
Origin of water course	within reserve	70.8% (48)	88.2% (34)
	outside reserve	29.2%	11.8%
Substrate of breeding site	rock shelf	0% (48)	14.7% (34)
	rocks	6.3%	2.9%
	pebbles	2.1%	0%
	soil	81.3%	82.4%
Sides of breeding site	rock shelf	2.1% (48)	2.9% (34)
	rocks	8.3%	2.9%
	pebbles	2.1%	0%
	soil	87.5%	94.1%
Pool	present	97.9% (48)	97.1% (34)
	absent	2.1%	2.9%
Water colour	clear	- (0)	70% (20)
	stained	-	30%
Water turbidity	clear	- (0)	95% (20)
	cloudy	-	5%

3.3 Medium scale habitat analyses

Medium scale habitat analyses revealed surprisingly little new information. To allow meaningful comparisons, absence sites were only chosen in places where water collects and thus were generally located within a drainage or creek line. As a result large tracts of land in the area studied did not qualify for analysis. *P. australis* non- track sites showed a tendency to be located in places where the canopy height was in the highest class (taller than 8 m) ($\chi^2_{(1)} = 3.9$; $P = 0.048$; also positive logistic curve: $P = 0.038$). Optimum value for maximum canopy height was 16.8 m. *P. australis* track sites showed no such relationship. Optimum slope for *P. australis* was in the category 3.1 – 6.0°, the species being absent from steep sites. There was a trend for soil texture 10 cm below the surface to be in the classes being dominated by sand ($\chi^2_{(6)} = 13.3$; $P = 0.038$)(track sites only). Erosion intensity tended to be "slight", rather than "negligible" for non-track sites ($\chi^2_{(1)} = 3.7$; $P = 0.054$). Shelter in the form of low vegetation tended to be greater then 5 clumps in track sites ($\chi^2_{(3)} = 10.2$; $P = 0.017$), and the probability of occurrence on non-track sites was positively correlated with increasing amounts of leaf litter ($P = 0.012$).

For *H. australiacus*, soil texture on the surface ($\chi^2_{(4)} = 12.4$; $P = 0.015$) and 10 cm below ($\chi^2_{(5)} = 14.3$; $P = 0.014$) tended to be dominated by sand. Animals were absent on rock. More presence sites had recently experienced fire than absence sites. This result is influenced by the fact that Bouddi, the section of the study area that remained unburnt, also contained no *H. australiacus*. This was not reflected in differences in vegetation cover or sheltering places (leaf litter, logs), but might have obscured such differences if indeed they normally exist. *H. australiacus* has an increased probability of utilising watercourses that experience slight to moderate erosion, as opposed to sites where erosion is negligible ($\chi^2_{(2)} = 7.5$; $P = 0.017$; also positive logistic curve: $P = 0.01$). In the study area, *H. australiacus* only occur where crayfish are present ($\chi^2_{(1)} = 22.3$; $P < 0.001$) in pools, creeks and pools in creeks but not in soaks and depressions ($\chi^2_{(5)} = 15.8$; $P = 0.008$). The hydroperiod of these water courses and bodies is ephemeral or semi-permanent, but generally not permanent ($\chi^2_{(2)} = 9.9$; $P = 0.007$).

3.3.1 Fine scale habitat analyses

Water temperatures of 28 *P. australis* breeding pools ranged from 9 to 30^0C over a twelve-month period. These pools frequently dried up (about 3 times over 12 months) but registered a mean annual depth of 11 cm (maximum depth: 50 cm) while holding water, and a surface area of 3.5 m^2.

H. australiacus breeding pools (n = 11) experienced water temperatures from 9 to 31^0C during the same period. Some pools were permanent, but most others dried up once or twice during the year. While holding water, these pools had an annual mean depth of 37 cm (maximum depth: 85 cm), and a surface area of 9.7 m^2.

Further details on the hydroperiods and other characteristics of these breeding pools and larval requirements, as well as site type comparisons of hydroperiods are given in Chapter 5.

Microhabitat details of the burrowing locations of 5 radio-tracked *H. australiacus* along Thommo's Loop (AMG 340000E, 6294000N) in Brisbane Water National Park show that the species shelters in open woodland (often with a heath understorey) and in open forest (Table 12). The vegetation structure utilised is representative of the types that were available. Canopy cover over the burrows ranged from <5% (many individual trees) to >75% after being burnt 12 months earlier. These data were collected as part of the work presented in Chapter 6.

Table 12 Microhabitat descriptions of individual burrows of 5 radio-tracked *H. australiacus*, including those occupied immediately prior to the study period (see Chapter 6 for more details). Canopy cover is classified as: **2** <5%, many individuals; **3** 5-25%; **4** 25-50%; **5** 50-75%; **6** >75%. All sites were burnt 12 months prior to analysis. Burrow identifications are preceded by the animal identification number.

Burrow ID	Micro habitat description	Canopy cover
#43-A	Bare sand, under fallen *Banksia ericifolia* with foliage. Open Woodland (sampled prior to study period).	6
#43-B	Bare sand, under fallen *Banksia ericifolia* with foliage. Open Woodland	6
#62-A	Bare sand, next to burnt/dead *Banksia ericifolia.* Open Woodland	3
#62-B	Track edge, soft clayey sand. Woodland.	4
#62-C	Outer edge of table drain, soft clayey sand. Open Woodland	3
#62-D	Cray burrows, sparse sedge cover. Open Woodland	3
#62-E	Bare sand in elevated position. Open Woodland	2
#160-A	Bare sand near *Leptospermum* sp. Woodland (sampled prior to study period)	5
#160-B	Bare sand near *Persoonia* sp. Woodland	5
#160-C	Network of cray burrows near creek line, sedges and *Ghania* sp. Open Woodland	4
#161-A	Sand, old track, holds moisture. Open Woodland (sampled prior to study period).	2
#161-B	Sand, old track. Open Woodland	3
#161-C	Sand, old track	2
#162-A	Bare sand, next to burnt branch (8 cm diameter). Open Forest	5
#162-B	Cray burrows, burnt bare patch in perched soak above sedge land. Open Woodland	4
#162-C	Bare sand in burnt heath thicket. Open Woodland	5
#162-D	Bare sand, under burnt branch. Open Forest	4
#162-E	Soft bare sand next to active ant nest at base of *Banksia marginata.* Open Forest	5
#162-F	Bare sand in burnt heath thicket. Open Woodland.	5
#162-G	Sand under leaf litter. Open Forest	4

3.4 Discussion

Both *Pseudophryne australis* (this study; Thumm & Mahony (1996 and references therein; 1999)) and *Heleioporus australiacus* in the Sydney Basin show a very strong association with the Hawkesbury Sandstone geology. Approximately 89% of locality records of both species coincide with this geology. In contrast, Hawkesbury Sandstone only covers about a quarter of the Sydney Basin surface, suggesting that sandstone, or some correlate of it is preferred. A small number of records (about 8%) coincide with the Narrabeen group. Parts of this group also include sandstone (NSW Dept. of Mines, 1966) and may explain why Narrabeen is also utilised. Moore (1961) recognised that *P. australis* and *H. australiacus* mostly occur on Hawkesbury Sandstone in the Sydney region. At Killara (northern Sydney) he had observed *H. australiacus* burrows among crevices in sandstone. From the Watagans, the northern limits of the distribution of *H. australiacus*, Mahony (1994) reported that this species utilises sandstone ridges and eroded sandstone drainage lines. In the southern limit of the Sydney Basin, the Shoalhaven region, Daly (1996b) observed *H. australiacus* on sandstone. Harrison (1922) observed that *P. australis*, *H. australiacus* and a third species (*Crinia signifera*) are the only frogs that inhabit the upper reaches of Hawkesbury Sandstone gullies in the Sydney region. More recently, Barker, Grigg & Tyler (1995) stated that *H. australiacus* is most common on Hawkesbury Sandstone in the Sydney region. Thumm & Mahony (1990, 1999) further elaborated on the geological association of *P. australis* and is not repeated here. The presence of a clay lens near some frog sites may be related to the Narrabeen group or the close proximity to a transition zone between different geological strata. Whether the habitat of the frogs is linked to transition zones remains to be further investigated.

The Hawkesbury Sandstone geology is often found in the higher parts of the topography, a fact reflected in the topographical distribution as well as the landscape morphology of the habitat of both species. Hawkesbury Sandstone is a Triassic formation which weathers into deep precipitous gorges with reasonably sized creeks that flood during rain and then dry to a series of pools. These creeks are fed by innumerable laterals of varying size and permanence (Harrison, 1922). Most locality records are placed within the top one third of elevated landscape where these laterals are found. Some variables in the study area, such as geology and elevation, are not independent of each other and may have a confounding effect on the distribution of the frogs. The evaluation of the relative influence of inter-dependent variables and their interactions was beyond the scope of this work.

H. australiacus were found to utilise flat ridges more often than *P. australis* do. There, *H. australiacus* utilise pools in hanging swamps or artificial small dams, whereas *P. australis* are absent from such places. These habits are responsible for the observed differences in the topographical distribution of both species (Table 6, Figure 2, Figure 3), where *H. australiacus* occurs above *P. australis*. In reality, however, *H. australiacus* rarely breeds above *P. australis* breeding sites at places where both species co-occur.

Both frogs are absent from only the highest mountain tops and never occur on low lying flats. Breeding sites are limited to less steep sections (up to 10°) throughout the Sydney Basin, an observation not previously reported for *P. australis*, but documented by Daly (1996b) for *H. australiacus* sites in the Shoalhaven. In south-eastern NSW, *H. australiacus* are absent from slopes that exceed 15° (Lemckert *et al.*, 1998). Broad scale distribution modelling based on slope will not reveal all potential habitat because traversing creeks (running at an acute angle to contours) may offer suitable gradients in areas that are otherwise too steep. Such sites were encountered during the survey. This limitation is reflected in the greater range of GIS derived values in comparison to the field measurements.

Both frogs mostly occur in areas that experience higher precipitation and associated moisture indices, and lower temperature ranges and lower temperature maxima compared to average values representative of the Sydney Basin. Milder climates with relatively higher minimum and mean temperatures appear to be favoured. Such preferences are likely to be beneficial to the aquatic larvae and terrestrial life stage of both species. Successful metamorphosis in habitat away from permanent watercourses in places where moisture holding capacity of soils are poor largely depends on replenishing rains, and temperatures that allow a relative reduction in evaporation rates. Dehydration is also a threat to the terrestrial life stage and both frogs should benefit from increased precipitation and reduced evaporation. Soil moisture levels must be important to *P. australis* which seeks shelter in a variety of moist places at or below ground level, and *H. australiacus* which burrows into soil. A milder climate is expected to convey benefits to tadpole development (see Chapter 3) and possibly offers extensions to breeding period and foraging time. Alternatively, both species may be constrained to areas that happen to feature these climatic properties for so far unknown reasons that are unrelated to climate.

The core habitat predicted by BIOCLIM surprisingly covers only a relatively small area of the overall distribution. The climatic core habitats of both frogs are relatively narrow, discontinuous strips that roughly follow the coast line a short distance inland (Figure 5, Figure 6). Much of the predicted core habitat overlaps with the greater metropolitan area of Sydney, which raises concerns regarding ongoing core habitat clearing and development.

Other similarities between both species are that they both utilise upper slopes and mid slopes. The effect of aspect on microclimate is probably less pronounced there than it is further down-slope and in gullies. This may be the reason why the placement of breeding sites appears to be independent of aspect. The structural vegetation types both species inhabit are open forest, woodlands and heaths where shrub layer cover is between 5 and 50%. Ground storey cover is high for both species, and slightly higher for *H. australiacus*. Both frogs therefore appear to be dependent on habitat with a complex vegetation structure.

Loose bush rocks provide shelter particularly for *P. australis*, and are present at about half the sites. The collection of bush rock for the ornamentation of suburban gardens is widespread around Sydney (Mahony, 1997; Schlesinger & Shine, 1994; Shine & Fitzgerald, 1989). Although this has not been tested specifically here, it is highly likely that the collection of rocks in the past and present has lead to a decrease of available rock cover. Bush rock removal is now a listed key-threatening process (*Threatened Species Conservation Act 1995*). The long-term implications of the reduction of rock cover are unclear.

Bare patches are rare. The soils are poorly structured and dominated by sand, a reflection of the associated geology. Such soils may facilitate burrowing, but have low water holding capacities (Beadle, 1962; White, 1987). A considerable proportion of breeding sites (17% of studied sites) are in man-made road and track structures. This is not surprising given that roads and tracks, at least in the Sydney Basin, are placed in the upper parts of the topography (Schlesinger & Shine, 1994). *P. australis* occasionally colonise table drains, many of which are regularly maintained. These frogs however are absent from the drainage systems of sealed roads. No breeding sites were found where drains were concrete lined, an observation also made on *P. australis* in the 1960's (Jacobson, 1963a). *H. australiacus* may utilise artificial, unlined dams, both in or outside creek systems, as well as mitre drains that allow water to pool (Chapter 5). The breeding sites of both species are subject to erosion. The flow of water imposes a disturbance along drainage lines (Krause *et al.*, 2003) which may play an important role in both frogs' habitats. *P. australis* occasionally lay their eggs under rocks where erosion has created small cavities. Furthermore, flowing water rearranges and refreshes leaf litter dams which are of great importance to this species for reproduction.

H. australiacus tadpoles benefit from the deep pools that are a direct result of erosion (see Chapter 5). Erosive forces at *P. australis* sites were classed as slight, but were higher (slight to moderate) at *H. australiacus* sites. These differences are likely to be due to some *H. australiacus* sites being located further downstream, where water flows during storm events can be higher as a result of the relatively larger catchment area.

Both frogs are absent from water courses that are dominated by exotic plants. Weeds, at least in the Sydney Region, favour modified areas resulting from physical disturbance (Buchanan, 1996) and / or nutrient enrichment, particularly that resulting from urban run-off water (Clements, 1983). Drainage lines below urbanised areas containing active *P. australis* and *H. australiacus* breeding sites were always weed-free and never contained gross pollutants such as plastics (A. Stauber, pers. obs.). On the other hand, these frogs were never observed to utilise watercourses dominated by weeds including privet (*Ligustrum* spp.) or lantana (*Lantana camara*). Clements (1983) found elevated phosphorus levels in the soils of watercourses with weeds. Incidental observations made over five years at a site near Berowra, Northern Sydney (328000 E; 6279000 N) are worth reporting here. Two hydrologically similar drainage lines run parallel to each other approximately 15 m apart. One supports natural weed-free vegetation carrying run-off water from natural bushland above and is regularly used by *P. australis* as a breeding site. The other carries water from a bitumen road into the bushland. This site is heavily overgrown with weeds and *P. australis* have never been seen or heard there (A. Stauber, pers. obs.). The actual influences of soil and water nutrient levels and the vegetation itself on the small-scale distribution of the frogs remain an area to be investigated further.

About half of the studied sites had been burnt within 3 years prior to this study. This may be a reflection of the hot and dry climatic conditions that had prevailed, but importantly, this does not demonstrate that fire is an integral component of the ecology of both species. High-frequency burning has been declared a key-threatening process (*Threatened Species Conservation Act 1995*) and may impact both frogs which were shown to rely on places with leaf litter piles and clumps of low vegetation in places with a well developed ground storey and shrub layer.

The habitat requirements of the two frog species differ in the following ways. *P. australis* habitat is often located within 200 m of cliffs (see also Thumm & Mahony, 1999), whereas *H. australiacus* shows no such association. Besides upper slopes and mid slopes, *H. australiacus* also inhabits flat ridges and gullies. The latter is the reason why *H. australiacus* is also found in closed forest, a structural vegetation type from which *P. australis* is absent. The percentage coverage of the top storey and the combination of the three strata reflect these differences, which are also supported by floristic differences (Jarvis & McNaughton, 1986; Woodward, 1987a). The coverage values for *H. australiacus* range more widely than those of *P. australis* due to some sites being on flat ridges with open vegetation structure (sparse coverage) and others in gullies supporting wet sclerophyll forest (dense coverage). *H. australiacus* were never found on sites where soils are less than 10 cm deep. These sites do not allow the species to burrow to normal depths (Chapter 6).

The amount of leaf litter on the ground is relatively higher at *P. australis* sites, with the probability of the species occurring increasing with increasing amounts of leaf litter. *P. australis* sites are characterised by large amounts of low vegetation and leaf litter piles. These are important for sheltering and egg deposition (Cogger, 1994; Moore, 1961; Ross, 1908; Thumm & Mahony, 2002b; Woodruff, 1978). *H. australiacus* breeding sites are characterised by the presence of crayfish burrows which at some sites occur in high numbers. *P. australis* breed in feeder creeks (not mapped on the 1:25000 topographic map series), natural and artificial gutters (including table drains), natural drains, soaks and depressions high up in the catchment where the hydroperiod is ephemeral (Cogger, 1994; Hoser, 1989; Jacobson, 1963a; 1963b; Mahony, 1994; Moore, 1961; Ross, 1908; Thumm & Mahony, 1999). *H. australiacus* utilise freestanding pools and pools in creeks, including feeder creeks where deep holes have formed through erosion, in the same places with *P. australis*. *H. australiacus*, however, also utilises habitat further downstream, where the hydroperiod of breeding pools is semi-permanent to permanent. *H. australiacus* breeding pools are free of fish and are generally located within ephemeral drainage lines but their hydroperiods can be ephemeral, semi-permanent or permanent. This finding is in general agreement with published accounts of localised observations (Daly, 1996a; Fletcher, 1894; Harrison, 1922; LeBreton, 1994; Mahony, 1994; Recsei, 1996). Two *H. australiacus* breeding sites visited are small spring-fed dams, both within natural drainage lines. This species is not known to utilise large dams (longer than 7 m) or dams placed away from drainage systems, unless these are associated with areas subjected to regular waterlogging (e.g., hanging swamps or near permanent springs).

The topographical position and underlying geology suggest that phosphorus levels in *P. australis* and *H. australiacus* habitat are lower in comparison to those found in valleys or on shale derived soils (see Clements, 1983). Soil phosphorus levels are one responsible factor determining the make-up of vegetation communities at least in the northern part of the Sydney Basin, also influencing the abundance of exotic plants and other weeds (Clements, 1983). Vegetation patterns on Hawkesbury Sandstone in the Ku-ring-gai Chase National Park are a function of complex environmental gradients which include environmental and site variables besides soil nutrients (LeBrocque & Buckney, 1994). These processes probably apply to Hawkesbury Sandstone vegetation communities throughout much of the Sydney Basin, but despite that, neither frog shows particularly strong associations with specific vegetation communities. Some associations were reported for relatively small areas (e.g., Daly, 1996a; Webb, 1983), but species assemblages of vegetation communities in forests, woodlands and heaths vary considerably across the Sydney Basin (Benson, 1986; 1992; Benson & Howell, 1994; Buchanan, 1980; Buchanan & Humphries, 1980; Burrough *et al.*, 1977; Keith, 1994; Keith & Benson, 1988; LeBrocque & Buckney, 1994; McRae, 1990; Outhred *et al.*, 1985; Thomas & Benson, 1985a; 1985b) and at a fine scale are not informative for predicting the potential distribution of either frog species.

Vegetation structure is somewhat influenced by topography (Jarvis & McNaughton, 1986; Woodward, 1987a). As a result, the range of vegetation structures recorded at the studied breeding sites is limited to what is available on the elevated locations of the habitat of both frogs. For this reason mangrove swamps, salt marshes and other low-lying wetlands and dunes are not utilised. *H. australiacus* are also absent from rainforests (but see Recsei (1996) who reported the species from sub tropical rainforest, a statement which has since turned out to be incorrect (Recsei, pers. comm.)). Vegetation types utilised by both frogs such as woodland and heath are relatively widespread among the remaining natural vegetation types in the Sydney Basin (*cf.* Howell & Benson, 2000). *H. australiacus* has also been reported from buttongrass swamps (LeBreton, 1994)(a site incorporated in the broad scale habitat analyses). Notable is the apparent absence of both species from cleared open land and pasture (see also Gillespie, 1996) which suggests a dependence on natural vegetation with a complex structure.

Both frogs are found in habitat that should be considered as marginal for the majority of amphibians: this habitat with ephemeral breeding sites indeed is only utilised on a large scale by *P. australis*, *H. australiacus* and one other frog, *Crinia signifera* (Harrison, 1922). *P. australis* and *H. australiacus* live in habitats which are strongly associated with Hawkesbury Sandstone with its characteristic sandy soils of poor water-holding capacities (White, 1987). The elevated topographical position of their habitat means that these places are generally well drained. In addition, the region's rainfall is highly unpredictable (Bureau of Meteorology, 2005a; Linacre & Hobbs, 1986). All these factors combine to produce a relatively dry and unpredictably variable environment.

The three frog species found in this habitat each exhibits different reproductive and early life-history adaptations as well as specific breeding pool preferences. *C. signifera* breeds throughout the year and colonises potholes and very small pools during rain (Barker *et al.*, 1995; Cogger, 1994). Rapid larval development and phenotypic plasticity in larval period in response to pool-drying allows these animals to metamorphose within 25 – 35 days (Lane & Mahony, 2002). *P. australis* has been categorised as a bet-hedger because of continuous iteroparity (repeated breeding throughout the year) (Thumm & Mahony, 2002b), staggered hatching dynamics (Thumm & Mahony, 2002a) and high variation in larval periods (Thumm & Mahony, 2006). Furthermore, *P. australis* lays eggs in terrestrial sites where embryonic development proceeds to a relatively advanced state, and hatching may be delayed until rain occurs (Jacobson, 1963b). *H. australiacus* generally utilises the largest and most permanent pools within its habitat and appears to time reproductive events with the onset of cooler and wetter weather. It has also demonstrated phenotypic plasticity in larval period in response to pool drying (Chapter 3).

The habitat occupied by both *P. australis* and *H. australiacus* is unusual in that only one other frog, the wide-ranging species *Crinia signifera*, is known to utilise it. Each of the three frogs has its own reproductive adaptations that allow it to persist in its own way in this marginal environment away from permanent water courses. Habitat specialisation by *P. australis* and *H. australiacus* require that their unique habitat requirements are taken into consideration in the management of urban impacts. These include the management of wild fires and fire hazard reduction operations, clearing of habitat and the collection of bush rock.

Chapter 3

ADAPTIVE PHENOTYPIC PLASTICITY IN THE LARVAL PERIOD OF *HELEIOPORUS AUSTRALIACUS*

Abstract

Heleioporus australiacus breed in ephemeral pools and their tadpoles are at risk of dying of desiccation if their pond dries out before the tadpoles metamorphose. A laboratory experiment was set up to test the response of *H. australiacus* tadpoles from three populations to decreasing water levels. Individually housed, half the tadpoles had water levels reduced at weekly intervals; levels for the other half stayed constant. Other variables were kept the same in both treatments. Larval periods ranged from seven to 13 weeks. The tadpoles responded to decreasing water levels by shortening their larval periods and metamorphosing from 2.6 to 4.4 days earlier ($P = 0.031$) than the tadpoles held in constant water level. Body size however was unaffected by treatment. In addition, a field population of tadpoles was monitored in the field. Over-wintering siblings left in the field took a minimum of 33 weeks to metamorphose and were 170% heavier than the laboratory animals. It appears that phenotypic plasticity in larval period is an adaptation of *H. australiacus* to its ephemeral breeding habitat.

1 Introduction

1.1 Population regulation in amphibians

Population regulation occurs by mechanisms that are mediated through both density dependent and density independent factors (Andrewartha & Birch, 1984). Amphibian population regulation through density dependent mechanisms acts particularly strongly on the larval stage (Berven, 1990; Wilbur, 1984). Several studies demonstrated that density effects on competition influence amphibian populations at the species level (e.g., Goater, 1994; Morey & Reznick, 2001; Relyea & Hoverman, 2003; Smith, 1987; Tejedo & Reques, 1994) and the community level (Wilbur, 1987), affecting survival, length of larval period and the growth rate of tadpoles. Similar effects are also attributed to predation, particularly where space is confined (Anholt *et al.*, 2000; Lane & Mahony, 2002; Laurila & Kujasalo, 1999; Relyea, 2001; Travis, 1981; Wilbur, 1987).

Density independent factors can also have a profound influence on tadpole survival and fitness. Density independent factors include hydroperiod (the length of time a larval pond continuously holds water), the physical and chemical environment, and other abiotic factors. In ephemeral or temporary habitats, uncertainty of pond duration is one of the most important density-independent factors that affect larval fitness and survival (Murphy, 2003; Newman, 1989; Tejedo & Reques, 1994; Thumm & Mahony, 2002b) although density dependent factors may become implicated as pond volume decreases (e.g., Leips, McManus & Travis, 2000). Catastrophic mortalities due to early drying of larval habitat are common in natural ponds (Newman, 1992; Tejedo & Reques, 1994; Thumm & Mahony, 2002b; Travis, 1981; Wilbur, 1984).

1.2 Ephemeral habitats provide growth opportunities

Even before the evolution of terrestrial life, aquatic organisms lived in ponds that were in danger of becoming too shallow for some of them. Such situations also occurred at times of no particular drought. Stranded fish that could save their lives by migrating to deeper pools were at an obvious advantage (Dawkins, 2004) and are thought to have given rise to the labyrinthodont amphibia (Ahlberg & Clack, 2006; Duellman & Trueb, 1994; Tyler, 1994).

But why do most of today's amphibians have an aquatic larval stage at all? Would amphibians with access only to breeding ponds of unpredictable duration not benefit from direct development that bypasses the aquatic tadpole stage altogether? A number of anuran species have indeed evolved direct development, a reproductive mode which has evolved independently in at least 12 groups or eight to nine families (Duellman & Trueb, 1994), including the Myobatrachidae (*Arenophryne rotunda* (Roberts, 1984); *Geocrinia rosea* (Watson & Martin, 1973); *Myobatrachus gouldii* (Roberts, 1981)). The majority of frogs however have an aquatic larval stage, including species which have access to ephemeral ponds only. The reason may well be that the aquatic habitat provides an opportunity for growth before the terrestrial phase of life (Wilbur & Collins, 1973), a growth opportunity with benefits that potentially outweigh the losses associated with larval predation and desiccation (Newman, 1992; Werner, 1986).

Evolutionary processes in ephemeral water bodies select for species which are adapted to the short-lived conditions of these habitats (Williams, 1987). In such habitats, natural selection would be expected to favour either rapid development, or phenotypic plasticity (Bradshaw, 1965; Stearns, 1989). Rapid development shortens the time span a tadpole is exposed to the risk of pond drying. Phenotypic plasticity in larval period is a more flexible alternative, where a tadpole quickly metamorphoses when its pond is drying up, but delays metamorphosis to exploit growth opportunities when water levels remain stable. Such plasticity may be adaptive (Newman, 1992; Stearns, 1989) and is subject to natural selection (Halkett *et al.*, 2004). Adaptation here is used as defined by Stearns (1986) as the product of natural selection that performs specific functions. The word "adaptive" is used as the corresponding adjective (for an alternative interpretation of "adaptive" see Gotthard & Nylin (1995).

1.3 Phenotypic plasticity in larval duration

Phenotypic plasticity was defined as "the ability of a genotype to develop different phenotypes in different environments" (Stearns, 1989). Environmentally-related phenotypic variation can express itself in two different ways in populations. Firstly, the response to an environmental cue may be systematic and repeatable (Bradshaw, 1965). The full range of phenotypes produced as a result of different values of the environmental cue is known as the norm of reaction (Stearns, 1989). Secondly, developmental noise can produce phenotypic variants as a result of developmental errors or in response to random environmental variation. These phenotypes are uncorrelated to any environmental cue (Bull, 1987). Via (1993) argued that the latter, developmental noise, should not be interpreted as phenotypic plasticity because it is not a systematic response to repeatable environmental change. Here, the term phenotypic plasticity follows Via's (1993) interpretation.

Phenotypic plasticity in larval period underlies physiological constraints (Wassersug, 1997) and usually leads to a trade-off between the length of time to metamorphosis and the size at metamorphosis. Age and size at maturation are key life-history traits affecting survival, growth rate and fecundity later in life (Stearns, 1992). Larger body size is highly adaptive in terrestrial habitats for amphibians and translates into increased survival, increased fecundity, and earlier sexual maturation (e.g., Álvarez & Nicieza, 2002; Berven, 1982; Goater, 1994;

Morey & Reznick, 2001; Newman, 1992; Newman & Dunham, 1994; Relyea & Hoverman, 2003; Smith, 1987; Werner, 1986). However, the ability to escape early from a drying pond at the expense of size directly improves the chances of survival at the time (Travis, 1981).

1.4 *H. australiacus* tadpole environment

Uncertainty of conditions is a key characteristic in variable habitats and forces organisms to select suitable conditions for reproduction. Such environmental variability can be temporal, spatial or both (Stearns, 1992). Appropriate reactions to temporal variability depend on the predictability of the environment. Environments that change periodically generally allow reproduction at particular and predictably successful times. In contrast, unpredictably variable environments, such as places where the variability lacks patterns of constant periodicity, or places where variability is erratic (no periodicity evident), may force organisms to assess and respond to rapidly changing conditions (Barandun & Reyer, 1998). Phenotypic plasticity is one possible mechanism that allows offspring to respond to such changing conditions.

Rainfall in the Sydney Basin (NSW National Parks and Wildlife Service, 2003) shows no distinct seasonal or annual patterns and annual totals vary considerably between years with heavy rain or drought potentially occurring any month of the year (Bureau of Meteorology, 2005a; Linacre & Hobbs, 1986)(see also Chapter 2). As a result pond duration is unpredictable and many *H. australiacus* breeding pools dry out during periods of low rainfall (Chapter 5). The ability of a tadpole to sense the deterioration of its habitat and to initiate metamorphosis, even at the cost of a small juvenile size, is an obvious adaptation for the use of such ephemeral habitats (Wilbur & Collins, 1973). In this Chapter, I investigate whether *Heleioporus australiacus* shows phenotypic plasticity in larval period in response to the hydroperiod (duration of pond) of its larval habitat. Given that this species breeds in ephemeral ponds in an area where rainfall is unpredictable, the ability of tadpoles to respond to pond drying by shortening their larval period would be a useful adaptation. Where there is such a response, a shorter larval period would be expected to result in smaller body size at metamorphosis.

Based on a laboratory experiment and field observations, I test the species' response to pond drying in terms of larval period and weight at metamorphosis, and establish the range of larval periods of *H. australiacus*. Such information allows for comparisons with other frogs and their habitat relationships and contributes to the growing understanding globally of the adaptive values of phenotypic plasticity. This information is also essential for appropriate habitat management. In order to quantify the minimum duration of suitable breeding pools, it is necessary to measure the duration of the larval period. These results complement the hydroperiod study (Chapter 5). I predict that *H. australiacus* has adapted to the climatic uncertainty of its habitat by either having a great range of genetically determined larval periods among siblings (asynchronous larval period *sensu* Thumm & Mahony (2006)), or by being able to plastically respond to pond drying.

The responses are discussed in relation to *H. australiacus* habitat features and those of other frogs. I then briefly address factors that influence development and growth rates and explore the fitness consequences and adaptive values of phenotypic plasticity in larval period.

2 Materials and methods

2.1 Pool drying experiment

The experiment took place in a temperature-controlled room at 22°C under a combination of natural light and an additional artificial light source (12 hour cycle, synchronous with daylight hours). A completely randomised block design with 20 replicates (20 animals x 3 populations x 2 hydroperiods: constant, decreasing) was used. The main reasons for this design were the light gradient and the possibility of a temperature gradient in the room. Each block was made up of a single row of six containers, each container holding one animal from one population and one treatment. The one hundred and twenty tadpoles were housed individually to eliminate crowding effects caused by animal interactions including competition (Gromko *et al.*, 1973; Woodward, 1987b), facilitation (Alford & Harris, 1988 and references therein; Newman, 1994), growth inhibitor production (Rose, 1960), and confounding variable density changes as individuals metamorphosed (Newman, 1989; Tejedo & Reques, 1994). I used 1 Litre rectangular plastic "take-away food" containers furnished with 75 mL of bleached, well washed natural sand and 2 dead eucalyptus leaves as substrate and shelter. Locations within each block were assigned using randomly generated numbers, and blocks were placed in the same sequence the sets of random numbers were obtained. The first 10 blocks were placed on a shelf above the second 10 blocks. Aged (aerated for 7 days), de-copperised tap water was used and replaced every 7 days. Initially, the water level (depth measured from the bottom of the container) in both the control and the drying treatment was 55 mm. This level was maintained for the control animals, but was gradually reduced on a weekly basis in the drying treatment (by 10 mm after first week, another 5 mm after second week, and then by 2-3 mm every following week). Levels were measured by pushing a plastic ruler, which was trimmed to the zero mark, through the substrate to the bottom of the container.

Water changes and level reductions were carried out simultaneously to keep disturbance consistent across treatments. The animals were checked and fed *ad libitum* on NUTRAFIN® turtle pellets 3 times weekly. The containers were completely covered with clear plastic sheets to reduce evaporation and related cooling, which may have varied among treatments. The sheets also became a necessity to stop the animals from jumping out of the containers. Despite this measure, some control animals managed to escape during the earlier stages of the experiment.

Tadpoles were collected in the field from 3 populations as detailed in Table 13. Individual populations were in different catchments, more than 7 km apart from each other, and were thus considered statistically independent. Much effort was put into finding the youngest tadpoles possible. Egg masses are extremely rarely encountered and were not available for this experiment. I therefore obtained tadpoles within a day of them being swept out of the burrows in which they had presumably hatched. Given the nature of the breeding sites it is unlikely that individual populations were made up of more than two clutches. Statistical tests are therefore assumed more robust due to minimal genetic variation within experimental populations. Developmental stages were determined one day before the start of the experiment on 20/3/2003 following Gosner (1960)(Table 13). It was estimated that the tadpoles had hatched 4 – 14 days earlier. Larval periods reported here begin at the estimated hatching date fourteen days before the experiment was started to allow comparisons with published values, and end with the emergence of the second front limb (Gosner (1960) stage

42). Statistical analyses, however, were carried out on the larval periods measured from the beginning of the experiment.

Table 13 Locality data and collection dates of *Heleioporus australiacus* tadpoles used in the laboratory experiment. Frequency distribution of developmental stages (Gosner, 1960) at the beginning of the experiment is given for each population.

Population	**1 - Kariong**	**2 - Pearl Beach**	**3 - Hornsby Heights**
AMG Easting	339 500	340 400	325 000
AMG Northing	6293 700	6286 400	6276 000
Date Collected	19/3/2003	19/3/2003	20/3/2003
n Stage 24	0	7	20
n Stage 25	30	33	20
n Stage 26	10	0	0

Information available at the time (later published as Green *et al.*, 2004) suggested that *H. australiacus* tadpoles are difficult to keep alive in the laboratory. For this reason, I avoided handling the animals during the course of the experiment and thus progressive size measurements were not taken.

Animals that had reached stage 42 (both front limbs emerged) were considered to have reached metamorphosis. The end of the larval period, here metamorphosis, is frequently defined as front limb emergence (e.g., Alford & Harris, 1988; Doughty, 2002; Hensley, 1993; Lane & Mahony, 2002) rather than complete tail resorption (Gosner stage 46), because the former is unambiguous and occurs abruptly (Hensley, 1993). Furthermore, animals are at risk from drowning if not removed after front limb emergence (Lane & Mahony, 2002) and at this developmental stage, *H. australiacus* were observed to burrow into wet sand and were no longer dependent on a water body (A. Stauber pers. obs.).

Metamorphs were removed from the experiment, with date and weight recorded. Animals were blotted with paper towelling and individually weighed on an electronic balance to 0.01 g. Their containers were emptied but returned to their location in order to maintain the integrity of the block design. Some of these metamorphs were euthanased using Chlorotone solution following the method outlined by Cogger (1994), set in formalin and preserved in

65% ethanol before lodging with the Australian Museum, Sydney as voucher specimens (registration numbers are given in Appendix 2).

Because data could not be normalised, a non-parametric Mann-Whitney test (M-W) was used to compare the experimental larval periods (from start of experiment to the day Stage 42 was reached) among control and drying treatment. Block and shelf effects were tested with Kruskal-Wallis test (K-W) and M-W respectively. Pearson correlation analysis and ANCOVA were carried out on body mass at metamorphosis and experimental larval period (ANCOVA dependent variable: mass; fixed factor: hydroperiod; covariate larval period) (Zar, 1996) to test the relationship between weight and larval duration and how it is affected by experimental treatment.

2.2 Duration of larval period in the field

The larval period of *H. australiacus* tadpoles was established by monitoring a field population in a pool in which there were tadpoles of similar ages from at least two egg clutches. This population was also the source of the sibling Pearl Beach animals (Population 2) used in the laboratory experiment (see Table 13).

The eggs were estimated to have been laid on 24/2/2003 and hatched on 7/3/2003. At each sampling session (n = 10), 40 tadpoles were caught haphazardly with a small net, weighed and the presence of hind limbs and emergence of front limbs (metamorphosis) recorded, as well as the date. Sampling took place at irregular intervals (1 - 8 weeks), determined by observed developmental rates of the tadpoles. Each tadpole was blotted dry on paper towelling before it was placed in a small plastic bag for weighing using Pesola™ 5g and 10g spring balances (precision 0.05 g and 0.1 g respectively). After the procedure, the tadpoles were returned to the water. Weight changes over time were analysed graphically.

Newly hatched tadpoles were found on 11/10/2003, 7 months after the experiment was started. These were distinguished from the study animals by their much smaller size, and were excluded from the experiment.

Water levels and temperature of the pool were recorded every fortnight for 12 months as part of the hydroperiod study (Chapter 5). Tadpoles and metamorphs were also briefly searched for during these additional visits.

2.3 Comparison of laboratory and field animals

Body masses at metamorphosis of laboratory and field animals were compared using one-way ANOVA.

3 Results

3.1 Pond drying experiment

Larval periods did not significantly differ among shelves ($U_{(n=113)} = 1583$, $P = 0.95$) or blocks ($K_5 = 6.33$, $P = 0.99$), therefore the measurements were pooled for further analyses.

Table 14 Summary statistics of *H. australiacus* larval periods in days since estimated hatching date by population and treatment. Water levels were constant in the control group and decreasing in the treatment.

Population	Measure	Control	Treatment
Kariong	Mean (SE)	59.1 (2.3)	55.6 (1.5)
	Median	55	54
	Minimum	50	48
	Maximum	87	73
	Range	37	25
	Sample size	20	20
Pearl Beach	Mean (SE)	52.5 (0.9)	49.9 (0.5)
	Median	52	50
	Minimum	48	48
	Maximum	61	56
	Range	13	8
	Sample size	19	20
Hornsby Hts	Mean (SE)	65.1 (2.6)	60.7 (2.0)
	Median	61	61
	Minimum	52	50
	Maximum	80	77
	Range	28	27
	Sample size	15	19

Tadpole survival was very high. In total, seven tadpoles were lost early in the experimental phase due to them escaping from their containers. The surviving tadpoles responded to a decrease in water level by metamorphosing earlier ($U_{(n=113)} = 1222$, $P = 0.031$)(Figure 9,

Table 14). The range of larval periods was also reduced in the treatment group of each population (Table 14). Estimated larval periods varied among populations (Figure 10, Table 14), presumably because of differences in hatching dates, but within each population-treatment pair, the response to pond drying was in a uniform direction (Figure 11, Table 14).

The weight at metamorphosis correlated positively ($R_{113} = 0.511$, $P < 0.01$, Pearson Correlation, 2-tailed) to the duration of the larval period (Figure 11), but was unaffected by experimental treatment (ANCOVA corrected model: $F_{2.112} = 19.5$, $P < 0.001$; hydroperiod: $F_{1.112} = 0.032$, $P = 0.859$).

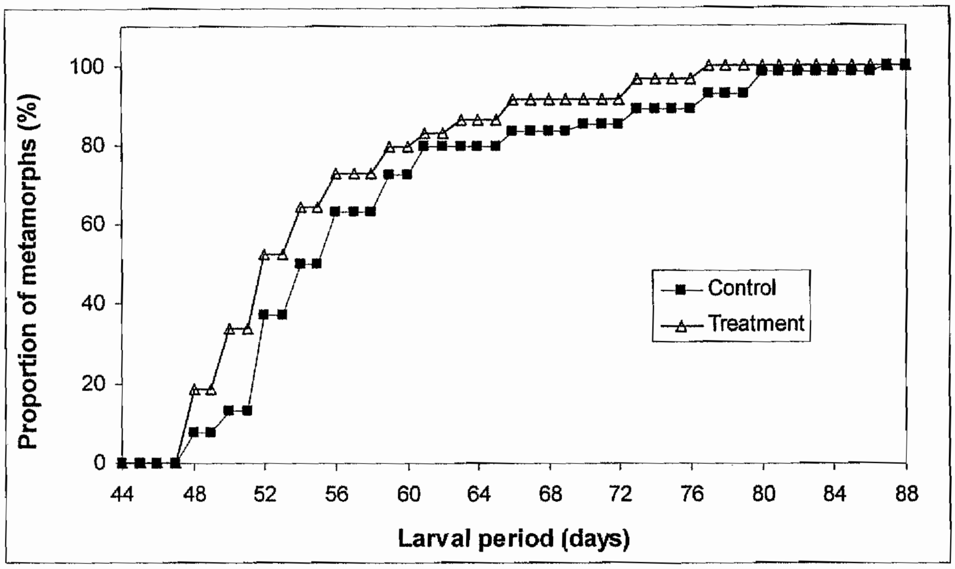

Figure 9 The larval periods and pooled proportions of *H. australiacus* tadpoles that had metamorphosed under simulated constant (Control) and decreasing (Treatment) water levels in the laboratory at 22^{0}C.

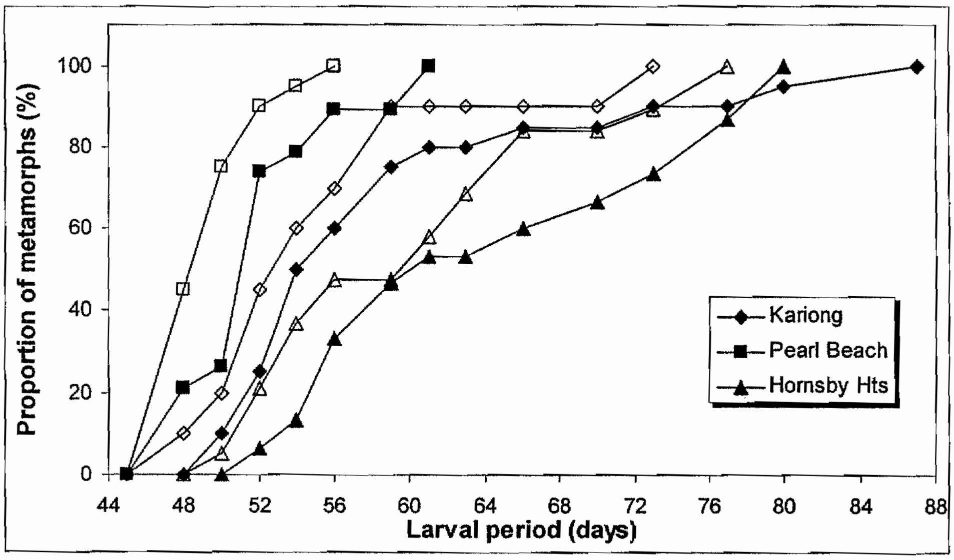

Figure 10 The larval periods and proportions of *H. australiacus* tadpoles from each of three populations that have metamorphosed under simulated constant (filled symbols) and decreasing (hollow symbols) water levels.

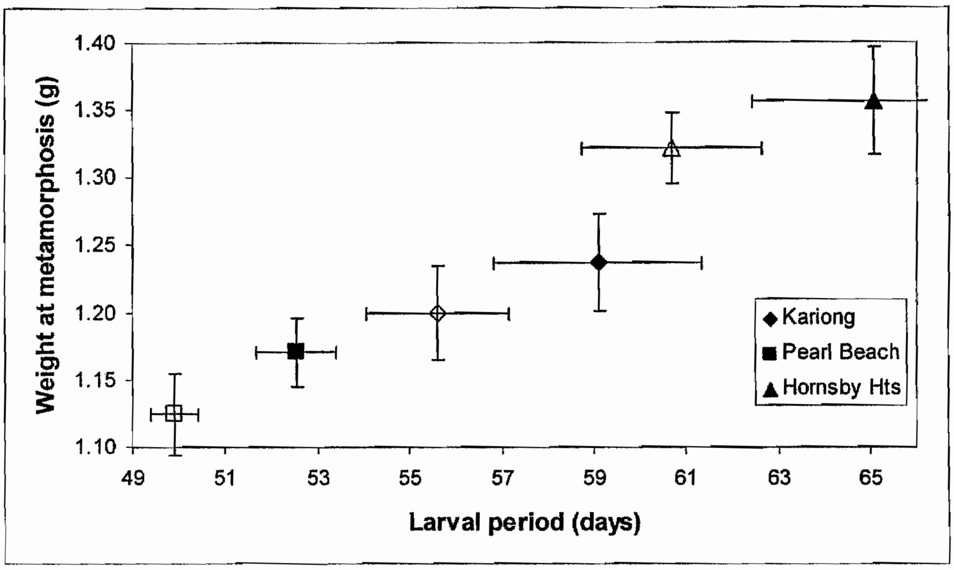

Figure 11 Mean body mass of *H. australiacus* metamorphs grouped by population and experimental treatment as a function of larval period (error bars are ± 1 SE). Manipulated water levels were: filled symbols – constant; hollow symbols - decreasing.

3.2 Duration of larval period in the field

The first metamorphs in the field were observed 33 weeks after their estimated hatching day. Over the following 4 weeks 23 metamorphs were recorded. Metamorphic transition peaked at week 35 with 13 metamorphs caught in a sample of 40 animals (Figure 12). The onset of metamorphosis occurred eleven weeks after the lowest water temperature was recorded and coincided with a sharp rate rise in water temperature increase (Figure 12).

3.3 Comparison of laboratory and field animals

The tadpoles in the laboratory developed much faster than their siblings in the field. The larval periods in the laboratory ranged from 7 to 13 weeks, whereas field animals metamorphosed from week 33 onwards (Figure 12). The range of larval periods in the laboratory was 66% of the mean duration, and about 11% in the field.

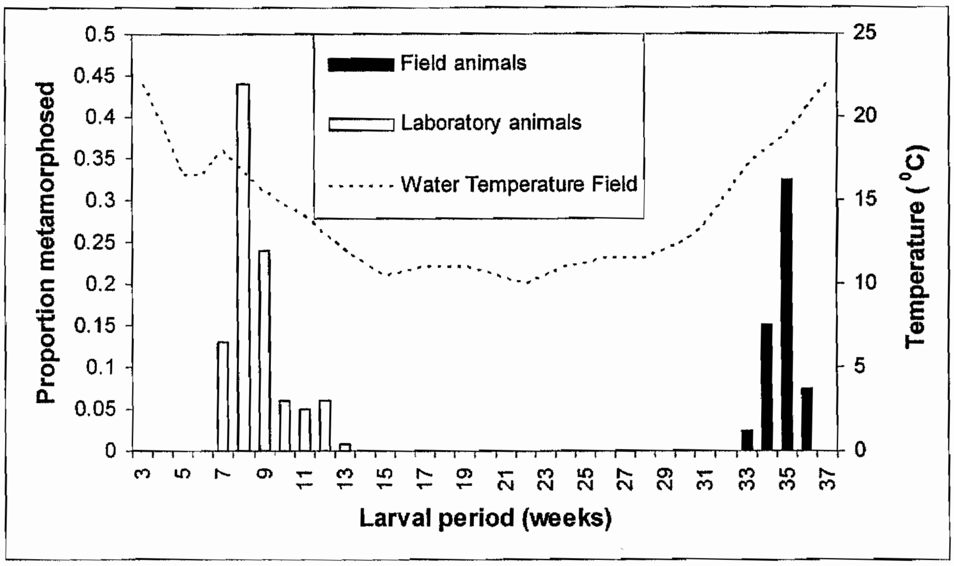

Figure 12 Comparison of *H. australiacus* larval periods in the laboratory and the field. Laboratory data were pooled across populations. The field animals were siblings of one of the populations represented in the laboratory. The temperature trace shows approximate water temperatures experienced by the field animals. Laboratory temperature was kept constant at 22°C. The proportions were calculated as the ratio of metamorphs from the final total of survivors for the laboratory animals, and as the ratio of each haphazardly chosen sample of 40 animals in the field.

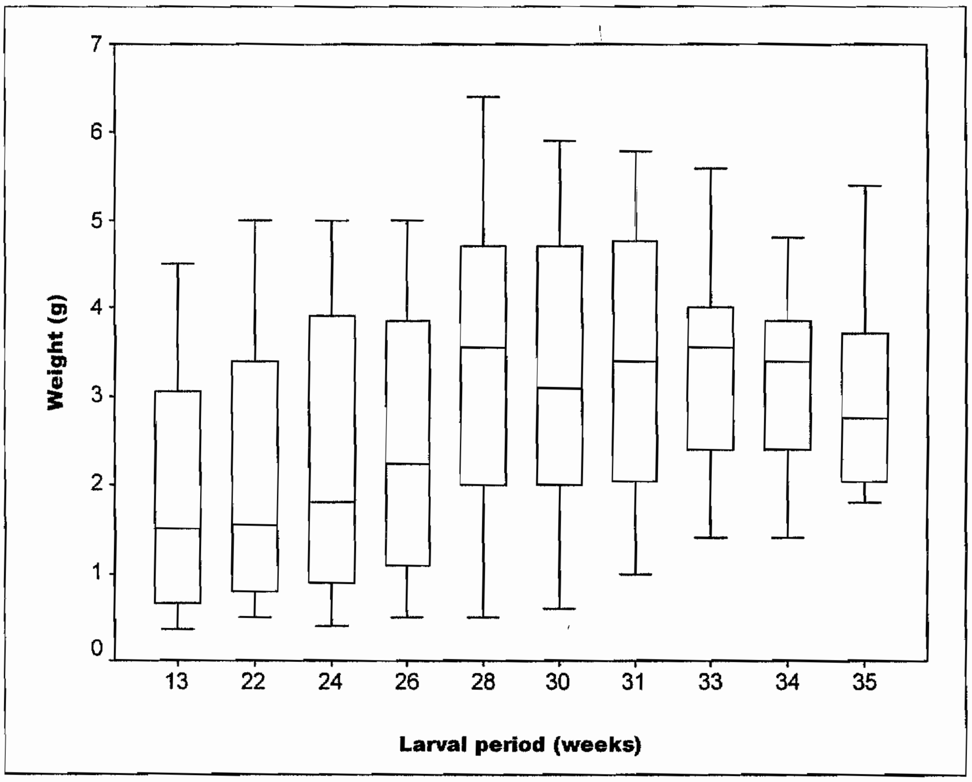

Figure 13 Boxplot of body mass changes in a wild population of *H. australiacus* tadpoles at Pearl Beach. Indicated are the median, interquartile range and the range. Each sample was made up of 40 haphazardly chosen individuals. Note: the x-axis is on a categorical scale.

Development in the field remained static at Gosner (1960) stages 26 – 30 (limb bud development) during the winter months (weeks 15 – 28). Toe development (stages 31 – 37) only started after winter in week 28, but growth was continuous throughout the winter months (Figure 13). The decrease in median body mass in weeks 33 and 34 coincided with the onset of metamorphosis, a time when tadpoles stop feeding to allow remodelling of mouth and intestines (Shi & Ishizuya-Oka, 1996) and when tissues undergo dehydration (Hensley, 1993). Another factor which may have influenced the observed weight loss is the possibility of the faster developing tadpoles suppressing growth in siblings, before they left the population which was then made up of smaller individuals (Thumm & Mahony, 2002b; Woodruff, 1972).

The slower developing field tadpoles (2.09 ± 0.05 g (mean ± SE of final weights)) clearly grew heavier than the laboratory (1.23 ± 0.01 g) animals. This 170% weight gain of the field tadpoles over the laboratory animals was significant (ANOVA $F_{1,131} = 429.2$; $P < 0.001$).

4 Discussion

4.1 Response of *H. australiacus* tadpoles to decreasing water levels

H. australiacus tadpoles are capable of phenotypically responding to decreasing water levels by shortening their larval period which allows them to move metamorphic climax forward in deteriorating ponds. The differences in mean duration of larval periods between the decreasing and constant water level treatments ranged among populations from 2.6 days (5.0%) to 4.4 days (6.8%). As a consequence the species is likely to benefit through increased rates of metamorphosis in slowly deteriorating breeding pools, allowing more recruits to escape death by desiccation.

Metamorphic responses to pond drying are thought to be driven by the activation of the thyroid and interrenal axes, the hormones of which control metamorphosis (Denver, 1998). Experiments on *Scaphiopus hammondii* showed a rapid response in hormone levels 48 hours after exposure to a drying environment (Denver, 1998). One environmental cue triggering this response appears to be the restriction of swimming volume in the drying habitat, constraining foraging. The associated cessation of feeding explained about 55% of the acceleration of development (Denver *et al.*, 1998). In my experiment, food intake did not differ among treatments, but the volume available for physical activity certainly decreased in the drying treatment, while the concentration of dissolved metabolic waste products there presumably increased between water changes.

While the response to decreasing water levels was uniform across all three populations, there were differences in larval periods as well as the duration of the metamorphic period (range in time between the first and the last individual of a group, i.e. population, to reach Gosner stage 42). Larval and metamorphic periods were always shorter in the drying treatments, with the Pearl Beach animals having the shortest metamorphic period of eight days, about one third of that of the other two populations. Similarly, larval periods in the constant water level treatment were much shorter in the Pearl Beach population when compared to the other two. The rate of accumulation of metamorphs during the metamorphic period (metamorphic curve) varied in shape and gradient among populations. The Kariong population plateaued after about 80% of animals had metamorphosed, whereas the Hornsby animals metamorphosed at a much lower rate than the others (Figure 10).

In an ecological context, such inter-population variation expresses itself in the different proportions of metamorphs each population can produce before a pool dries out if its hydroperiod is shorter than the requirements of the slowest developing tadpole. A further consequence is the weight difference observed among metamorphs from different populations. Populations with longer larval periods produced heavier metamorphs (Figure 11) that may be fitter in terrestrial life (fitness consequences are discussed later).

Many of these differences may possibly be attributed to differences in the age of tadpoles among populations. As pointed out earlier, hatching dates among populations were estimated to range over ten days, which finds some support in the different proportions of developmental stages of the field-collected animals (Table 13). Age differences would best explain the time differences of metamorphic onset. Age differences perhaps also account for some of the variation in the shape of the metamorphic curves because individuals of different early developmental stages may have responded variably to their introduction to the novel habitat of the laboratory. Leips (1994) found that in *Hyla cinerea* and *H. gratiosa* (Hylidae) differentiation rates are sensitive to changes in food levels early during the larval stage, becoming fixed after a certain point in development. Developmental rates of *Pseudacris crucifer* (Hylidae) are also flexible early and only become fixed after about 66% of the larval period (Hensley, 1993). On the other hand, the growth history during the early larval period had no influence on the time to metamorphosis in individually raised tadpoles of *Bufo woodhousei fowleri* (Bufonidae) (Alford & Harris, 1988) and *Scaphiopus hammondii, S. intermontanus* and *S. couchii* (Pelobatidae) (Denver *et al.*, 1998; Morey & Reznick, 2000).

Berven *et al.* (1982; 1979) compared *Rana clamitans* and *R. sylvatica* from high and low elevation breeding ponds where they show vastly different life history characteristics (including larval period and size at metamorphosis) in their natural habitat. They demonstrated that these differences were interpretable as a direct effect of temperature alone, and also that populations differed genetically in their thermal sensitivities. Genetic variation within sampled *H. australiacus* populations was thought to be low because of the low likelihood that within each population more than two breeding pairs had contributed to the animals used for the experiment. Across populations, however, these animals most likely differed genetically from each other. It is unknown how much of the observed differences in larval periods and metamorphic periods are due to genetic variation at the population level rather than presumed age differences. There is evidence for frogs that genetic variation among breeding pairs can translate into different lengths of offspring larval periods (e.g., Berven, 1982; Newman, 1988; Travis, 1981; 1983).

Furthermore, presumed age differences are not necessarily supported by the well defined trend indicated by the metamorphic age to weight relationship (Figure 11). Were we to adjust the estimated hatching dates so that the three populations metamorphose simultaneously (by manipulating the larval periods in shifting Pearl Beach to the right and Hornsby Heights to the left in Figure 11), we would record significant weight differences among metamorphs (of presumably equal ages) from different populations. Parental provisioning is a possible cause for such variation in larval growth (Semlitsch & Schmiedehausen, 1994; Travis, 1981). While it could have contributed to the observed population differences generally, parental provisioning in combination with genetic variation may also explain significant weight differences among metamorphs of equal age (see also Berven, 1982). Unfortunately, data on egg size variability do not exist for *H. australiacus*.

Metamorphosis in *H. australiacus* ranged over weeks because each tadpole developed at its own rate. If the range of larval periods is expressed as a percentage of the mean larval period (laboratory animals: 66%; field animals 11%), then the values for *H. australiacus* are considerably lower than the 85% derived from data reported for over-wintering *Pseudophryne australis* in an outdoor laboratory (Thumm & Mahony, 2006). The authors described *P. australis* as having an asynchronous larval period mediated by genetic variation and possibly maternal provisioning. *P. australis* did not show shortened larval periods in response to pond drying, but decreasing water levels produced higher proportions of metamorphs within a set time (Thumm & Mahony, 2006). Within-clutch variation in larval periods may be an additional strategy to phenotypic plasticity that allows *H. australiacus* to reduce the risk to reproductive effort associated with pond drying. Asynchrony in larval period, however, did not obscure the plastic response to pond drying in *H. australiacus* and may possibly be a secondary survival strategy to phenotypic plasticity in larval period.

4.2 Responses of other anuran tadpoles to decreasing water levels

4.2.1 Species that accelerate development with pond drying

H. australiacus is not the only frog that is able to accelerate larval development in response to pond drying. At least nine other species from five families are known to show this capability. The larval habitats of each of these species are ephemeral ponds of variable duration (see Table 15 for details and references).

4.2.2 Species that do not accelerate development with pond drying

Not all ephemeral pond breeders seem to be capable of responding to pond drying by metamorphosing earlier (Table 16). These include *Bufo punctatus, Hyla gratiosa* and *Pseudophryne australis.* At least five species that utilise permanent ponds for breeding appear to be unable to shorten their larval period in response to pond drying, whereas others (e.g., *Bufo calamita, Rana temporaria*) may or may not respond, depending on geographic location (possibly genetic variation among populations) or perhaps due to differences in experimental design. *B. calamita* for instance only responded at low densities (references in Table 16).

4.3 Size at metamorphosis and pond drying

A shortening of the larval period is not the only plastic response seen in frogs due to pond drying. Pond drying can also increase the larval period. Leips (2000) found extended larval periods and smaller body size in two closely related *Hyla* spp. as an indirect effect of increased density due to pond drying. Under crowded conditions, pond drying also reduced metamorph size in *Bufo calamita, B. bufo, Rana temporaria* (Brady & Griffiths, 2000), *Hyla pseudopuma* (Crump, 1989), *Scaphiopus couchii* (Newman, 1989) and *S. hammondii* (Denver *et al.*, 1998). The latter three examples also showed shortened larval periods (Table 15) which suggests that larval duration may be implicated in the relationship between competition and size at metamorphosis.

Table 15 Anuran species that accelerate larval development in response to decreasing water levels. Larval periods, relative size (based on length or weight measurements) of metamorphs and details of housing conditions are given where available.

Family	Species	Pond duration	Larval period	Relative size in drying treatment	Housing	Comments	Reference
Bufonidae	*Bufo americanus*	Variable	32.6-98.8 d	Unchanged	Crowded	Density variable, predators	Wilbur, 1987
Bufonidae	*Bufo calamita*	Variable	29-42 d	Smaller	Crowded	Shorter larval period at low density	Tejedo & Reques, 1994
Ranidae	*Rana temporaria*	Variable	8-10 w	Unchanged	Crowded		Loman, 1999
Ranidae	*Rana temporaria*	Variable	33-36 d	Smaller	Crowded	Drying produced more metamorphs	Laurila & Kujasalo, 1999
Hylidae	*Hyla pseudopuma*	Variable	25-27 d	Smaller	Crowded	One clutch	Crump, 1989
Pelobatidae	*Scahiopus couchii*	Variable	8-16 d	Smaller	Crowded	Texas	Newman, 1988; 1989
Pelobatidae	*Scaphiopus hammondii*	Variable	< 30 d	Smaller	Crowded Individually	Laboratory, constant temperature	Denver, 1998; Denver *et al*., 1998
Pelobatidae	*Scaphiopus holbrooki*	Variable	35.3 – 54.1 d	Unchanged	Crowded	Density variable, predator	Wilbur, 1987
Myobatrachidae	*Crinia georgiana*	Variable	29-34 d	Smaller (early ones only)	Individually	Decreased food levels, decreased larval period	Doughty, 2002
Myobatrachidae	*Crinia signifera*	Variable	25-35 d	Smaller	Crowded	Drying decreased juvenile survival	Lane & Mahony, 2002
Myobatrachidae	*Heleioporus australiacus*	Variable	48 – 87 d	Unchanged	Individually		This study

Table 16 Anuran species that do not accelerate larval development in response to decreasing water levels. Larval periods, relative size (based on length or weight measurements) of metamorphs and details of housing conditions are given where available.

Family	Species	Pond duration	Larval period	Relative size in drying treatment	Housing	Comments	Reference
Bufonidae	*Bufo bufo*	Variable to permanent	46.6 d (Semlitsch and Reyer, 1992)	Smaller	Crowded	Increased development rate, smaller size	Brady & Griffiths, 2000
Bufonidae	*Bufo calamita*	Variable	—	Smaller	Crowded	Increased development rate, smaller size	Brady & Griffiths, 2000
Bufonidae	*Bufo punctatus*	Variable	2 m	—	Crowded	Field experiment	Tevis, 1966
Ranidae	*Rana esculenta complex* LR	Permanent	45-58 d	Smaller	Crowded	Survival not affected; competition reduced developmental rate	Semlitsch & Reyer, 1992
Ranidae	*Rana lessonae* LL	Permanent	47-59 d	Smaller	Crowded	Reduced survival in drying treatment; competition reduced developmental rate	Semlitsch & Reyer, 1992
Ranidae	*Rana temporaria*	Variable to permanent	—	Smaller	Crowded	Increased development rate, smaller size	Brady & Griffiths, 2000
Ranidae	*Rana utricularia*	Permanent	83 – 123.6 d	Unchanged	Crowded	Density variable, predator	Wilbur, 1987

Table 16 continued

Family	Species	Pond duration	Larval period	Relative size in drying treatment	Housing	Comments	Reference
Hylidae	*Hyla cinerea*	Permanent	37-49 d	Unchanged	Crowded	Drying affected density, extending larval period and reducing size; outdoor tanks	Leips *et al.*, 2000
Hylidae	*Hyla gratiosa*	Variable	60-61 d	Unchanged	Crowded	Drying affected density, extending larval period and reducing size; outdoor tanks	Leips *et al.*, 2000
Myobatrachidae	*Limnodynastes tasmaniensis*	Permanent	60-300 d	Smaller	Crowded	Juvenile survival not affected	Lane & Mahony, 2002
Myobatrachidae	*Pseudophryne australis*	Variable	39-106 d	Unchanged	Individually	Drying produced more metamorphs; increased larval period, larger metamorphs	Thumm & Mahony, 2006

In *H. australiacus*, weight at metamorphosis is positively correlated with length of larval period even in the absence of competition (Figure 11). An increase in larval period generally leads to an increase in size at metamorphosis in other frogs also (Blouin, 1992: *Hyla cinerea, H. gratiosa, H. squirella*; Hota & Dash, 1981: *R. tigrina*; Leips & Travis, 1994: *H. cinerea, H. gratiosa*; Morand *et al.*, 1997: *Bufo bufo*, *B. clamitans*, *Rana dalmatia*, *R. temporaria*; Smith-Gill & Berven, 1979: *R. clamitans*; Thumm & Mahony, 2006: *Pseudophryne australis*; Wilbur, 1977: *R. sylvatica*).

While weight differences in *H. australiacus* were not significant between treatments in the laboratory, the modest relationship with larval period suggests that an increase in the difference of the mean duration of the larval period among treatments (for instance possibly under lower temperatures) would from some point in time onward be expected to produce significant weight differences among treatments. Further experimentation is required to test how temperature affects the magnitude of the phenotypic response to pond drying in *H. australiacus*. Denver (1998) reduced temperature to increase the resolution of developmental measurements in a series of tadpole experiments investigating the response of *Scaphiopus hammondii* to pond drying. In *Rana temporaria*, different temperature regimes may explain why pond-drying may or may not decrease metamorph size (Laurila & Kujasalo, 1999; Loman, 1999).

4.4 Size at metamorphosis and larval period

The over-wintering siblings that remained in the field were 1.7 times heavier than the laboratory animals. Over-wintering of tadpoles increased body mass also for instance in *Rana clamitans* (Smith-Gill & Berven, 1979).

Logistical constraints meant that only one field population could be monitored at the time, but size comparisons among tadpoles in other pools and over a number of years, as well as a review of published values (Anstis, 2002; Daly, 1996a) confirmed that the maximum sizes of the monitored tadpoles in the field are comparable to those in other locations, and that the laboratory animals metamorphosed at very small sizes.

Based on laboratory tadpole data, the duration of the larval period accounts only for a little more than a quarter of the observed weight gain. Clearly there are other factors that influence mass at metamorphosis. Environmental conditions that differed considerably between the laboratory and field include temperature regimes, nutrition and density of conspecifics and possibly stress levels.

4.5 Other determinants of phenotypic plasticity in tadpoles

Other factors may influence plasticity in tadpole development and growth besides pond drying. These include temperature, food quality and availability, and predation. Following is a brief summary of these effects based on work by others, and where applicable, how these effects relate to the *H. australiacus* tadpole experiment reported here and how these were dealt with in the experimental design.

4.5.1 Temperature effects on larval development

High temperature always accelerates development in the fully viable range and results in smaller body size in invertebrates, even where large size would seem advantageous (Levins, 1968). In other ectotherms, such as anuran tadpoles, higher temperatures also generally shorten the larval period and produce smaller metamorphs (e.g., Álvarez & Nicieza, 2002: *Discoglossus galganoi*; Berven, 1982: *R. sylvatica*; Blouin, 1992, also Leips & Travis, 1994: *Hyla cinerea, H. gratiosa, H. squirella*; Morand *et al.*, 1997: *Bufo bufo*, *B. calamita*, *Rana dalmatia*, *R. temporaria*; Smith-Gill & Berven, 1979: *Rana clamitans*, *R. pipiens*; Tevis, 1966: *Bufo punctatus*).

Anuran metamorphosis is a process highly sensitive to temperature. Water temperature acts directly on rates of biochemical and physiological processes that underlie metamorphosis and is therefore rate limiting (Smith-Gill & Berven, 1979). For this reason, temperature was controlled for the duration of the experiment and potentially confounding temperature effects among treatments eliminated by the block design and the prevention of variations due to evaporative cooling. The latter, although usually not taken into consideration (e.g., Doughty, 2002; Lane & Mahony, 2002; but see Berven, 1982, who used incubators), is particularly important in a temperature-controlled environment where humidity can be quite low (relative humidity in the room was around 50%).

The thermal profile of drying ponds in the field may change dramatically as water levels start to decrease (Newman, 1989)(see also Chapter 5) and it may be possible that an acceleration in larval development in the wild is entirely due to temperature effects. My results, however, do not support this hypothesis because larval periods differed significantly among treatments, whereas temperature did not. Therefore, temperature increases may accelerate larval development, but are not necessary to initiate a response to pond drying in *H. australiacus*.

Temperature differences experienced by the laboratory and field animals best explain the observed differences in growth and development of *H. australiacus* tadpoles. The laboratory animals were kept at a relatively high, constant temperature, whereas the field tadpoles were exposed to changing and considerably lower temperatures (up to 12^0C lower in winter). Winter temperatures in the field effectively stalled development and tadpoles only increased body mass. This observation fits well with Smith-Gill & Berven's (1979) discovery that low temperatures retard differentiation more than growth. As a result, over-wintering field tadpoles metamorphose at a larger size due to a prolonged period of mass accumulation.

It is not clear whether natural temperature differences among the hatching sites of the three studied populations and possible acclimatisation of hatchlings to these differences account for some of the differences in larval periods observed in the laboratory.

4.5.2 Food and competition effects on larval development

Higher food levels or decreased competition increase growth rate, shorten the larval period and produce heavier metamorphs (Alford & Harris, 1988: *Bufo woodhousei fowleri*; Álvarez & Nicieza, 2002: *Discoglossus galganoi*; Beachy *et al.*, 1999: *Hyla versicolor*; Goater, 1994: *Bufo bufo*; Hensley, 1993: *Pseudacris crucifer*; Hota & Dash, 1981: *Rana tigrina*; Leips *et al.*, 2000: *Hyla gratiosa*, *H. cinerea*; Loman, 1999: *Rana temporaria*; Morey & Reznick, 2001: *Scaphiopus hammondii*; Murphy, 2003: *Edalorhina perezi*; Nyström & Åbjörnsson, 2000: *Rana temporaria*; Relyea & Hoverman, 2003: *Hyla versicolor*; Semlitsch, 1993: *Rana lessonae*, *R. esculenta*; Semlitsch & Reyer, 1992: *Rana esculenta* complex; Wilbur, 1977: *Rana sylvatica*). However, sudden food withdrawal was shown to accelerate development in *Scaphiopus* once a developmental threshold was reached (Morey & Reznick, 2000).

In *Hyla cinerea* and *H. gratiosa* early increases in food levels shortened the larval period, demonstrating that differentiation rates are sensitive to changes in food levels. Beyond a certain point in development, however, the rate of development is set, and changes in food level affect only body size at metamorphosis (Leips & Travis, 1994).

Food availability to individuals is usually influenced by the density of competitors. Hence an increase in developmental rate and metamorph size resulting from density reduction was measured in several frogs (e.g., Loman, 1999; Nyström & Åbjörnsson, 2000: *Rana temporaria*; Murphy, 2003: *Edalorhina perezi;* see also Table 15 and Table 16). Density and food levels may act independently on growth and development rates (Hota & Dash, 1981: *Rana tigrina*) or produce significant interactions (Wilbur, 1977: *Rana sylvatica*).

Laboratory animals were fed equal amounts simultaneously and because individuals were free of any competition, food availability can be ruled out as a factor influencing the observed shortening of the larval period in the drying environment.

It is likely, however, that differences in food levels and quality among laboratory and field animals influenced growth and development patterns in *H. australiacus*. In the field, *H. australiacus* tadpoles feed on vegetation and sediment (Anstis, 2002). Low protein foods can have an inhibitory effect on tadpole growth (Steinwascher & Travis, 1983). The food provided to the laboratory animals presumably contained more protein (NUTRAFIN®: 34% min. crude protein) than what may have been available in the field. The laboratory animals, which never refused food, should therefore have grown larger. I suspect that nutritional differences between the field and laboratory animals influenced growth less than temperature differences did.

4.5.3 Predator effects on tadpole behaviour and morphology

The presence of predators may induce alterations to the behaviour and / or morphology of tadpoles. Behavioural responses may be a decrease in swimming or foraging activity when predators are present (Anholt *et al.*, 2000: *Rana catesbeiana, R. clamitans, R. pipiens, R. sylvatica*; McCollum & Van Buskirk, 1996: *Hyla chrysoscelis*; Relyea, 2001: *Bufo bufo, R. catesbeiana, R. clamitans, R. pipiens, R. sylvatica, H. versicolor*; Van Buskirk *et al.*, 1997: *Pseudacris triseriata*). Predator-induced morphological changes include variations in colouration and tail shape. In the presence of odonate predators, *H. chrysoscelis* tadpoles develop relatively large and brightly coloured tailfins with dark spots, a phenotype with a reduction in overall survivorship, but an increase in survival when exposed to free odonates (McCollum & Van Buskirk, 1996). Changes in body shape were also observed in *Hyla versicolor* (Relyea & Hoverman, 2003) and *Pseudacris triseriata* (Van Buskirk *et al.*, 1997).

4.5.4 Stress-related developmental rates

Stress experienced by tadpoles may also influence development rates. *Scaphiopus hammondii* tadpoles stopped feeding in response to stress caused by decreasing water levels (Denver, 1997). *Crinia georgiana* tadpoles experimentally exposed to decreasing water levels also stopped feeding. Food withdrawal and decreasing water levels combined to increase the rate of development, shortening the larval period in that species (Doughty, 2002).

It is to be expected that the procedures necessary to set up the experiment, and the novel environment in the laboratory caused stress in *H. australiacus* tadpoles. While no animal ever showed lack of appetite it cannot be ruled out that increased hormone levels in response to stress may have increased the underlying development rate in both the control and treatment groups. Possible stress influences however did not obscure the observed acceleration in larval development in response to pond drying.

4.6 Benefits of plasticity in larval period

H. australiacus frequently breed in ephemeral ponds of variable duration (Chapters 2 and 5; see also Daly, 1996a). The ability to accelerate larval development in response to pond drying is clearly an advantage to this species by allowing individuals to leave that deteriorating and potentially lethal habitat sooner. In the laboratory, tadpoles exposed to pond drying metamorphosed 2.6 to 4.4 days earlier compared to their siblings in constant water. Even such a seemingly small reduction in the larval period, relative to the larval periods determined in the field, can at times be a deciding factor between life and death in slowly deteriorating ponds.

Phenotypic plasticity in larval period, however, does not always guarantee reproductive success, because ponds may dry out before metamorphosis is possible. Tadpoles in 45% of monitored breeding pools died due to early pond drying during a drought (Chapter 5). Pond durations of 23 to 29 weeks were too short to allow metamorphosis, hydroperiods of 33 weeks were the minimum required to produce metamorphs (Chapter 5, Table 30). In the field, *H. australiacus* has a relatively long larval period, which on its own would restrict the species to breed in permanent pools, a rarity in its habitat. Phenotypic plasticity in larval period, however, reduces this limitation and potentially allows the species to exploit much more commonly-found temporary pools. Phenotypic plasticity, coupled with the temporal and spatial heterogeneity in the hydroperiod of breeding ponds, allows this species to persist in a much broader geographic range than if it was restricted to permanent water bodies.

Given the unusually short larval period observed in the laboratory animals, it is worthwhile to further investigate whether the larval period reduction in response to pond drying is of fixed duration or whether the time gain is proportional to the larval period. A proportional reduction would be more advantageous than a fixed one to this frog in the field, because there, a time advantage of one week would surely be better than that of one day.

4.7 Duration of the larval stage of *H. australiacus*

The larval duration in frogs is thought to affect overall lifetime fitness of individuals. It is thought that the larval period reflects genetic adjustments to interactions between mortality risks and relative growth rates of aquatic tadpoles in ponds, compared to those most likely experienced by terrestrial juveniles (Werner, 1986). The larval periods of *H. australiacus* in the laboratory were shorter than expected. Daly (1996a) reported a minimum larval period for *H. australiacus* in the field of 92 days, ranging up to 12 months for over-wintering tadpoles. Larval periods in my laboratory experiment at a constant temperature which was set in the upper range of temperatures measured in natural breeding ponds (Chapter 5) ranged from 48 to 87 days. The laboratory animals therefore all metamorphosed earlier than Daly's (1996a) most rapidly developing tadpoles in the field, some taking a little more than half that time. The laboratory animals also exhibited a much tighter range of larval periods. Captive *H. australiacus* tadpoles kept by others took a minimum of approximately 80 days to reach Gosner (1960) stage 42 (J. Recsei, unpubl. data), again recording longer larval periods than the majority of animals in my study.

Over-wintering field tadpoles (also siblings to some of the laboratory animals) required a hydroperiod of 33 to approximately 40 weeks to metamorphose. In Chapter 5 I show that hydroperiods of 29 weeks in two locations were too short to produce any metamorphs despite the species' ability to shorten its larval period in response to pond drying. All populations monitored for three years (including the subjects of this study) bred in late summer and autumn. None of their offspring metamorphosed before cool water temperatures set in. Only very rarely did pairs produce egg clutches in spring. The resulting spring hatchlings developed quite rapidly in the warmer waters and presumably metamorphosed at about the same time as the over-wintering relatives.

4.8 Is phenotypic plasticity in the larval period of *H. australiacus* adaptive?

4.8.1 Factors influencing fitness

Larger size at metamorphosis may have fitness consequences. Relyea (2003) provides evidence that larval environments can have profound impacts on traits and fitness of organisms later in ontogeny. In frogs, larval history can influence subsequent fitness (e.g., Beck & Congdon, 2000; Goater, 1994; Lane & Mahony, 2002; Relyea & Hoverman, 2003).

While the majority of experiments that tested the response of tadpoles to pond drying (including this study) did not investigate the fitness consequences later in ontogeny, the number of studies exploring the relationship between metamorph size and various fitness parameters has recently increased. Consequences of environmental variation in the larval habitat can extend to the terrestrial phase and influence juvenile survival (Álvarez & Nicieza, 2002), a good correlate of fitness (Endler, 1986). In *Bufo bufo*, post metamorphic survival to first hibernation was higher in larger metamorphs (Goater, 1994). Higher survival rates for larger juveniles were also documented in *Scaphiopus hammondii* (Morey & Reznick, 2001), *Scaphiopus couchii* (Newman & Dunham, 1994), *Crinia signifera* (Lane & Mahony, 2002) and *Hyla versicolor* (Relyea & Hoverman, 2003). However, no such relationship was found in *Pseudacris triseriata* (Smith, 1987). Larger *Bufo terrestris* metamorphs have higher sprint speeds and endurance when compared to smaller siblings (Beck & Congdon, 2000).

Larger metamorph size is likely to lead to greater survival in *H. australiacus* also. The ability to metamorphose early in order to escape a drying environment is clearly an advantage affecting larval survival rates. Larger individuals however have several advantages over smaller conspecifics once the terrestrial life stage is reached. The risk of dehydration is lower in larger juveniles, and may be a critical feature in this species considering the time available in locating patchily distributed moist microhabitat (Newman, 1994). Larger juveniles are likely to have a foraging advantage over smaller ones because of the reduced dehydration risk. They may be able to increase foraging activity spatially and temporally and be able to ingest larger prey items than their smaller siblings. Larger individuals may also benefit from lower predation rates due to being active less frequently (Morey & Reznick, 2001) or by being too large for some predators.

Small size at metamorphosis is also generally associated with lower adult fitness but may differ with gender and terrestrial food availability (Morey & Reznick, 2001). Larger frogs of both genders seem likely to reproduce more successfully, although energetic costs of reproduction are proportionally higher for larger individuals (Humphries, 1979). In *Pseudacris triserata*, larger metamorphs grow into larger adult size and males which mature earlier (Smith, 1987), and female *Uperoleia rugosa* always select calls of heavier males (Robertson, 1986). It is not known whether larger size at metamorphosis increases fitness or reproductive success in *H. australiacus*, but based on the review provided above, it seems unlikely that this species defies such a widespread and uniform trend among anurans. A small number of field observations (A. Stauber, pers. obs.) do suggest that small males may be restricted to marginal habitat where they call only from streams that offer no breeding pools of suitable duration.

4.8.2 Adaptive plasticity

To be adaptive, phenotypic plasticity in larval period as a response to hydroperiod must combine both a physiological buffering to poor habitat qualities and an improved response to favourable conditions (Thompson, 1991). As a result, phenotypic plasticity involves fitness costs (Newman, 1992). In the case of *H. australiacus*, its buffer to environmental degradation is its ability to respond to pond drying, a response which allows it to escape a potentially fatal habitat sooner at the expense of smaller body size. The improved response to favourable conditions is a relatively longer larval period which was shown to at least marginally increase body size at metamorphosis. Large body size may increase fitness in the terrestrial environment (see previous section) and therefore phenotypic plasticity in larval period may be an adaptation to the uncertainty of pond duration (Crump, 1989; Newman, 1992; 1989; 1988). But is phenotypic plasticity in the larval period of *H. australiacus* adaptive or just beneficial?

Adaptations are products of natural selection that perform specific functions (Stearns & Koella, 1986). Differences between genotypes in their ability to express plasticity across a range of environmental conditions will result in different reaction norms (Stearns, 1989; Stearns & Koella, 1986). If these are heritable they will form the basis for the evolution of phenotypic plasticity (Bradshaw, 1965; Halkett *et al.*, 2004; Newman, 1992). The genetic nature of reaction norms is controversial and has been the subject of much discussion (Gotthard & Nylin, 1995 and references therein). The more widely accepted view expressed (Gotthard & Nylin, 1995) is that genes for plasticity can respond to selection (e.g., Scheiner, 1993). As an alternative, Via & Lande (1993; 1985) had earlier offered a model where phenotypic plasticity is only a by-product of selection on trait means within environments, and not the result of plasticity itself (Gotthard & Nylin, 1995). Whichever view is adopted, there appears to be agreement that gene expression plays a part in phenotypic plasticity.

Plasticity may be beneficial without being the result of natural selection if it is entirely due to constraints (Smith-Gill & Berven, 1979). Beneficial but non-adaptive plasticity has been termed “spandrels” (*sensu* Gould & Lewontin, 1979) by Newman (1992). Non-adaptive influences can be rejected as underlying causes of phenotypic plasticity in the larval period of *H. australiacus*. It was demonstrated that neither food levels nor temperature could have been responsible for the observed shortening in the larval period as a response to pond drying. Hence temperature, a major influence on developmental rates (Smith-Gill & Berven, 1979), and resource limitations are unlikely factors to have influenced the outcome. It could be argued that resource limitations may have applied due to the possibility of differing solute concentrations (e.g., O_2, but also metabolic waste products, CO_2) among the treatments; however, work on *Scaphiopus hammondii* suggested that these are probably not essential for a response (Denver *et al.*, 1998).

I agree with Bradshaw (1965) and Newman (1992) that for plasticity to evolve there must be genetic variation for the norm of reactions within a population. Although it is possible that populations may have evolved phenotypic plasticity in the past but no longer show genetic variation for the trait. There seems to be a genetic basis to phenotypic plasticity in the larval period of *H. australiacus*. The observed response to pond drying was uniform across populations and is also found in other ephemeral pond-breeding frogs from a range of families (Table 15). Given that the majority of breeding pools in *H. australiacus* habitat are ephemeral or semi-permanent, I conclude that phenotypic plasticity in larval period in this species is an adaptation that resulted through selective forces imposed by variable and unpredictable pond duration.

Chapter 4

SPATIAL DISTRIBUTIONS, HABITAT ASSOCIATIONS AND MOVEMENT PATTERNS OF *PSEUDOPHRYNE AUSTRALIS* AND *HELEIOPORUS AUSTRALIACUS*

Abstract

The spatial distributions and associations with certain habitat features, and movement patterns of *Pseudophryne australis* and *Heleioporus australiacus* were investigated in order to determine the habitat use by these threatened frogs.

Seven *P. australis* breeding sites were regularly monitored over 44 months. Animals were marked using ventral patterns and had their locations and shelter type recorded. Overall, 394 frogs were marked. These predominantly selected leaf litter piles despite their relatively low availability, and to a lesser extent vegetation, logs, rocks and soil cavities. Leaf litter piles in drainage lines moved over time through natural processes and the animals moved with the piles. Nearest-neighbour distances between individuals were less than 20 cm for 78% of captured animals. These aggregations were mostly related to leaf litter piles and the data suggest that these habitat features are a limiting resource.

In contrast, *H. australiacus* did not form aggregations. Three 2.4 km transects (unsealed tracks) were regularly sampled over 36 months. Individuals were marked using Passive Integrated Transponder (PIT) tags, and had their locations recorded using permanent distance markers. Overall, 138 individuals were marked. These animals showed no preference for any of the three structural vegetation types (woodland, heath, forest) in which they occur. Statistical tests of standardised distances showed that for each transect, the locations of first capture were independent of relative distances to the closest creek and mitre drains. However, males appeared to be more common near culverts. Individuals were randomly distributed along the transects and nearest-neighbour distances were greater than 50 m for 88% of individuals. Individuals apparently did not share their space with conspecifics.

Individuals of both species moved distances which were greater than their recorded net displacements in space, which indicates site fidelity. The results are discussed in relation to the spatial requirements of both species and the protection of utilised habitat features. The differences in spatial dynamics of the two threatened frog species with overlapping habitats highlighted in this study require species-specific management approaches.

1 Introduction

Generally, animals are non-randomly spaced through their habitats, a distribution pattern which is often associated with the heterogeneous distribution of predation risk and or resources (Bertram, 1978; Levins, 1968; Wiens, 1976). If habitat patches differ in quality, then individuals should exhibit some degree of habitat selection: a response which imposes the effects of habitat structure on the distribution of individuals toward non-randomness in space (Wiens, 1976). Therefore, organisms may form aggregations (Wilson, 1975) that are closely linked to environmental factors (e.g., Aberg *et al.*, 2000; Moody *et al.*, 1997; Orians & Wittenberger, 1991; Parris, 2001).

In principle (and in the absence of social interactions (Blaustein & Walls, 1995)), clustering by consumer organisms (*sensu* Wiens, 1976) usually indicates habitat patches that contain resources of relatively higher quantity or quality by supporting higher densities of consumers. Such habitat patches may also contain critical but limited habitat features (e.g., Orians & Wittenberger, 1991), or they may indicate avoidance of uninhabited patches (Aberg *et al.*, 2000). Logically, it follows that habitat patches where individuals aggregate are of considerable value to populations of that species.

Information on an organism's habitat use and spatial distribution, coupled with the identification of high-value habitat patches, are integral components of ecological and conservational research (Aberg *et al.*, 2000; Harding *et al.*, 2001), have application in habitat restoration efforts (e.g., Matthews & Pope, 1999) and allow the identification and ranking of sites where individuals are more likely to occur within their habitat (e.g., Aebischer *et al.*, 1993). Such information also facilitates metapopulation analysis and the prediction of recolonisation patterns (Hanski & Gilpin, 1997).

In this Chapter, the spatial distributions and associations with certain habitat features, and movement patterns of two frogs, *Pseudophryne australis* and *Heleioporus australiacus*, are investigated in order to assess the habitat use of these threatened species (*Threatened Species Conservation Act 1995*). Both frogs occupy similar habitat (Chapter 2) although usage occurs at different scales. Representing opposing extreme ends of the size scale of Sydney Basin frogs (Cogger, 1994), the species vary in their behaviour and detectability. The methodological approaches taken consider these differences among species as well as the limitations imposed by the small size of *P. australis*.

1.1 Habitat associations

1.1.1 Pseudophryne australis

P. australis are associated with ephemeral drainage lines (Thumm & Mahony, 1999)(Chapter 2) and deposit their eggs in concealed positions under leaf litter, logs or rocks (Harrison, 1922; Woodruff, 1972; 1978). Here I examine the frequency distribution of available shelter types used by the species and compare this with actual usage frequencies in order to rank them according to their relative importance to the species.

Microhabitat associated with leaf litter piles in ephemeral watercourses was expected to be subject to frequent disturbance, such as rearrangement through flood waters, scratching birds and fire. Disturbance of leaf litter, measured as its temporal stability, was qualitatively assessed and related to site loyalty of individual frogs inhabiting these. Here, I predict that *P. australis* which are found to inhabit leaf litter show site loyalty to leaf litter piles, rather than a particular fixed spot along a drainage line.

1.1.2 Heleioporus australiacus

Vegetation structure and its classification provide a useful tool for evaluating the conservation status of habitats and impacts to these both at small and large scales (Specht *et al.*, 1995). The structural complexity of vegetation can vary considerably within *H. australiacus* habitat (Chapter 2). The classification of vegetation into broad structural types does not require special skills and could be a useful tool in the identification of high conservation value habitat patches should *H. australiacus* show an association with any particular vegetation structure. The distributions of individuals from three populations, each inhabiting an environmental mosaic of patches (*sensu* Wiens, 1976) that differed in vegetation structure, were analysed to test whether the species shows any association with vegetation structure.

Like *P. australis*, *H. australiacus* has an aquatic tadpole stage (Anstis, 2002; Watson & Martin, 1973) and requires access to water in order to reproduce. Breeding sites utilised by *H. australiacus* include creeks (Gillespie, 1990; Littlejohn & Martin, 1967) and track drains, such as culverts or mitres (Daly, 1996a; Recsei, 1996)(Chapter 5). In contrast to *P. australis*, *H. australiacus* is often encountered long distances from suitable breeding sites (Gillespie, 1990; Lemckert & Brassil, 2003; Lemckert *et al.*, 1998; Webb, 1991). Because fertilisation takes place externally (Duellman & Trueb, 1994), both genders must visit the breeding sites. Amphibians are usually associated with water (Daugherty & Sheldon, 1982) and adult frogs commonly form aggregations with respect to breeding (Sullivan *et al.*, 1995). For this reason it is expected that *H. australiacus* would be more commonly encountered near breeding sites. Therefore, I tested the prediction that *H. australiacus* aggregate near potential breeding sites.

Alternatively, if *H. australiacus* do not form aggregations near water bodies, then breeding individuals that are located away from potential breeding sites would need to move longer distances in order to reproduce. In order to test this, movement distances and relative distances from the closest breeding site were examined to determine if the two variables are related.

1.2 The spatial distribution of *Pseudophryne australis* and *Heleioporus australiacus* individuals

At the broad-scale level, animals often form spatial clumps, but within these clumps, individuals may be widely separated from each other (Campbell, 1990; Conder, 1949; Pulliam & Caraco, 1984). At the population level, the spacing of individuals influences the spatial requirement of the population and its density. Here, I also investigate the spatial distribution of *P. australis* and *H. australiacus* in relation to other conspecific individuals in order to explore the spatial requirements of populations.

1.3 Movement patterns of *Pseudophryne australis* and *Heleioporus australiacus*

Movement patterns of individuals are fundamental components of the ecology and evolution of a species (Daugherty & Sheldon, 1982; MacArthur, 1972). In conservation biology, an understanding of movement patterns identifies the full range of habitats that are essential to a species' persistence (Spieler & Linsenmair, 1998). Such information allows the design of conservation areas that include all essential habitat components, including buffer zones, which are all linked by suitable corridors (Dodd & Cade, 1998). Movement patterns also give an insight into space utilisation, site fidelity and dispersal (Dodd & Cade, 1998). The movement patterns of *P. australis* and *H. australiacus* and their displacements were also analysed to gain an understanding of the spatial requirements of individuals.

In summary, this chapter comprises a comparative study of dispersion and dispersal relative to habitat in both frog species, addressing the general research question "How do *P. australis* and *H. australiacus* use their habitat?" The aim was to quantify spatial distributions as well as the movement patterns of these threatened frogs and to identify associations with certain habitat features. The knowledge gained will contribute to a better understanding of each species' basic biology, and to improve the planning for their conservation management. Tested were microhabitat associations for *P. australis*, some macrohabitat associations (vegetation structure; natural and artificial water courses and drains) for *H. australiacus*. Furthermore, the spatial distribution and movement patterns of individuals of both species were investigated at the population level.

2 Materials and methods

2.1 *Pseudophryne australis*

Seven *P. australis* breeding sites on the NSW Central Coast were chosen to include the range of site types the species most commonly utilises across its range (Table 17). Several years of observations of each site prior to this study suggested that the sites were permanently inhabited by the species. For simplicity, it was assumed that each site supported its own population, except for one (PB, a single population which was divided into PBl and PBu by a track) (Table 17). The populations were regularly monitored between August 2001 and April 2005. Sampling intervals were irregular because they were dictated by weather conditions. Most of the time, wet weather and mild temperatures combined for short periods (one to several days) and lasted only long enough to allow sampling of a single population before the return of dry conditions. Within these constraints, sampling effort and intervals were kept the same across populations as closely as possible.

All Pearl Beach sites (PA, PB, PC) were located in the same catchment but in different drainage lines. This provided the opportunity to examine whether individuals utilise more than one site by noting any frogs which moved between these sites. A track linked the sites by approximately the shortest route. Sites were located in alphabetical order along the track and distances between sites were 500 m and 200 m respectively in the order of sites stated. These distances were determined in the field to 10 m precision with a bicycle-mounted CATEYE Mity2® computer calibrated for wheel size.

All sites, except T and P, were of a linear nature. For linear sites, a permanent zero mark was chosen in the field and recorded on maps. Other permanent landscape features (e.g., rocks, large trees) were also mapped as additional reference points. A tape measure was rolled out during each sampling session to establish the locality (chainage) of animals and habitat features to the nearest 10 cm.

Table 17 AMG coordinates and main characteristics of seven monitored *P. australis* breeding sites. Because the site of population PB was dissected by a track, the lower (l) and upper (u) sections were sampled separately.

Site	Locality	AMG (m)		Character
PA	Pearl Beach	342300E	6286200N	Deep, sparsely vegetated table drain above culvert in natural drainage line
PBl, PBu	Pearl Beach	342000E	6286200N	Natural ephemeral drainage line
PC	Pearl Beach	341800E	6286100N	Natural ephemeral drainage line
T	Berowra	326800E	6277000N	Depression, pool forms occasionally
I	Kulnura	333900E	6333700N	Frequently maintained mitre drain, pools occasionally
P	Martinsville	344400E	6340000N	Large depression, rarely floods

Two-dimensional maps showing logs, vegetation clumps and trees were drawn for sites T and P. Distance measures obtained by measuring tape were included. These maps were used to record animal locations there.

Males were located by their calls. Leaf litter, vegetation, logs or rocks were removed by hand to uncover the animals. Large leaf litter piles, vegetation patches and hollow logs were also systematically searched for animals.

Animals were temporarily held individually in labelled containers and their locations of collection in the field were flagged with labelled wire pegs. *P. australis* usually stop calling while their shelter is being disturbed. Places where calling animals were heard but could not be found were left for a while and revisited a short time later when animals were calling again. The aim of each sampling session was to capture as many frogs as possible from the site (including all calling frogs and those encountered by chance). Some sites were sampled over three consecutive nights to achieve this. All animals were returned together after the last night's sampling. Occasionally, animals could not be recovered without causing major destruction to their habitat. Those animals were usually in rock crevices and were not captured, but their presence was recorded. Females were recovered by chance. These were recognised by their rounded body shape and larger sizes (Stauber, 1999).

The captured animals were marked by recording their ventral patterns using pencil and paper (Stauber, submitted). Recaptured animals were recognised by matching the new pattern maps (or the individual) with pattern maps from previous sessions. An evaluation of this technique is given in Appendix 1.

Before the animals were returned to their exact location of capture, their habitat was restored as close to its original condition as possible. Besides locality, the type of cover was recorded for each animal and the distribution of potential habitat features was mapped for each transect. These were leaf litter (at least 2 cm deep when lightly compressed by hand), low vegetation (usually the base of sedges or the inside of *Ghania* spp. thickets; at least 2 cm deep when lightly compressed by hand), logs, rocks and soil cavities of suitable sizes. The hygiene protocol (NSW National Parks and Wildlife Service, 2001) was followed to minimise disease transmission between individuals and populations.

2.1.1 Microhabitat associations

P. australis are very rarely observed in the open. They usually hide under leaf litter or vegetation, rocks, logs or in crevices in the soil or rocks. The frequency distribution of shelter type was analysed based on the location of first capture of each individual from all sites.

The spatial distribution of *P. australis* along three transects (PBl, PBu, PC) was analysed graphically in relation to the distribution of leaf litter at the transects. Goodness-of-fit chi-square tests (Zar, 1996) were also carried out on observed animal-leaf litter association frequencies for each transect separately using unequal expected frequencies based on the relative abundance of leaf litter versus the remainder of shelters and open space. Site PA was excluded from these analysis because it offered mostly rock crevices and cavities under rock, and only sometimes had accumulations of leaf litter. Site I was excluded also because leaf litter was uniformly distributed along one side (50%) of the breeding area. The two depressions (T, P) never accumulated deep leaf litter and were therefore excluded from leaf litter analysis; the animals there used alternative shelters.

2.1.2 Temporal stability of microhabitat

The distribution of leaf litter piles along the three transects in natural drainage lines (PBl, PBu, PC) was compared over time using four maps of potential habitat features obtained at different dates for each site (mapping dates are stated with the results). Leaf litter was overwhelmingly the most utilised shelter where available (see Results). The data presented here therefore exclude the other features for clarity. Leaf litter piles are subject to rearrangement (by flood waters, birds, etc.), decomposition, and are susceptible to fire. Sites PBl and PC were partially burnt by the NSW Rural Fire Service in early November 2001. The range of available leaf litter in lineal metres and its coefficient of variation (CV) were calculated for each transect to qualify the temporal stability of these shelters and potential egg deposition sites.

2.1.3 Nearest-neighbour distances

For each individual, nearest-neighbour distances (Moody *et al.*, 1997) were calculated from the chainage values for linear transects and estimated from the maps produced of the two-dimensional sites. No nearest-neighbour distances were calculated for sampling sessions when only one animal was found. A frequency histogram was produced from data pooled across sampling sessions and sites to summarise the distribution of the actual distances between active animals.

A measure to quantify the spatial distribution of individuals was proposed by Clark & Evans (1954)(see also Krebs (1999)). Using nearest-neighbour distances for all individuals, their method allows the calculation of an aggregation index R, which measures the deviation of the observed pattern from the expected random pattern. The spatial pattern is random if R = 1, and clumping occurs when R approaches zero. A regular pattern is indicated when R approaches its upper limit (a value of 2). Their formula (designed for two-dimensional space) was adapted to suit the uni-dimensional "space" of the transects:

$R = \frac{\bar{r}_A}{\bar{r}_E}$ aggregation index (Equation 3)

$\bar{r}_A = \frac{\sum r_i}{n}$	mean distance to nearest neighbour (m)
r_i	distance to nearest neighbour for individual i (m)
n	number of individuals along transect
$\bar{r}_E = \frac{1}{2\rho}$	expected distance to nearest neighbour (m)
$\rho = \frac{n}{l}$	density of organisms (animals per m)
l	transect length (m)

All transects were sampled beyond their limits for the presence of frogs. The distances calculated for individuals nearest to the beginning or end of a transect are therefore true nearest neighbour distances (between observable individuals along the transect). Hence a boundary strip was included and possible bias favouring regular patterns reduced (see Sinclair, 1985). Aggregation indices were calculated for the linear sites for each sampling session when at least nine animals were captured. Statistical tests were not applied to the aggregation indices because of low sample sizes and occasional non-independent data points generated by recaptured individuals.

2.1.4 Individual movements

Animals which were captured at least twice provided information on the time between captures and the displacement distance moved within that time. Pearson correlation (Zar, 1996) was used to test whether the net displacement (displacement between the locations of first and last capture) of individuals was related to the length of time between first and last capture.

The sum of displacement distances of each individual that was captured more than twice was compared to its maximum displacement (difference between highest and lowest chainage) using a paired Wilcoxon Signed Rank Test (Zar, 1996).

All ventral pattern drawings of the Pearl Beach animals (PA, PB, PC) were compared against each other to establish whether animals migrate between populations. The comparisons included 52 animals that were marked prior to this study (from January 1999 onwards). These additional records did not provide information on cover or chainage, and were therefore only included in the analysis of migration among Pearl Beach populations.

2.2 *Heleioporus australiacus*

A transect of 2.4 km in length was established in each of three study areas on the Central Coast of NSW. Fixed distance transects were used to standardise sampling effort among areas. The chosen areas were located in Brisbane Water National Park (two areas) and Reeves Road Reserve, all in the Gosford Local Government Area. The transects were: Warrah (340860E, 6286120N), Thommo's (339200E, 6293880N) and Reeves (342490E, 6302770N) (AMG coordinates (in m) are of the transect mid-points). The three transects were all in different catchments and were at least 7.5 km apart from each other. Furthermore, *Atlas of NSW Wildlife* records suggested that *H. australiacus* individuals from the three areas were not part of one continuous larger population. For these reasons the three transects were considered as independent units. Each transect followed a track (unsealed road) through natural bushland along which *H. australiacus* were observed prior to this study. Preliminary spot lighting data (presence of *H. australiacus*) were used to decide on the length and end points of the transects, thus maximising the likelihood of encountering animals.

Aluminium tags with a small piece of reflective self-adhesive tape served as permanent distance markers. The tags were nailed to shrubs and trees 15 to 20 metres apart. Distance measures (from here on referred to as chainages) were obtained with a trundle wheel and transcribed to the tags using felt pen and a metal scribe.

Sampling always took place at night. Transects were sampled once in both directions on foot at three-week intervals for 12 months (September 2002 – 2003). Opportunistic additional sampling took place between December 2001 and December 2004. No more than one transect was visited in a single night. Animals were searched for using a head torch fitted with a halogen bulb. *H. australiacus* juveniles and adults alike were generally detected by eye-shine. The search area was the width of the track including table drains and mitre drains along the full length of the transects.

H. australiacus with snout-urostyle lengths (SUL) greater than 40 mm were marked using Passive Integrated Transponder (PIT) tags. The pre-sterilised TROVAN® ID 100® tags were implanted under the skin into the dorsal lymph sac (Camper & Dixon, 1988; Donnelly *et al.*, 1994) by use of a sterile hypodermic needle. The back was swabbed with BETADINE® SwabAid® to clean the skin and to reduce the risk of infection. The hygiene protocol (NSW National Parks and Wildlife Service, 2001) was followed to minimise disease transmission between individuals and populations.

Animals were captured by hand and temporarily held in a plastic bag. The following data on each individual were recorded: ID number (PIT), date, several body measurements, gender, reproductive state of females (eggs visible through abdominal wall), and location (transect and chainage (± 1 m). A hand-held scanner identified the PIT numbers. Pesola® spring balances (100±0.5 g; 300±1 g) were used to weigh the frogs in the bags. Fibreglass callipers (± 0.05 mm) provided measurements on snout-urostyle length (SUL), tibia length and head width (head width between both mouth corners). Males were identified by their distinct nuptial spurs (Moore, 1961 p. 180). Animals without nuptial spurs were classified as females if they had SUL of at least 60 mm. The smallest male observed with nuptial spurs had a SUL of 49.1 mm. Most large females were also recognised by eggs that were visible through the abdominal wall. The remaining animals were classified as juveniles.

The location where each individual frog was captured for the first time was digitally mapped for further processing in ArcView 3.2 (Environmental Systems Research Institute, Inc.). This map will be referred to as LMF (location map of first capture).

2.2.1 Association with vegetation structure

Broadly, three structural vegetation types were encountered in the field along each transect. These were woodland, heath and forest as defined by Walker & Hopkins (1998). Digital maps of the spatial (linear) distribution of each vegetation type along the transects were produced, following measurements taken in the field using the chainage markers. The relative abundance of each type along each transect was calculated. The LMF was used to assign a vegetation type to each animal. Goodness-of-fit chi-square tests (Zar, 1996) were carried out on observed animal-vegetation association frequencies for each transect separately using unequal expected frequencies based on the relative abundance of each structural vegetation type.

2.2.2 Association with creeks and artificial track drainage structures

Potential breeding sites creeks, mitre drains and culverts are collectively referred to as features. The chainage of each feature was recorded in the field for each transect. The locations of the nearest features beyond both ends of each transect were also included. Distances between features and animal-to-feature distances were calculated from the chainages. In some situations where the nearest creek was beside the track, the distance was measured in the field with a tape measure. Because distances between features differed greatly within transects, I used relative distances to statistically analyse whether animal locations were associated with features. First, the half-distance between neighbouring features of the same type was calculated. The distance of the animal location to the closest feature was then divided by the corresponding half-distance, producing a ratio between zero and one. Ratios were grouped into 10 equal size classes based on their values. The frequencies of ratio-classes were compared using goodness-of-fit chi-square tests with equal expected frequencies for each transect and feature type where possible. Goodness-of-fit chi-square tests were also applied to the pooled data (all transects together) for males and females separately.

2.2.3 Nearest-neighbour distances

Nearest-neighbour distances (Moody *et al.*, 1997) were calculated from the chainage values where animals were captured. A frequency histogram was produced to summarise the distribution of actual distances between active animals for all sampling sessions when more than one animal was encountered.

All transects were sampled beyond their limits for the presence of animals. The distances calculated for individuals nearest to the beginning or end of a transect are therefore true nearest neighbour distances (between observable individuals along the transect). Hence a boundary strip was included, and possible bias favouring regular patterns reduced (see Sinclair, 1985). Other conditions necessary in identifying animal – habitat associations are that the study area includes sufficient habitat variation and that the sampled area is at least the size of a home range (Aberg *et al.*, 2000). These conditions were met by transect choice and length. A home range is defined as the area in which an animal normally lives, excluding migrations (Brown & Orians, 1970).

Aggregation indices *R* were calculated separately for each transect following the method detailed in 2.1.3, but in order to boost sample sizes, data were pooled (location of first capture) as if all marked individuals were observed at the same time. I expect this biases *R* toward zero (aggregation) because of those individuals which may utilise the same space at different times. This possible bias does not detract from the identification of habitat features that may encourage individuals to aggregate there, but may influence conclusions drawn on animal behaviour. Statistical tests were not applied to the aggregation indices because of low sample sizes and occasional non-independent data points generated by recaptured individuals.

2.2.4 Individual movements

Individual movements of *H. australiacus* were analysed as outlined in Section 2.1.4.

2.2.5 Do individuals located far from creeks move further than those near creeks?

Animals that are found far away from creeks are expected to visit those creeks in order to reproduce, and may therefore register longer movements. Pearson correlation was used to describe the strength of a linear relationship between maximum displacement and mean distance from closest creek (arithmetic mean of chainage positions) for each animal that was captured at least twice.

3 Results

3.1 *Pseudophryne australis*

This study witnessed the disappearance of population PA. Animals were heard and seen there regularly between April 1999 and June 2003. Egg masses were also observed on several occasions. No *P. australis* has been heard or seen there since June 2003, even on nights when the species was calling in relatively large numbers at all other nearby sites (7 sampling sessions between June 2003 and December 2004). Another population, PA1, became established 120 m from PA (380 m from PB) in an ephemeral, natural and rocky drainage line. Calling activity was first recorded there in August 2001, and continued throughout the study period. No animals from neighbouring populations PA or PB were recaptured at PA1. The data of PA1 were added to those of PA for continuity and to boost sample size.

Overall 394 frogs were marked (PA: n = 10; PA1: n = 17; PB: n = 99; PC: n = 159; T: n = 41; I: n = 28; P: n = 40). These numbers include 52 animals that were marked prior to this study.

3.1.1 Microhabitat associations

P. australis (mostly calling males) predominantly associated with leaf litter (Table 18). Leaf litter piles were commonly made up of sclerophyllous dead leaves at various stages of decay, and often included woody debris, such as small branches. Leaves and branchlets of the Casuarinaceae were also present at some sites. Leaf litter piles retained moisture for longer periods than the leaf litter on the forest floor nearby. An overwhelming majority of animals was recovered from leaf litter, despite the relatively low occurrence (< 14% of site coverage) of this type of shelter along the drainage lines (Table 18). The association with leaf litter was highly significant at each transect where leaf litter coverage could be measured (PBl: $\chi^2_{(1)} = 237$, $P < 0.01$; PBu: $\chi^2_{(1)} = 247$, $P < 0.01$; PC: $\chi^2_{(1)} = 680$, $P < 0.01$). Other types of shelters utilised were hollow logs, soil cavities under logs and rocks, rock crevices, and holes and cracks in soil. The animals at Site I were always captured along the same side of the breeding area, the side that was uniformly covered in leaf litter. The other side near the track was always bare and not utilised by the frogs. Sites T and P offered little leaf litter cover. At these sites, low vegetation and logs were the most utilised shelters. Leaf litter dwelling *P. australis* were not found there because of other permanent features at those particular locations. Site PA only offered transient leaf litter piles. The animals there sheltered predominantly under rocks, but were also found in leaf litter when that was available.

Table 18 Mean leaf litter availability at three transects and the proportions of shelter types utilised by *P. australis*. Details are stated for three transects along natural drainage lines. Pooled data are also presented for all seven monitored sites, two of which were depressions and one a mitre drain. See Table 19 for more details on leaf litter availability along the drainage lines.

Site	**Number of frogs**	**Available leaf litter**	**Distribution of population (%)**				
		(%)	Leaf litter	Log	Vegetation	Under rock	In soil
PBl	53	13.7	86.8	0	3.8	9.4	0
PBu	29	7.2	82.8	6.9	0	3.4	6.9
PC	143	13.1	86.7	1.4	7.0	3.5	1.4
All	342	na	66.7	9.9	19.0	3.2	1.2

Animals were mostly associated with leaf litter piles (Figure 14, Table 18) and maintained that association even if piles were relocated (next section) through natural disturbance. The few individual frogs shown in Figure 14 that were not in leaf litter utilised much less abundant shelters such as logs or rocks, soil cracks or vegetation.

3.1.2 *Temporal stability of microhabitat*

Leaf litter availability along the three transects varied over time (CV in Table 19). Not only did the patches of leaf litter vary in numbers and sizes, their positions also changed slightly over time (Figure 14). Most of the changes were attributed to water action, but bird disturbance (most likely by superb lyrebird *Menura novaehollandiae*; or alternatively the

Australian brush-turkey *Alectura lathami*) was also recorded for the lower end of the PC transect prior to the last sampling period.

Table 19 Leaf litter availability (in lineal metres) along three natural drainage lines inhabited by *P. australis*. Means, ranges and the coefficients of variation (CV) were determined from 4 sampling sessions held at each site between February 2002 and October 2004.

Population	**Transect length (m)**	**Leaf litter availability**		
		Mean (m)	Range (m)	CV (%)
PBl	30	4.1	1.4	17.1
PBu	30	2.15	1.4	31.7
PC	25.6	3.35	0.6	9.0

3.1.3 Nearest-neighbour distances

The majority of *P. australis* (67%) at the study sites were found within 10 cm of each other; 78% of individuals were within 20 cm of their nearest neighbour (Figure 15). Animals clearly formed aggregations within breeding sites which is illustrated by the *R* values from a subset of animals from the linear transects (sites PBl, PBu, PC and I) (Table 20). Those animals aggregated in leaf litter piles as was previously shown. Numerous egg masses were encountered in these while searching for animals. Calling sites in leaf litter that had become vacant by the temporary removal of individuals were again occupied by new frogs the following night. Such replacement was observed repeatedly during the study.

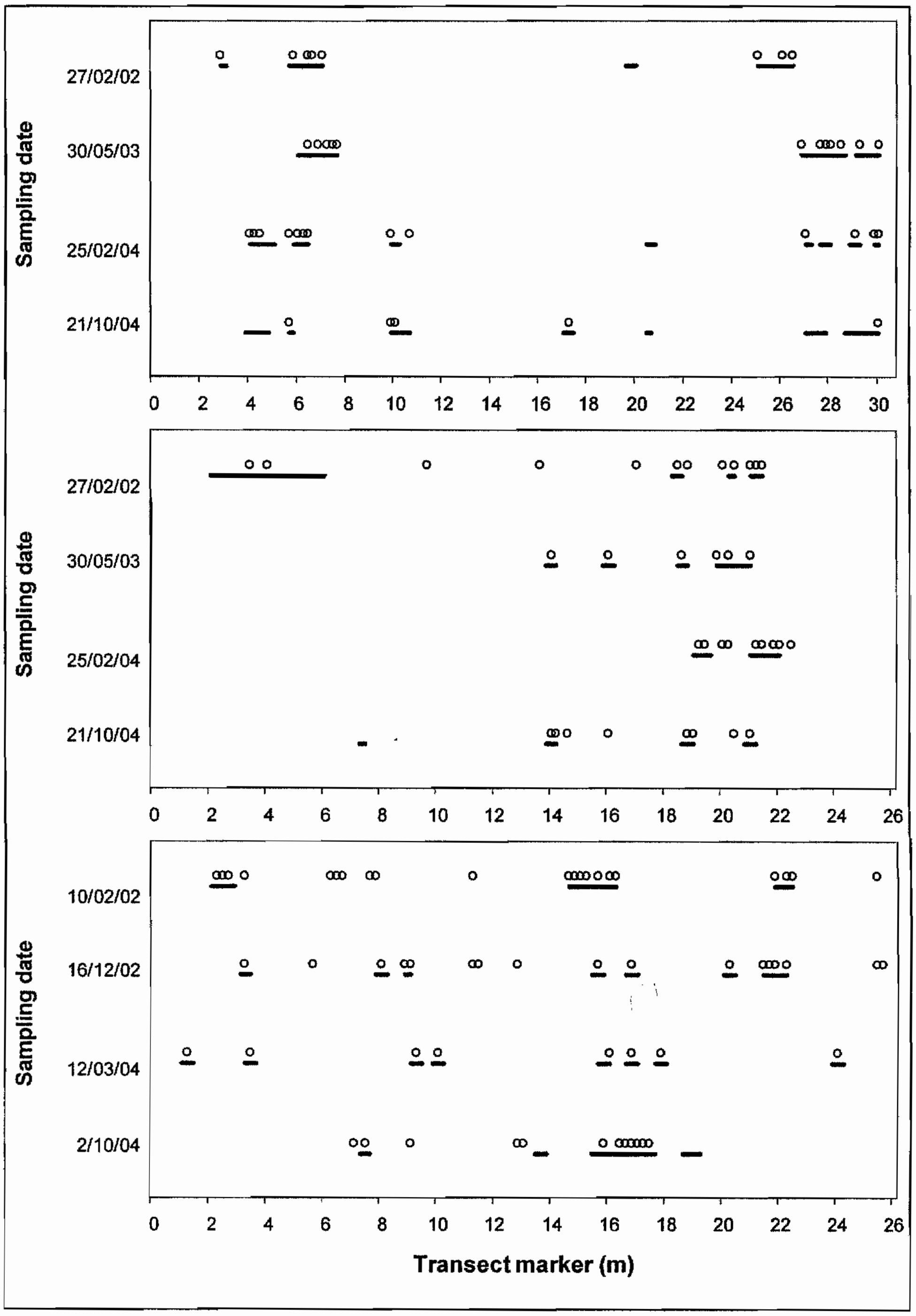

Figure 14 Association of *P. australis* locations (hollow circles) with leaf litter piles (solid lines), and temporal changes in leaf litter location along three transects (top: PBl; centre: PBu; bottom: PC). The transects were sampled repeatedly over time.

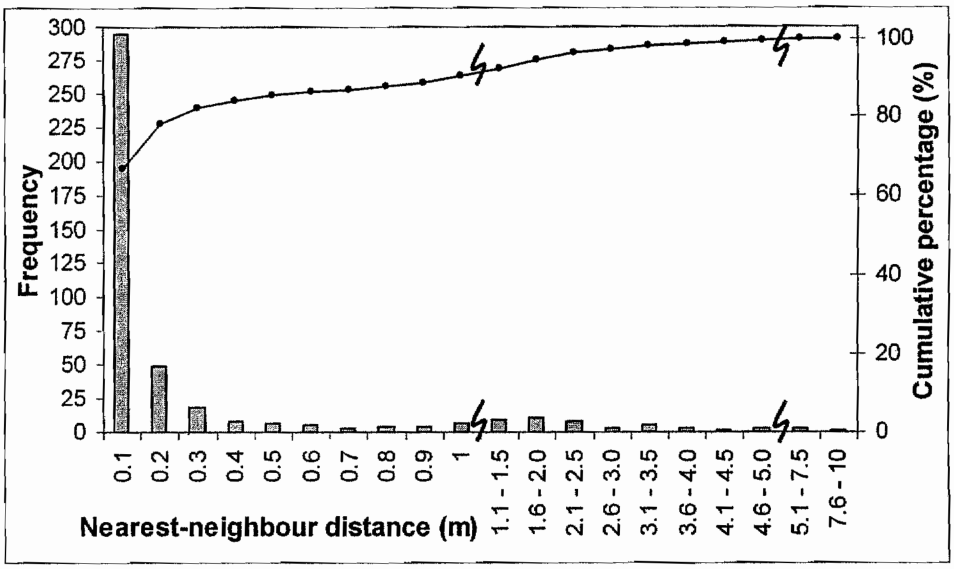

Figure 15 Frequency distribution of nearest-neighbour distances (bars) of active *P. australis* (n = 442). The cumulative percentage is indicated by the line. Data were pooled for all sampling sessions (n = 27) at seven study sites. Note that the x axis is not on a linear scale.

Table 20 Sample sizes, densities and aggregation indices *R* based on nearest-neighbour distances (Clark & Evans, 1954) of *P. australis* along three natural drainage lines and an artificial mitre drain. Means and ranges stated are based on four sampling sessions at sites PBl and PBu, and three at PC, where values of one session were excluded because of low (n = 7) sample size. Site I provided data on two sessions when at least nine animals were caught. SD values are in ().

Site	**PBl**	**PBu**	**PC**	**I**
Number of animals	12 - 22	9 - 22	26 - 97	11 - 14
Mean nearest-neighbour distance (m)	0.16 (0.09)	0.27 (0.20)	0.17 (0.17)	0.11 (0.02)
Mean density (animals per 1 m)	0.52 (0.12)	0.52 (0.22)	1.94 (1.55)	0.92 (0.16)
Aggregation index *R*	0.18 (0.11)	0.30 (0.25)	0.44 (0.31)	0.21 (0.07)
Transect length (m)	33	26	26	13.6

3.1.4 Individual movements

In total, 104 males (of 322) and 10 females (of 72) were captured more than once (Figure 16). This equates to a recapture rate of 33% for animals marked during this study period. Mean time (± SD) between first and last capture of these animals was 564 ± 348 days. The recorded mean net displacement between both locations was 5.7 m (range: 0 m – 34 m). Net displacement was not correlated to the time between captures (R = 0.048; P = 0.611; Pearson correlation). Figure 16 indicates that possibly two groups of animals exist in the populations, based on their movement distances. A large group moved less than 10 m, whereas individuals of the other group moved further. In addition, a single female first recorded and marked in December 2002 at site PC was recaptured 200m further at PB on February 2004. No other movements between populations were recorded.

The sum of displacement distances of individuals captured more than twice was higher than the maximum spatial displacement recorded (Z = -4.38; P < 0.001; Wilcoxon signed rank test) (Table 21). The female that had migrated from PC to PB was excluded from this analysis because of the potentially strong influence of this outlier on the test result.

Table 21 Summary statistics of the total distances moved by *P. australis* which were captured more than twice (n = 39) and their displacements. Not included is a single female that had migrated 200 m from one population to another.

	Mean (SD)	Min. – max.
Total distance moved (m)	11.8 (15.0)	0.2 – 73.0
Maximum displacement (m)	6.3 (7.4)	0.1 – 24.2

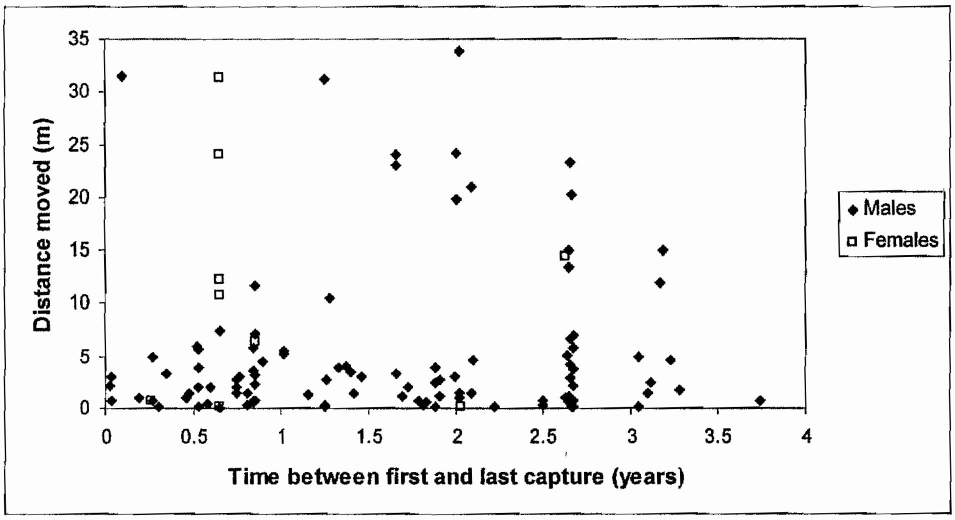

Figure 16 Distances moved by recaptured male and female *P. australis* over time. Six populations were regularly monitored. A single female that moved 200 m over 1.2 years is not shown.

3.2 *Heleioporus australiacus*

3.2.1 Association with vegetation structure

Based on the locations of first capture of 138 *H. australiacus* along three 2400 m transects that all included a mosaic of woodland, heath and forest, this species' spatial distribution is random and shows no preference for any of the three structural vegetation types (Table 22). Excluded from these analyses were sections of rock slab (Warrah: 50 m; Thommo's: 150 m) and one animal on rock at Warrah.

Table 22 Association of *H. australiacus* with structural vegetation types. Observed and expected frequencies and goodness-of-fit chi-square test statistics from three transects indicate that this frog's spatial distribution is random in respect to the three structural vegetation types encountered in their habitat.

Transect:	**Warrah**		**Thommo's**		**Reeves**	
Frequencies:	Observed	Expected	Observed	Expected	Observed	Expected
Woodland	59	55.7	22	23.9	7	11.3
Heath	12	17.2	8	10	7	5.3
Forest	6	4.1	11	7.1	6	3.4
χ^2 statistic (2 df)	2.65		2.69		4.17	
P value	0.27		0.26		0.12	

3.2.2 Association with creeks and artificial track drainage structures

H. australiacus appear to form aggregations near creeks, mitre drains and culverts (Figure 17), a pattern that is largely influenced by the wide range of distances between features in the field (Table 23). A comparison of mean and median values (Table 23) demonstrates that track sections with short half-distances between features were much more common than sections with longer distances. Hence animals were more likely to be found relatively close to features.

Statistical tests of the standardised distances show that within each transect, the locations of first capture of *H. australiacus* are independent of relative distances to the closest creeks and mitre drains (Table 24). However, an association with culverts is suggested at Warrah and in the pooled data. This is entirely due to males being more common near culverts (males: $\chi^2_{(9)} = 27.4$; $P = 0.001$; females: $\chi^2_{(9)} = 8.97$; $P = 0.44$) (data pooled across transects). Figure 18 shows that while both males and females were found throughout the full range of relative distances available to them from the nearest culvert, males were more abundant nearest to culverts.

Males, females and juveniles were found along the full range of available distances from creeks (up to 348 m). Mean distance (± SD) to the nearest creek was 64.8 ± 86.0 m. The locations of males and females ranged up to 310 m from mitres; the five juveniles were all found within 60 m of mitres. Females were found further away from culverts than juveniles and males (Figure 17).

Table 23 Summary statistics of half-distances between creeks, mitre drains and culverts along three *H. australiacus* transects.

	Creeks	**Mitres**	**Culverts**
Mean ± 1SE (m)	73.3 ± 12.3	47.9 ± 9.8	45.2 ± 9.6
Median (m)	45.5	22	26
Min. – max. (m)	1 – 413	7.5 – 407	8.5 – 469
Sample size	52	60	58

Table 24 Chi-square statistics (9 df) of *H. australiacus* associations with creeks and artificial track drainage structures along three transects. Animal numbers for the combined results (all transects) are given in the order creek / mitre / culvert. Warrah only had one mitre drain and Reeves had no culverts. These combinations were therefore excluded from analyses.

Transect		**Warrah**	**Thommo's**	**Reeves**	**All**
Creek	χ^2	8.92	10.5	14.0	9.99
	P	0.44	0.31	0.12	0.35
	number of	20	14	15	49
Mitre drain	χ^2	-	6.07	8.00	9.00
	P	-	0.73	0.53	0.44
	number of	1	39	17	57
Culvert	χ^2	17.4	12.9	-	19.6
	P	0.043	0.17	-	0.021
	number of	45	11	0	56
Animal numbers		78	41	20	139/61/119

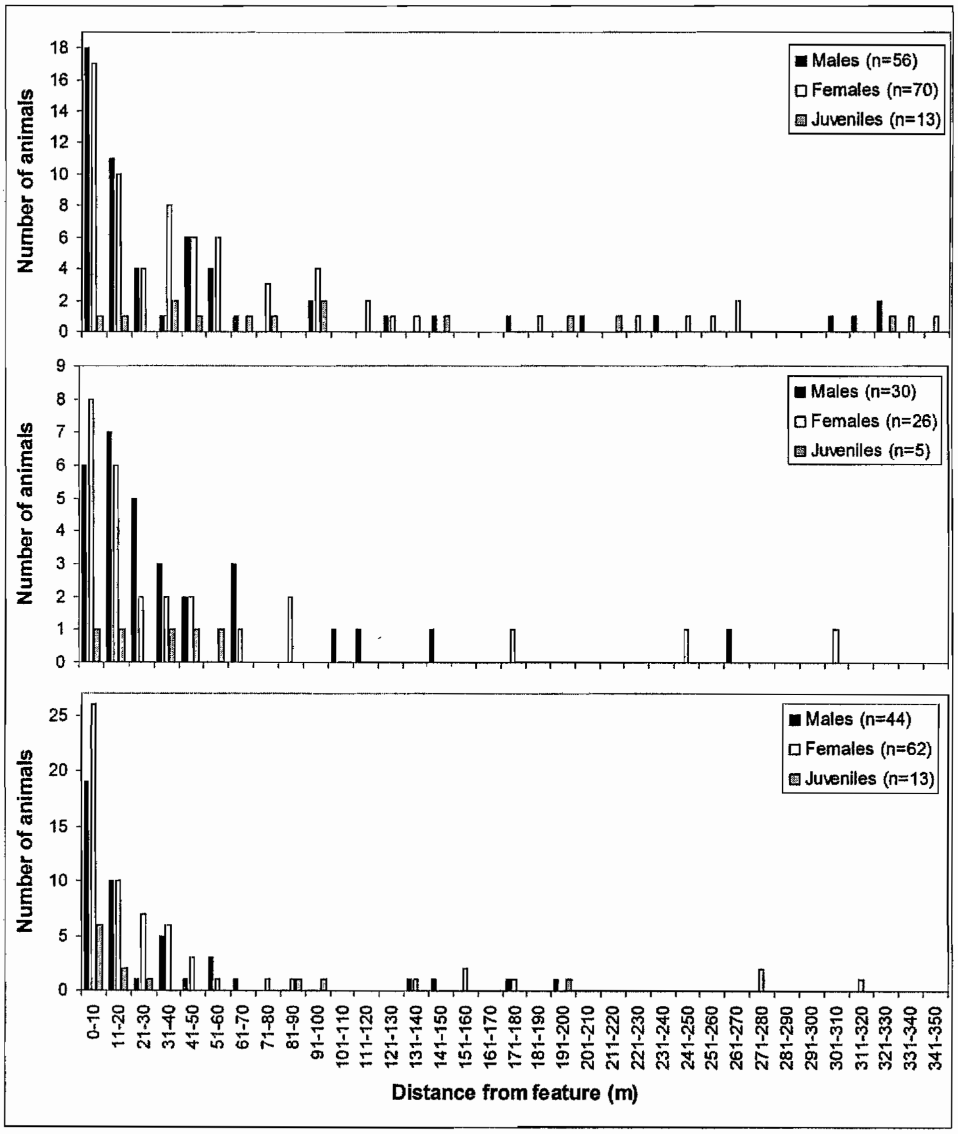

Figure 17 Frequency distributions of *H. australiacus* locations as a function of distance to the nearest creek (top), mitre drain (centre) and culvert (bottom). Sample sizes vary because not all features were present at each transect.

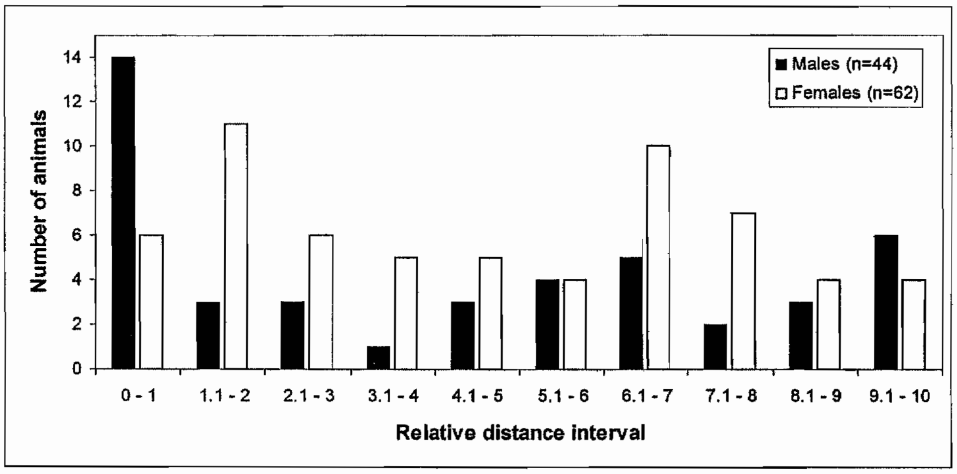

Figure 18 Relative distances of male and female *H. australiacus* from the nearest culvert. Relative distances were calculated as proportions (x 10) of the maximum distance along the transect an individual could be from the closest culvert.

3.2.3 Nearest-neighbour distances

During 52 sampling sessions more than one animal was encountered along the three transects. A total of 216 animals (including recaptured individuals) were recorded. Only six times were nearest-neighbour distances of less than 10 m recorded. The majority of individuals (88%) were more than 50 m from their closest active neighbour (Figure 19). Half the recorded distances between individuals were greater than 250 m.

For Warrah and Thommo's, the aggregation indices based on nearest-neighbour distances between pooled animal locations are close to one, indicating that these animals are randomly distributed along those transects (Table 25), and do not form aggregations. *R* for Reeves indicates a random distribution that tends toward even spacing of individuals, but is influenced by a small sample size.

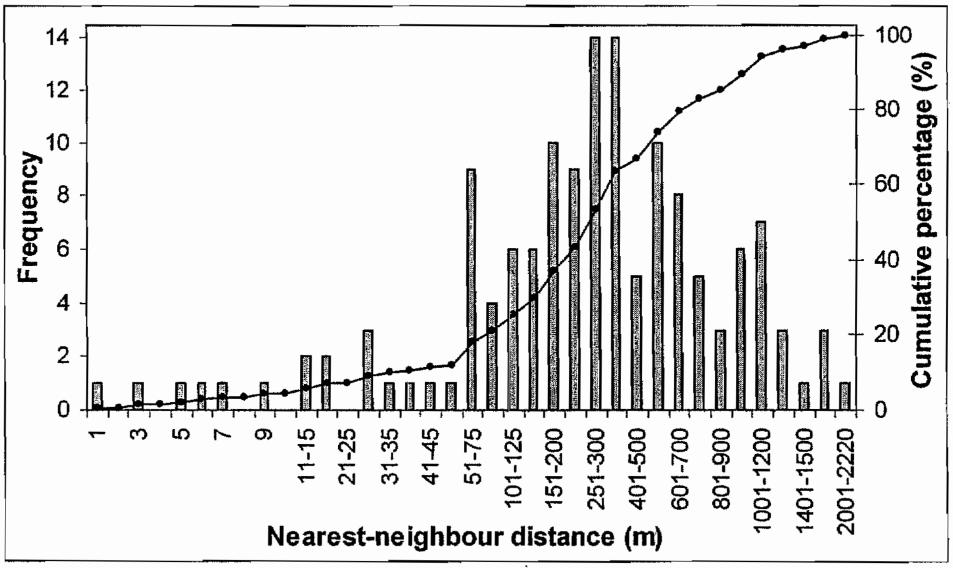

Figure 19 Frequency distribution of nearest-neighbour distances of active *H. australiacus*. Distances are one-dimensional and were determined along transects. Data were pooled for all sampling sessions (n = 52) during which at least two animals were encountered. Note that the x axis is not on a linear scale.

Table 25 Sample sizes, densities and aggregation indices based on nearest-neighbour distances (Clark & Evans, 1954) of *H. australiacus* along three 2400 m transects. SD in ().

Transect	**Warrah**	**Thommo's**	**Reeves**
Number of animals	78	41	20
Mean nearest-neighbour distance (m)	13.8 (17.9)	28.1 (32.5)	84.3 (143.2)
Density (animals per 100 m)	3	1.7	0.8
Aggregation index *R*	0.897	0.961	1.41

3.2.4 Individual movements of H. australiacus

In total, 43 individuals were captured more than once (31% of all marked animals). Mean time (± SD) between first and last capture of these animals was 280 ± 237 days. The recorded mean net displacement between both locations was 45.3 m (range: 0 m – 637 m). Net displacement was not correlated to the time between captures (R = 0.135; P = 0.389; Pearson correlation; natural logarithm of distance + 1). One male moved more than 600 m (Figure 20). That individual was first recaptured 13 m from the location where it was marked 12 months earlier. Another three months later it was recorded 637 m away from the site of its previous capture. In general, displacement distances for males were less than 100

m. A number of males were re-captured at the location where they were first caught. Females generally moved less than 100 m and displacement distances were considerably less (Figure 20).

The sum of displacement distances of individuals captured more than twice was higher than the maximum spatial displacement recorded (Z = -3.18; P = 0.001; Wilcoxon signed rank test) (Table 26). The exclusion of one outlier did not influence this test result.

Table 26 Summary statistics of the total distances moved by recaptured *H. australiacus* and their displacements. One animal moved an unusually long distance, influencing mean, SD and maximum values; therefore these statistics were calculated with and without that individual included.

		Mean (SD)	**Min. – max.**
Total distance moved (m)	All (n = 21)	93 (141)	13 – 663
	1 outlier excluded	65 (55)	13 – 210
Maximum displacement (m)	All (n = 21)	73 (137)	13 – 663
	1 outlier excluded	43 (27)	13 – 105

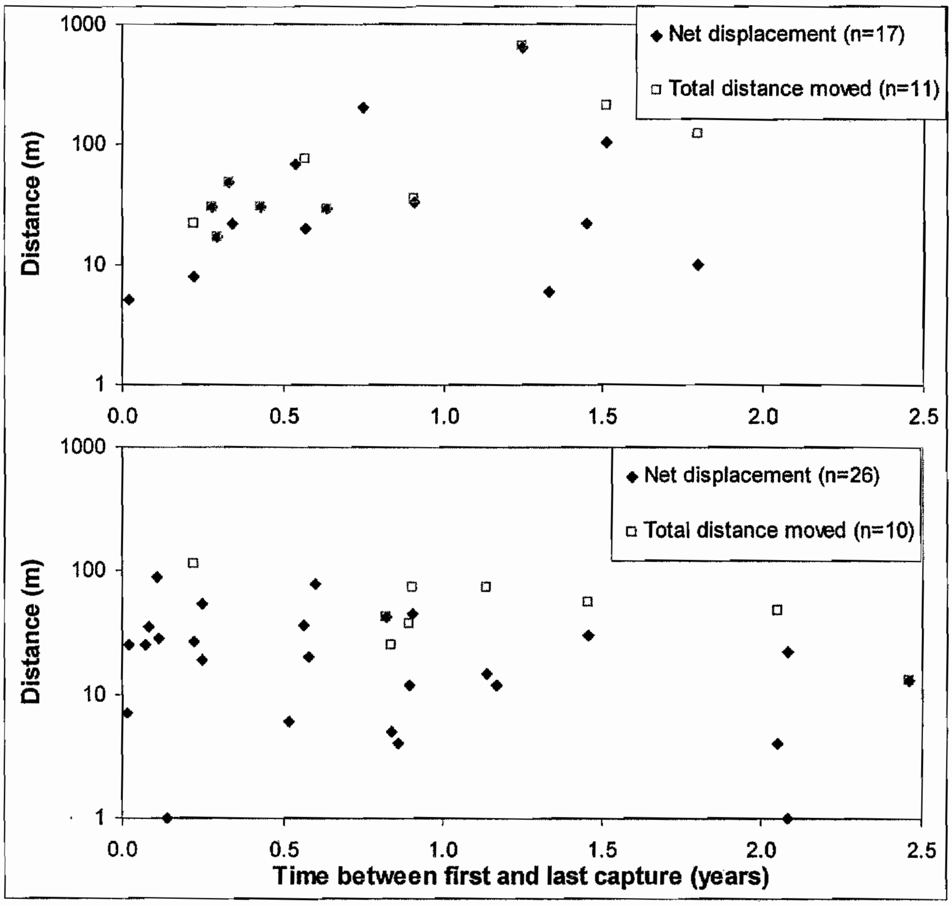

Figure 20 Displacement distances between locations of first and last capture as a function of time between captures for *H. australiacus* males (top) and females (bottom). The total distances moved are also shown separately for individuals that were captured more than twice. The y-axis is represented on a logarithmic scale.

3.2.5 Do individuals located far from creeks move further than those near creeks?

There was no correlation between the maximum displacement distances and the mean distances to the nearest creek for the 43 individuals which were captured at least twice ($R = 0.247$; $P = 0.111$; Pearson correlation). If there was a relationship, the animals ($n = 12$) that live far from creeks would also move further and should therefore be located close to the line in Figure 21.

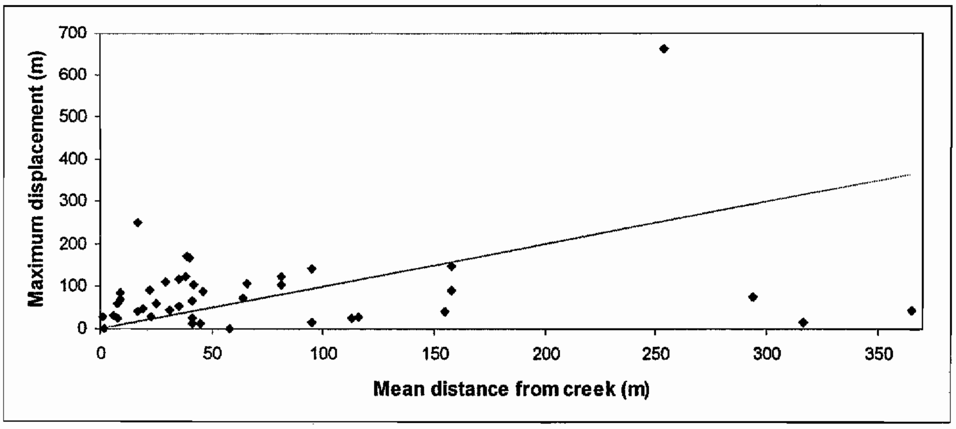

Figure 21 Maximum displacement distances of 43 *H. australiacus* as a function of their location from the closest creek. The line represents places where displacement and distances from creeks are equal. Symbols below the line represent the 12 animals that were never observed to have moved to a creek.

4 Discussion

4.1 Habitat associations and movement patterns of *Pseudophryne australis*

4.1.1 Microhabitat associations

Pseudophryne australis associate with ephemeral drainage lines and are only rarely encountered elsewhere (Harrison, 1922; Thumm & Mahony, 1999; Woodruff, 1972; 1978). It should be noted however, that non-calling individuals (juveniles, non-calling males, and females) are very difficult to detect. These are extremely rarely encountered in the open, or under rocks or logs away from breeding sites (A. Stauber, pers. obs.). Pit traps used for general survey work are not effective at retaining individual *P. australis*, unless the buckets are modified.

Here, I examined microhabitat associations for *P. australis*, concentrating on known breeding sites which included a range of site types (Chapter 2) utilised by this frog across its range.

None of the studied *P. australis* individuals were observed in the open. The ones that called always did so from concealed positions. Others, including a small number of females, were also found hidden in leaf litter or hollow logs, in soil cavities under logs or rocks, in rock crevices and in holes and cracks in soil. Elsewhere, only four individuals were ever observed in the open over the past five years. One female was observed feeding on active termites at the base of their mound approximately 150 m from the closest known breeding site. The others were males swimming in pools, each at a different location.

It follows that the distribution of the individuals studied was strongly linked to sheltering locations. This was shown to be the case in several different ways. Site I provided the simplest and most obvious example. The site, an elongated mitre drain, provided leaf litter along one side only, with the track side always being bare. Animals at that site were always calling from the side which had leaf litter cover and were never observed or heard on the bare side. The three sites studied along natural drainage lines showed that, with only rare exceptions, animals stayed with leaf litter piles, even after these piles had been moved through natural forces to new locations (Figure 14). This association is strengthened when one takes into consideration the relatively low abundance of leaf litter along these transects. However, other utilised shelters were even less abundant.

Despite leaf litter offering the most utilised microhabitat, *P. australis* also persisted at sites where leaf litter was rare. There they were observed to predominantly utilise vegetation, and to a lesser extent logs and rocks. Places chosen in vegetation were usually at the base of thick clumps of grasses, sedges or *Ghania* spp, where dead and decomposing plant matter has accumulated. Such places are usually well shaded and may remain moist for longer periods than more open spaces nearby.

Leaf litter piles and most of the other cover types provide deposition sites for the terrestrially laid eggs (Barker *et al.*, 1995; Harrison, 1922; Woodruff, 1978)(also observed during this study). Potentially higher moisture levels under these types of cover presumably help protect the eggs from desiccation. Embryos can indeed remain within their eggs for several months awaiting rain before they hatch (Fletcher, 1889; Harrison, 1922; Thumm & Mahony, 2002a). The choice of terrestrial "nest" sites may also afford increased anti-predator protection to the eggs. This is particularly true for aquatic predators.

Elevated moisture levels in these shelters were also expected to provide a favourable microclimate for juvenile and adult frogs. However, *P. australis* juveniles are very rarely seen (A. Stauber, pers. obs.) and none were encountered during this study. Frogs have highly permeable skin (Duellman & Trueb, 1994) and small species, such as *P. australis*, and especially their juveniles, are particularly vulnerable to desiccation. Once the shelters dry out, the frogs may retreat to lower clay layers or into crevices in cliffs (Thumm & Mahony, 1999).

During the searches for frogs, a multitude of sometimes very abundant invertebrates were found in the leaf litter and under the logs. These included ants, beetles, cockroaches, mites, springtails, termites and worms. The diet of *P. australis* consists mostly of these organisms (Webb, 1983). The shelters and breeding sites utilised by *P. australis* therefore also provide foraging opportunities.

Leaf litter piles and logs are clearly important to *P. australis* because they provide shelter, egg deposition sites and foraging opportunities. Once dry, they are also highly combustible. Fire hazard reduction burning, and wild fires alike, potentially reduce population sizes (Thumm & Mahony, 1999; A. Stauber, pers. obs.). An indirect effect of such disturbances is likely to be the temporary loss of leaf litter piles and logs. It has been stated that the congener *P. corroboree* may be more vulnerable to dehydration following fire (Osborne, 1991). Whether this also applies to *P. australis* remains to be tested, but it is highly likely that the temporary and perhaps even partial loss of sheltering, feeding and breeding habitat may negatively affect population size, which, in the worst case may also affect population persistence. Given the importance of these habitat features to the species, managers should aim at reducing fire impacts on natural drainage lines and table drains that are colonised by *P. australis*. High frequency fire has been listed as a key threatening process by the NSW Scientific Committee (*Threatened Species Conservation Act 1995*). Thumm & Mahony (1997b, 1999) recommended that fire hazard reduction burns should be implemented only after careful planning taking into consideration exclusion zones to protect the species, and that no more than one fire management activity (including burning, slashing, clearing) should be carried out at a single site within [about] 10 years. These recommendations are obviously designed to minimise the temporary loss of important microhabitat features and should be adopted across the species' range. Ideally, fire management activities within an area are carried out in small patches at different times to form a temporal mosaic pattern at a metapopulation scale.

It was shown that microhabitat features can undergo disturbances. Leaf litter piles are subject to being rearranged and relocated by the forces of water, or to a lesser extent by scratching birds. Individual *P. australis* showed some resilience to such disturbances by persisting at these sites and even moved with, or resettled in relocated piles. Resilience to such small scale, patchy disturbances however does not demonstrate resilience to disturbances in general.

4.1.2 Nearest-neighbour distances

P. australis formed small groups of very closely spaced individuals at all sites studied. The three drainage line sites that were studied in more detail demonstrated that animal aggregations were confined to leaf litter piles. Such leaf litter piles provide critical and perhaps even limiting resources to the species (see above).

When resources are used disproportionately to their availability, then their use is said to be selective (Johnson, 1980). Resource selection is the process in which an animal choses a resource, whereas resource preference is the likelihood that a resource is chosen if offered in equal proportions with others (Johnson, 1980). The variability in shelter type availability and their use among the study sites suggests that *P. australis* did not necessarily prefer one type over another. Animal aggregations in concealed locations however clearly demonstrated selection of such resources by *P. australis*.

While not specifically tested, limitations of such resources in suitable breeding areas are indicated in two ways. Firstly, sheltering locations were patchily distributed and covered only small proportions of utilised breeding sites. The patchy distribution of sheltering sites corresponded well to the patchy distribution of animal aggregations. Secondly, frequent observations were made during this study where calling sites that had been made vacant through the temporary removal of animals, were again occupied by new individuals from the same population only 24 hours later. Such replacement was also observed elsewhere (Thumm & Mahony, 1999).

The close proximity of individuals to other conspecifics may lead to antagonistic behaviours. Thumm (2004) indeed observed aggressive behaviour in *P. australis* between males, and members of both genders and ovipositing pairs. The author concluded that territoriality has evolved in both males and females of this species in response to limited resources, including egg deposition sites.

4.1.3 Individual movements

One third of all marked animals were recaptured within their breeding sites. However, there was one exception: a single female was observed to have utilised two neighbouring sites 200 m apart. The majority of recaptured individuals (82%) were resighted less than 7.5 m from the location where they were first captured. Furthermore, the movement distances of individuals recorded were higher than their respective spatial displacements. These results suggest strong site fidelity. White & Garrott (1990) define site fidelity as a tendency of an animal to either return to an area previously occupied or to remain within the same area for an extended period of time. With one exception, all recaptured frogs demonstrated fidelity to a breeding site, and some even to a single leaf litter pile. Many frog species show site fidelity to at least some components of their habitats (see Sinsch, 1990 and references therein), but generally this is not for the length of time observed in *P. australis*. More generally, most animal species indeed show site fidelity (references in White & Garrott, 1990). The evolution of site fidelity among animals is the subject of many questions and competing theories (Shields, 1983).

At least some of the distances moved by individuals were related to the relocation of habitat features, particularly leaf litter piles. This is not unexpected in a mobile species that utilises transient or shifting habitat features.

Individual movement distances and the aggregation behaviour observed in *P. australis* suggest that populations may be able to persist in relatively small areas of suitable habitat. An exceptionally high number of 97 individuals was collected at one 26 m long site over several consecutive nights. Normally, however, similarly-sized sites yielded a maximum of about 20 calling individuals. Other workers recently produced similar counts of up to 20 individuals (see Thumm & Mahony, 1996). In the early 1900s, Ross (1908) reported finding colonies of 30 or more animals. It is not clear whether the relatively higher numbers 100 years ago were due to sampling differences or favourable weather conditions then, or whether the species has undergone a decline since.

The spatial requirements of individuals and therefore populations however are most likely to be much higher than the space and resources offered by breeding sites alone. Extensive search efforts through the leaf litter did not produce any frogs during prolonged dry weather conditions. Unfortunately, the fossorial habit and small body size make it extremely difficult to track individuals to their retreats during unfavourable climatic conditions. It has been reported however, that these frogs may retreat to lower clay layers or into crevices in cliffs (Thumm & Mahony, 1999). It can only be speculated that frogs seek such refuges as close to breeding sites as possible. The closeness of an individual to a potential breeding site can affect the time required to acquire and defend a high-value egg deposition site when weather conditions turn favourable. High-quality habitat is usually occupied very quickly in other animals (e.g., Orians & Wittenberger, 1991). Proximity to breeding sites is likely to be an important factor influencing individual reproductive success in species such as *P. australis* because the timing of reproduction in this frog is independent of season but strongly linked to prevailing weather conditions (Thumm & Mahony, 2002b). The spatial requirements of this species therefore do not only include a suitable breeding site, but also suitable dry-weather refuges nearby.

Little information is available in relation to the foraging behaviour of *P. australis*. Foraging may indeed further increase the spatial requirements of individual *P. australis*. Ross (1908) described *P. australis* as "a great wanderer" with individuals found half a mile (approx. 800 m) from any water. On several occasions, *P. australis* females were observed considerable distances (Watagans: 100 m; Stauber, pers. obs., Hornsby: 72 m; Thumm, unpubl. data) away from the nearest breeding sites feeding on termites at the base or even on top of their mounds. Perhaps females range further than males to seek out high quality food items for egg production. Such foraging behaviour further increases the spatial requirements of a species.

This study witnessed the disappearance of a population, and the formation of a new one nearby. It is unclear why the former experienced a decline. It was observed that the site offered no place that allowed water to form temporary pools, which are needed for tadpoles to complete that life stage. It is quite possible that the site had one or two temporary pools in the past, but these had become defunct because of sedimentation. *P. australis* are long-lived.

In captivity, males and females reached more than 9 years in age (Thumm & Mahony, 2002b). One captive female was indeed still laying eggs at age 13 years and 4 months (Thumm, pers. comm.). It is possible that this population declined as adults reached the ends of their lives, and then disappeared because it failed to produce new recruits due to the absence of a pool.

A new population was formed 120 m away from the declining one. I had monitored that site as part of previous research for four years prior to this study. The origin of these animals remains a puzzle because none of the individuals were members of the two neighbouring populations. This leaves open many questions that relate to dispersal of this species, which of course also relates to the spatial requirements of populations.

4.1.4 Limitations

This investigation of habitat associations in *P. australis* focussed on breeding sites only and was mostly based on the locations of calling males. It should be recognised, and was mentioned earlier, that this species also utilises habitat away from breeding sites. Usage patterns, location and type of these habitats remain to be investigated.

Two thirds of the marked animals were never seen again. The fate and the whereabouts of these individuals remain unresolved, but because these animals make up a significant proportion of the sample, their consideration is important. Dispersal, relocation and death are the most obvious explanations why these frogs were not recaptured. Dispersal is a one-way movement of individuals from their natal place or an area that has been occupied for a period of time (White & Garrott, 1990). Dispersal fundamentally influences gene flow and the genetic structure of populations (Berry, 2001; Driscoll, 1998; Ibrahim *et al*, 1996; Lacy & Lindenmayer, 1995; McCauley *et al*, 1995; Neigel & Avise, 1993; Peterson & Denno, 1997), their spatial arrangement through colonisation and recolonisation (Hengeveld, 1994; Shaw, 1995), and population demography and persistence (Hansson, 1991). In amphibians, a reliance on dispersal seems highly likely because of the patchy distribution of breeding sites (Hughes, 1990). For amphibians, dispersal is generally thought to be primarily achieved by juveniles (Berven & Grudzien, 1990; Breden, 1987; Gill, 1978). No juvenile *P. australis* were encountered during this study. Juveniles do not call and would only be detected by chance. Given the longevity of *P. australis* and the low recapture rate of adults, it is highly likely that adult dispersal is an important element in this species ecology and population demographics. Dispersing individuals had a very low probability of being recaptured in the present study, unless they dispersed to a neighbouring population which was monitored. Some individuals were recorded to have moved distances greater than the lengths of some of the shorter study sites, which suggests that individuals were quite capable of moving out of the study sites. In many cases this would have been the result of individuals moving further up or down the drainage lines.

Some individuals may have relocated because of the trauma associated with their capture and marking. However, a lack of relationship between net displacement and time since capture suggests that marking had little impact on dispersal behaviour in both frogs. Some individuals may have relocated because of experiences unrelated to this study. Furthermore, death due to predation and other causes was expected to remove some individuals from the study populations.

4.2 Habitat associations and movement patterns of *Heleioporus australiacus*

4.2.1 Association with vegetation structure

In Chapter 2 it was shown that *Heleioporus australiacus* inhabit a range of forests, woodlands and heaths. The distribution of animal locations across the three structural vegetation types was unequal, which suggests that either forest, woodland and heath availability varied across the sampled range, or that *H. australiacus* tolerates a range of structural vegetation types, but prefers one type over another.

The three populations sampled in this experiment all inhabited areas that were covered by a mosaic made up of forest, woodland and heath. Structurally, the major differences among the three structural vegetation types were tree height and the densities of canopy cover, understorey and ground cover (Benson & Fallding, 1981). At ground level, these differences are most likely to influence the temperature regime and the effort required by active frogs to move through the habitat. Differences in food type and availability among the habitats remain to be investigated.

Despite the physical differences between forest, woodland and heath, *H. australiacus* did not show an association with any particular vegetation structure. Therefore, while being dependent on habitat with a complex vegetation structure (Chapter 2; see also Gillespie (1990)), no preferences are evident for a particular vegetation type within the range of types the species inhabits.

The specificity to vegetation structure varies greatly among frogs. *Litoria pearsoniana* for instance appears to prefer a vegetation type that is structurally and floristically very specific (Parris, 2001), whereas *Mixophyes fasciolatus* is found across a variety of forests (Parris, 2002). A general overview of the variation in the specificity to broad vegetation characteristics for a number of eastern Australian frogs can be taken from Ehmann (1996), Hines *et al.* (1999) and Lemckert & Morse (1999).

The lack of association of *H. australiacus* with a particular vegetation structure makes it more difficult to identify high-value habitat. Much of the remaining natural vegetation is located in the upper parts of Hawkesbury Sandstone in the Sydney region is a mosaic of forests, woodlands and heaths, with patterns largely influenced by soil, aspect, drainage and fire history (Benson & Fallding, 1981; Benson & Howell, 1994). *H. australiacus* potentially inhabits all these areas of remaining natural bushland because it is a habitat generalist as far as vegetation structure is concerned.

4.2.2 Association with creeks and artificial track drainage structures

The spatial distribution of *H. australiacus* individuals showed no association with creeks throughout the year, except when mating, which is somewhat surprising considering this frog's reproductive requirements for such watercourses (Gillespie, 1990; Littlejohn & Martin, 1967). This result shows that *H. australiacus* is widely distributed in the landscape. Other workers have also observed this species considerable distances away from creeks (Gillespie, 1990; Lemckert & Brassil, 2003; Lemckert *et al.*, 1998; Webb, 1991). The result also suggests that breeding individuals migrate to creeks in order to reproduce, rather than maintain home ranges that are clustered around breeding sites. At the peak of the breeding season, I had heard choruses of up to 5 individuals within a 30 m stretch of creek in the study area, which may indicate that animal density at these kinds of sites increases during breeding activity. Such a relatively high density of animals was never observed along the transects otherwise, although detection methods differed (compare densities of pooled data in Table 25).

The spatial distribution of *H. australiacus* also showed no association with mitre drains. A small number of mitre drains were utilised as breeding sites (Chapter 5) and others provided sheltering opportunities (Chapter 6), but despite this, these artificial structures do not seem to provide sufficient resources to support groups of individuals.

The lack of association with creeks and mitres encumbers the identification of high-value habitat. Access to creeks is clearly essential to the reproductive success of any *H. australiacus* population, but it appears that the placement of individual home ranges is not related to their proximity to a water course. Corridors that link home range sites with breeding sites are expected to play an important role in the habitat of this species. Essentially, *H. australiacus* inhabit areas that may be long distances from breeding sites. Furthermore, the number of breeding sites available to the studied populations may not be a resource that is restricted enough to influence the spatial distribution of this frog (see Orians & Wittenberger, 1991).

The locations of male *H. australiacus* were associated with culverts or concrete pipes that are buried below the track. Some of these culverts (43%) were located at creek crossings, but only 16% of the surveyed creeks were at culverts. Thus more than half of the culverts were located in natural drainage lines or depressions which only carry water during heavy rainfall, and to a lesser extent near soaks or where they drain track runoff. Most of the culverts in the study area had artificially excavated channels up to 1 metre deep leading to or from them. The sides were generally vertical, unlined exposed soil without vegetation cover. Crayfish holes were found in many of these banks. Pools had formed on the lower side of some of the culverts as a result of erosion and observations confirmed that several of these pools were utilised by *H. australiacus* as breeding habitat. In summary, culverts usually had the following characteristics: they contained a concrete pipe of several metres in length, were within areas resembling deeply eroded drainage lines with crayfish burrows, and may also have had a pool of varying hydroperiod. It is difficult to rank the importance of these features to *H. australiacus* males, but it seems likely that each may play a role in either breeding activity or sheltering. The pipe may help amplify the individual's call (see Bailey & Roberts, 1981), although males were never observed to call from within these pipes. The pipes may also offer foraging opportunities in a unique microclimate and with fewer predators compared to the open track surface or the surrounding bushland. The crayfish burrows offer calling sites (Gillespie, 1990; Hoser, 1989; Moore, 1961; A. Stauber, pers. obs.), egg deposition sites (Hoser, 1989; A. Stauber, pers. obs.), and possibly sheltering opportunities. The pools are essential for tadpole development.

The association with culverts was only observed at one transect – where the numbers of animals and culverts were highest – and not at the other two. The influence of sample size on the result is not known, it is therefore not clear whether this association applies to a few, or indeed all populations of this species.

4.2.3 Nearest-neighbour distances

The aggregation indices based on nearest-neighbour distances for the three transects do not support the finding that *H. australiacus* associate with culverts. Indeed, *H. australiacus* did not form aggregations anywhere within their occupied habitat which further supports the conclusion that at the population scale, these animals show no preferences for any particular features within their general habitat, unless individuals are avoiding conspecifics except at breeding times. Based on aggregation indices, individuals were randomly spaced at the population scale. The higher value for the Reeves population is most likely inflated due to a bias towards regularity with decreasing sample size (Sinclair, 1985).

The spacing of individuals within populations is not solely influenced by the location, quality and availability of resources. Behavioural interactions such as social interactions (Blaustein & Walls, 1995; Brown & Orians, 1970), including avoidance (e.g., Aberg *et al.*, 2000), also influence the spatial distribution of mobile organisms (Moody *et al.*, 1997). The effects of behaviour on spatial patterns were not investigated in this study, but would make an interesting subject of further research. The large values of the actual nearest-neighbour distances measured in the field do suggest that avoidance behaviour to conspecifics may be implicated in the spatial distribution of *H. australiacus*.

Nearest-neighbour distances demonstrate just how widely and sparsely individuals are spaced. Nearest-neighbour distances for about ¾ of the animals (Figure 19) were greater than the maximum weekly displacement distances measured in the field during a radio-tracking study (Chapter 6). Less than 3% of the sampled animals were occupying space within 10 m of each other and half the animals were more than 250 m from their nearest neighbour. Given that individuals show site fidelity (see below and Chapter 6) and that individuals generally do not share their space with conspecifics, the spatial requirements of individuals is additive at the population level. This translates into substantial spatial requirements of viable populations.

4.2.4 Individual movements

Across the three transects, all of the recaptured *H. australiacus* (31% of all marked animals) showed that they each were associated with their own habitat patch. Several individuals were resighted within about 20 m from where they were first marked more than two years earlier. Furthermore, individuals that were resighted more than once had moved significantly greater distances than their net spatial displacements. In other words, they moved around without really leaving their area. These observations, together with the lack of any correlation between time and distance moved, support the hypothesis that individual frogs show high site fidelity over time. Many frogs show site fidelity to at least some components of their habitats (see Sinsch, 1990 and references therein), but generally this is not for the length of time observed in *H. australiacus*.

Whether site fidelity in *H. australiacus* translates to territoriality remains to be tested. If a territory is defined as a “defended space”, the definition adopted by Noble (1939), then territoriality describes behaviour which includes the defence of the site and the exclusion of competitors (Gergits, 1982). Resource limitations linked to particular sites (a resource may be space itself or any biotic or abiotic feature (Begon *et al.*, 1996)) and resource defence by *H. australiacus* remain to be investigated in order to demonstrate territoriality in the species. Male *H. australiacus* do possess prominent cone-shaped nuptial spines on their fingers (Moore, 1961), which could be used as weapons against each other to possibly defend resources. Captive juveniles were observed repeatedly head-butting each other when a limited number of prey items were made available (A. Stauber, unpubl. data). It is not clear how females would defend resources because they do not possess nuptial spines, nor do they call to advertise their presence. Perhaps they use head-butting or possibly even chemicals. Territoriality would explain the sparse distribution of individuals. At densities that are higher than those encountered during this study, territoriality would be expected to translate into a regular spatial distribution pattern. Territoriality in frogs is not uncommon (see references in Brown & Orians, 1970; Mathis *et al.*, 1995 and references therein; Roithmair, 1994; Thumm, 2004).

The majority of marked individuals were never resighted. The fate and the whereabouts of these individuals remain unresolved. Dispersal, relocation, migration and death are the most obvious explanations why these frogs were not recaptured. For amphibians, dispersal is generally thought to be primarily achieved by juveniles (Berven & Grudzien, 1990; Breden, 1987; Gill, 1978). No juvenile *H. australiacus* were recaptured. Dispersing individuals had a very low probability of being recaptured in the present study, unless they dispersed along the transects.

Some individuals may have relocated or given up using the track because of their experience associated with their capture and marking, or experiences unrelated to this study. Such "track-shy" animals could have simply altered their behaviour to a minimal extent in the way they use their home range and remained undetected for the remainder of the study.

Death due to predation and other causes was expected to remove some individuals from the study populations. A list of known and potential predators of *H. australiacus* was given in the species profile. The difficulties of estimating mortality rates based on a study that gets its data from active animals of open populations are obvious.

Migrants may have been intercepted as they moved across the track from non-track home ranges to breeding sites. The probability of recapturing such an animal is expected to be much lower than that of an animal that maintains its home range along a track. One male was observed to migrate over 600 m to a breeding area, after demonstrating site fidelity for one year. This single record is important because it indicates that mature males which are confined to a home range far from any breeding site have the ability to disperse to participate in breeding activity. It is expected that breeding males and females with home ranges that offer no breeding site migrate to a suitable site nearby. Hence the following question arises.

4.2.5 Do individuals located far from creeks also move further?

Almost 28% of the animals that were captured at least twice had home ranges that did not include creeks or other breeding sites, and their recorded maximum displacement distances were less than the distance of the animal's location to the closest creek. Hence animals located further away from creeks did not move longer distances. It is quite possible that populations contain a number of non-breeding adults, which would not need to visit breeding sites. It is also possible that migrations to breeding sites were not observed due to the rarity of encountering individuals.

Support for the latter explanation is found when the proximity of individuals to creeks is compared to the maximum displacements recorded for all individuals. Figure 21 shows that displacements of up to 150 m were not uncommon for *H. australiacus*. The majority of marked animals (90%) were located within 160 m from a creek. They were all adults. At least 90% of adults therefore lived within reach of a breeding site without showing a clustered distribution.

4.2.6 Differences among transects

The data presented here demonstrate differences in animal density among the three transects. The area sampled was constant, but the number of sampling sessions differed slightly among areas. The research for this chapter was focussed on maximising animal locality data collected, and not on transect comparisons. However, the differences in animal densities among the transects indicated by Table 25 are repeated in the dataset (not presented here) for the period when sampling effort (number of sessions) was kept constant across transects. The difference in the density of the populations studied may be influenced by habitat quality and quantity, but also by stochastic processes (Harding *et al.*, 2001). Determination of the magnitude of each on the observed pattern was not explored for in this chapter.

4.2.7 Limitations

Data were collected along a linear transect through *H. australiacus* habitat. The sampled section was open space, the surface of unsealed tracks, surrounded by natural bushland. The sampling area was therefore a unique feature within *H. australiacus* habitat. The majority of sampled animals did not simply cross the track to move from one vegetated patch to another, but spent considerable time on the track, either resting or perhaps waiting to ambush prey (see also Hoser, 2002). Indeed, many animals were encountered on the track (usually at the same location) during both the inward and outward journey while sampling. These observations strongly suggest that *H. australiacus* incorporates and uses the track as part of its habitat. Unfortunately, visual surveys were not possible in vegetated areas. It is therefore not known what proportion of the population avoids the track and was not detected. There must clearly be animals for which the home range does not include a track section simply due to their distance from the tracks. There may be others that deliberately avoid the open space of the track.

The interpretations of the data offered here assume that the number of “track avoiders” within the sampling areas was insignificant, and that tracks do not act as “magnets” to the species. However, roads may provide benefits to the species, such as open foraging ground, or a unique microclimate, or factors associated with the edge-effect. If such benefits influence the spatial distribution of *H. australiacus* by attracting them to roads, then the population density would be lower in natural bushland. This would influence the overall spatial requirements of *H. australiacus* populations. On the other hand, roads may also act as ecological traps (*sensu* Donovan & Thompson, 2001), by attracting individuals to places where they may get run over by vehicles or are easily taken by predators. This topic clearly needs more work.

4.3 Conclusions

Calling *P. australis* are predominantly found in leaf litter piles, but they also utilise vegetation, logs, rocks and soil cavities. The relatively low abundance of these shelters at breeding sites suggests that *P. australis* select these resources. The species also forms aggregations in these sheltered locations. Leaf litter piles offer breeding habitat, shelter to eggs and frogs alike, and foraging opportunities. It is likely that leaf litter piles are a limiting resource to this species. It seems reasonable to assume that *P. australis* benefits from measures that minimize the impacts of fire, particularly fuel hazard reduction burns, on breeding sites.

The spatial requirements of *P. australis* populations remain uncertain. Apart from breeding sites, the frogs also need access to shelters nearby that provide refuges during adverse climatic conditions. Additional foraging space seems to be another requirement. Habitat protection should therefore not be restricted to breeding sites alone, but also needs to incorporate shelter and foraging areas. Individuals demonstrated site fidelity and may not be able to relocate to nearby sites when conditions in their home ranges change.

While being dependent on natural bushland, *H. australiacus* do not show any preference for heath, woodland or forest. Vegetation structure based on growth form and crown separation of woody plants (*sensu* Walker & Hopkins, 1998) is therefore a poor predictor for species occurrence in bushland. Within their habitat, populations are made up of randomly, or possibly evenly, spaced individuals. Individual home ranges are located independently of their proximity to creeks, mitre drains and culverts, although males in one study area appeared to be more common near culverts. While the protection of breeding sites is important, it is also a necessity to consider the presence of individuals up to several hundreds of metres from potential breeding sites.

H. australiacus have demonstrated site fidelity and it appears that individuals do not share their space with conspecifics. Given that individual home ranges may exceed 2000 m^2 (Chapter 6) with little overlap, the minimum spatial requirements of a viable population is at least a hundred hectares. The reduction of habitat availability by several house block sized allotments may therefore negatively impact on population persistence, even if these developments are located considerable distances away from water courses.

Chapter 5

PSEUDOPHRYNE AUSTRALIS, HELEIOPORUS AUSTRALIACUS AND THE TRACK ENVIRONMENT: DO NATURAL AND ARTIFICIAL TRACK-SIDE BREEDING SITES ALLOW EQUAL REPRODUCTIVE SUCCESS?

Abstract

Twenty eight *Pseudophryne australis* and eleven *Heleioporus australiacus* artificial track-side breeding sites (track sites) and natural breeding sites located away from tracks (non-track sites) were monitored fortnightly for twelve months to determine the hydroperiod, or pond duration, and other physical characteristics of these sites. Hydroperiods were compared among site types (track and non-track sites) and related to the larval requirements of both frogs. Records were made of sites which held tadpoles; only some of these sites had hydroperiods of sufficient length to produce metamorphs.

P. australis track sites had shorter hydroperiods than non-track sites in the warmer half-year only. Across the whole year, about half of each site type had hydroperiods long enough to produce metamorphs. Of the 15 pools that contained tadpoles, only three were in the track environment. One track and four non-track sites produced metamorphs. *H. australiacus* non-track breeding sites had longer hydroperiods than track sites, and included the only permanent pools encountered. All sites contained tadpoles but only four non-track and two track sites had hydroperiods of sufficient duration to produce metamorphs.

Non-track breeding sites were more heavily shaded and thus provided a much more thermally stable aquatic habitat. All track sites were subject to traffic of varying intensity and a range of maintenance works. Management options are suggested to mitigate the impacts associated with the operation and maintenance of track sites, taking into consideration the species' ecology and life history.

1 Introduction

Pseudophryne australis frequently colonises man-made table drains and other structures associated with track drainage systems (Thumm & Mahony, 1996) as long as they are not concrete lined (Jacobson, 1963a). Breeding occasionally occurs in and around these artificial structures. *Heleioporus australiacus* has also been reported to breed in man-made drainage ditches and culverts (Daly, 1996a; LeBreton, 1994; Recsei, 1996).

Within the distribution range of both frogs, the majority of roads and tracks are placed in the upper parts of the topography (Schlesinger & Shine, 1994) where gradients are gentle. The habitat of both *P. australis* and *H. australiacus* is largely restricted to these elevated sites (see Chapter 2). As a result, road or track density can be high in the frogs' habitat. A considerable part of the Sydney Basin is within the Reserve System with its vast areas of mostly natural bushland (exceptions are plantations in some SF compartments). Even there the road and track system can be extensive (Upitis, 1980) serving for park and fire management, recreational purposes, and providing access for forestry operations and to utility infrastructure (Department of Conservation and Land Management, 1994). Main roads excepted, the majority of roads within the Reserve System are unsealed. It is these unsealed roads (here termed tracks) that offer breeding habitat to both frogs in the Reserve System and also on privately-owned bushland.

The placement and construction of roads and tracks force structural changes onto the environment affecting its hydrology within and beyond the boundary of the road and track reserve (Bennett, 1991; Carr & Fahrig, 2001) resulting in the destruction or creation of wetlands (Trombulak & Frissell, 2000). Breeding sites in the track environment (track breeding sites) are regularly exposed to anthropogenic disturbances including traffic and maintenance works, usually by heavy machinery. It is unclear whether these man-made breeding habitats are of benefit to the study animals. On one hand, it is possible that table drains offer additional breeding habitat to the species, allowing them to successfully exploit previously unsuitable places. The outcome could be an increase in population size or number where breeding sites are otherwise a limiting factor. Alternatively, the track environment may appear to the frogs as suitable breeding habitat, leading them to abandon their natural breeding sites, while losses of offspring due to the desiccation of eggs or tadpoles may be increased. In this case, roads would act as ecological traps (*sensu* Donovan & Thompson, 2001) and the outcome could lead to a decrease in animal numbers and possibly local extinctions.

Pond durations are in part a function of rainfall (Tejedo & Reques, 1994) and can have profound influences on tadpole survival (Newman, 1992; Tejedo & Reques, 1994; Thumm & Mahony, 2002b; Travis, 1981; Wilbur, 1984). Rainfall in the Sydney Basin (NSW National Parks and Wildlife Service, 2003) is unpredictable because it shows no distinct seasonal patterns, and annual totals vary considerably between years with heavy rain or drought potentially occurring any month of the year (Bureau of Meteorology, 2005a; Linacre & Hobbs, 1986). This unpredictability results in lack of seasonality and uncertainty of pond duration in ephemeral situations.

Is the road habitat beneficial to *P. australis* and *H. australiacus*? The complex relationships between these frogs and the artificial track habitat are poorly understood. Ecologists and managers alike are interested in knowing whether tracks provide habitat enhancement or ecological traps for these species. Here I investigate the hydroperiod of *P. australis* and *H. australiacus* breeding pools in the field both within the track system and away from tracks. Hydroperiod, or pond duration, is the length of time a pond continuously holds water. A hydroperiod that is shorter than the minimum time required for an aquatic tadpole to successfully metamorphose under given environmental conditions leads to certain death of the tadpoles by desiccation. Tadpole mortalities due to early pool drying were reported for both *P. australis* (Thumm & Mahony, 2002b) and *H. australiacus* (Daly, 1996a).

I used hydroperiod as an indirect measure to comparatively assess reproductive success (successful metamorphosis) of track and non-track sites. The aim was to determine whether artificial track breeding sites allow equal reproductive success compared to natural breeding sites away from tracks. The hydroperiods of 39 breeding pools which were utilised by the frogs at least once during the two years prior to the study were monitored for twelve months. This allowed a temporal characterisation of the breeding pools and comparisons of their characteristics between the track and non-track environment. The hydroperiods measured in the field were related to larval requirements. The study also provided the opportunity to identify those sites that actually held tadpoles during the study period, only some of which produced metamorphs. Records were also made of sites which held tadpoles to determine whether they produced metamorphs. Impacts related to traffic and road works were also assessed. Management options are suggested to mitigate the impacts associated with the operation and maintenance of track sites, taking into consideration the species' ecologies and life histories.

2 Materials and methods

Field sites for the hydroperiod study of *P. australis* were chosen from the *Broken Bay* and *Cowan* 1:25000 topographic map sheets (Land Information Centre, 2000). Sites had to be located within 2.5 km of the nearest public road (or track) for access. I was familiar with 56 sites (30 track, 26 non-track) that satisfied these criteria and where I had heard *P. australis* calling at least once during the two-year period prior to the commencement of the hydroperiod study. Meaningful pairing of sites based on local variation in precipitation was not possible, thus a subset of 14 track and 14 non-track sites was chosen using random numbers.

Eleven (6 non-track and 5 track sites) *H. australiacus* sites were also monitored. These were all the sites that I was familiar with at the time within the *Broken Bay* and *Cowan* 1:25000 topographic map sheets. One site from the *Hornsby* sheet and six from *Gosford* (Central Mapping Authority of New South Wales, 1982-1989) were also included. The total number of sites (including *P. australis* sites) and their placement allowed them all to be visited in a single day (Figure 22).

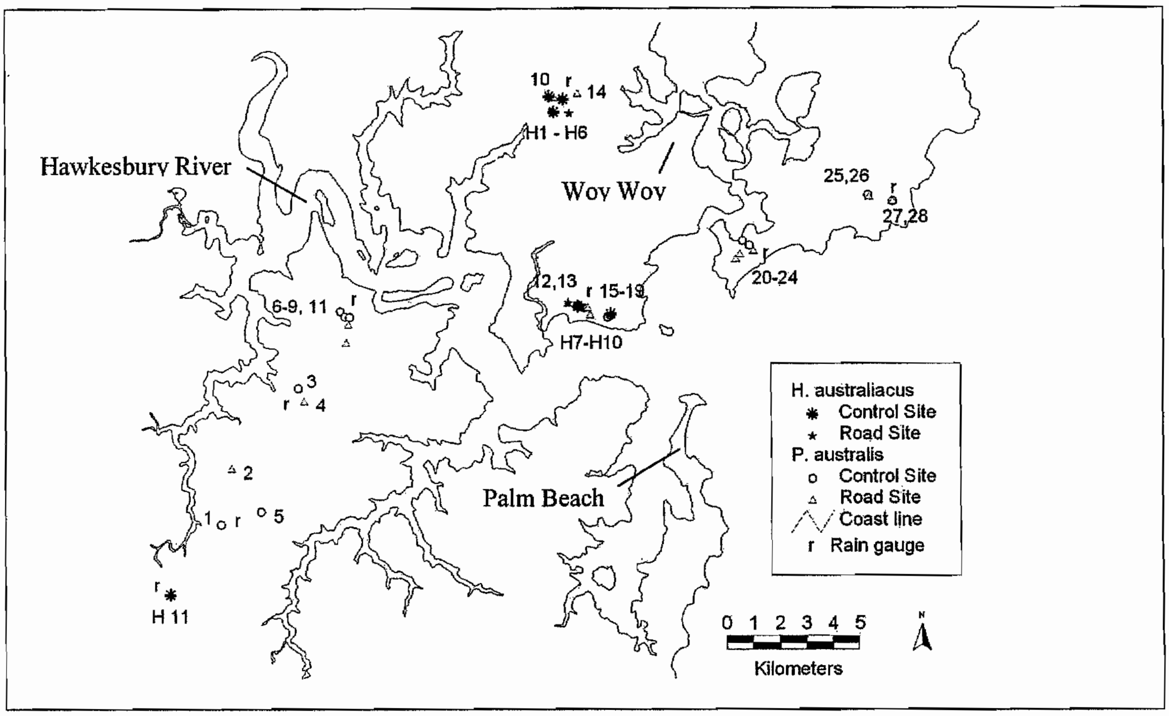

Figure 22 Locations of hydroperiod sampling sites of *P. australis* (Sites 1 – 28) and *H. australiacus* (Sites H1 – H11) in the Broken Bay area of NSW, approximately 35 km north of Sydney..

Track sites were artificial structures (culverts, table drains, mitre drains) associated with the track drainage system and pools that form on the track surface. Non-track sites were depressions and natural drains and creeks. Sites were permanently labelled and marked in the field with aluminium tags. Eight rain gauges (maximum reading 97 mm) were strategically placed for best coverage of the study sites. Seven of the gauges applied to *P. australis* and three to *H. australiacus* sites.

All sites were visited on the same day once every fortnight for twelve months (31/3/2003 – 13/3/2004). One interval in November – December was 39 days. The following data were recorded: presence or absence of water; water temperature; pool length, width and depth; the presence of relevant tadpoles; shading (none, 1 - 33%, 34 - 66%, 67 - 100%); percent coverage of leaf litter and vegetation along the edges (none, 1 - 33%, 34 - 66%, 67 - 100%); track work activity including type; traffic intensity (none; 1 – 5 movements; > 5 movements over 14 days) for cars and motorbikes separately; and rainfall from the nearest gauge.

2.1.1 Data analyses

The fortnightly sampling regime did not record all changes to the state (water present or absent) of pools. Here it was assumed that changes did not occur unless detected during routine sampling. When water was present at a site during a single sampling session, but not immediately before or after, then the hydroperiod was taken as 7 days. Otherwise, hydroperiods were calculated as the difference in days for the period water was continuously recorded as present by subtracting the date water was first recorded from the date water was last recorded.

Hydroperiod requirements of *P. australis* tadpoles were related to Thumm & Mahony's (2006) values determined during an experiment with captive tadpoles carried out at field temperatures during the autumn and winter months. Larval durations for *P. australis* were taken as 45 days as a minimum value, 78 days for the mean and 110 days for the maximum. *H. australiacus* larval hydroperiod requirements were determined during the course of this study.

Goodness-of-fit Chi squares test statistics (Zar, 1996) were calculated for site-type comparisons (2 levels: track and non-track) for each individual sampling session using presence / absence of water. The numbers of dry episodes were also compared among site types in the same way.

Among-site comparison (two levels) of the longest hydroperiod of each *P. australis* site was carried out using one-way ANOVA after initial assumption testing (normality: Kolmogorov-Smirnov and Shapiro-Wilks statistics; homoscedasticity: Levene statistic). Maximum hydroperiods of *H. australiacus* sites, and the total number of dry days (for both species) were compared among site types using nonparametric Mann-Whitney (M-W) tests, because data did not meet the assumption of normality (Zar, 1996).

Surface area estimates were calculated from pool length and width, assuming elliptical shape. Annual mean values of surface area and depth were calculated for each site limited to sessions when water was present.

Modal values for vegetation cover and leaf litter cover at the edges of breeding pools, and shading, were taken from the 24 values of each individual site. For *P. australis*, the mode values were analysed statistically using M-W tests for separate comparisons among site types (track, non-track) and the presence or absence of tadpoles.

Coefficients of variation (CV) were calculated from the water temperature data for each sampling session and site type. Site type comparisons spanning the full study period were carried out with Wilcoxon tests for matched pairs (Zar, 1996).

Motor bike and car traffic were assessed separately for each sampling period based on the number of recent vehicle tracks found on the track surface. A zero score was recorded when no vehicle tracks were observed. A score of 1 was assigned for one to five vehicle movements, and 2 was the score for six or more vehicle movements. Yearly traffic scores were calculated by summing the scores, then multiplying the sum by the number (n) of non-zero scores and taking the square root of the product. This way, repeated light traffic (one to five movements) was weighted slightly heavier than single episodes of heavy traffic, because of the possibility that repeated traffic, regardless of vehicle numbers may have a greater impact on the breeding sites.

3 Results

3.1 Hydroperiod of *Pseudophryne australis* breeding pools

One track site (#8) was filled with soil as part of track maintenance works on 19/8/03 and did not allow water to pool for the remainder of the sampling period. During no sampling session was there a significant difference between the track and non-track environment in the number of sites holding water (Goodness-of-fit Chi square tests, $\alpha = 0.05$). The total number of dry episodes was equal among site types ($\chi^2_{(1)} = 0.33$, $P = 0.564$) ($n_{(track)} = 45$; $n_{(non-track)} = 46$; Table 27).

The difference in the duration of the maximum hydroperiods between track and non-track sites (Table 27) was not significant (ANOVA $F_{1,26} = 0.38$; $P = 0.55$). Six track and seven non-track sites had maximum hydroperiods of sufficient duration to allow all tadpoles to metamorphose (Figure 23), including one of the non-track sites which had two hydroperiods long enough to allow 100% metamorphosis. Eight track and nine non-track sites had hydroperiods greater than that required for a mean number (50%) of tadpoles to metamorphose, three of the non-track sites lasted that long for two different episodes. The hydroperiods of five track and three non-track sites were too short to allow any individuals to metamorphose (Figure 23). Hydroperiods were longest during the autumn – winter period when rainfall was highest (Figure 24). Non-track sites had longer hydroperiods during spring – summer (ANOVA $F_{1,26} = 5.1$; $P = 0.03$) when five non-track sites provided the opportunity for successful metamorphosis (hydroperiods ranging from 67 – 109 days). During that period, only one track site had a hydroperiod (67 days) long enough to allow some tadpoles to metamorphose. The total number of dry days (Table 27) did not vary significantly among track and non-track sites (M-W $U_{(n=28)} = 69$; $P = 0.18_{\text{2-tailed}}$).

P. australis tadpoles were seen during four hydroperiod episodes (three sites) in the track environment, one hydroperiod of 28 days producing metamorphs. Tadpoles were recorded during 23 episodes in 12 non-track sites. Metamorphs were observed in four cases. One flooded non-track site held water for 98 days during which adult *P. australis* were regularly heard calling along the perimeter of the pool, but the site could not be reliably sampled for tadpoles or metamorphs during that time because of issues with visibility and access. No track site and five non-track sites had hydroperiods longer than 45 days during which tadpoles were present. Some sites were in flood during a sampling session when tadpoles were observed to be washed in and out of pools. *Crinia signifera* tadpoles were occasionally observed in *P. australis* breeding pools mainly during short hydroperiods, but *H. australiacus* tadpoles were always absent.

Table 27 Summary of hydroperiod maxima, number of dry episodes and their duration for monitored track and non-track breeding pools used by *P. australis* or *H. australiacus*.

		P. australis		***H. australiacus***	
Site type		Track	Non-track	Track	Non-track
Maximum hydroperiod (days)	Mean	90.4	102.5	155	286
	(SE)	(14.2)	(13.6)	(8.9)	(39.3)
	Range	14 - 169	28 - 169	127 – 169	155 – 348
Number of dry episodes	Mean	3.2	3.3	2	1.2
	(SE)	(0.35)	(0.24)	(0.45)	(0.75)
	Range	1 – 5	2 – 5	1 – 3	0 – 4
Number of dry days (days)	Mean	162	120.3	49.4	10.5
	(SE)	(22.2)	(22.8)	(22.3)	(7.2)
	Range	28 - 306	14 – 214	7 – 113	0 – 42

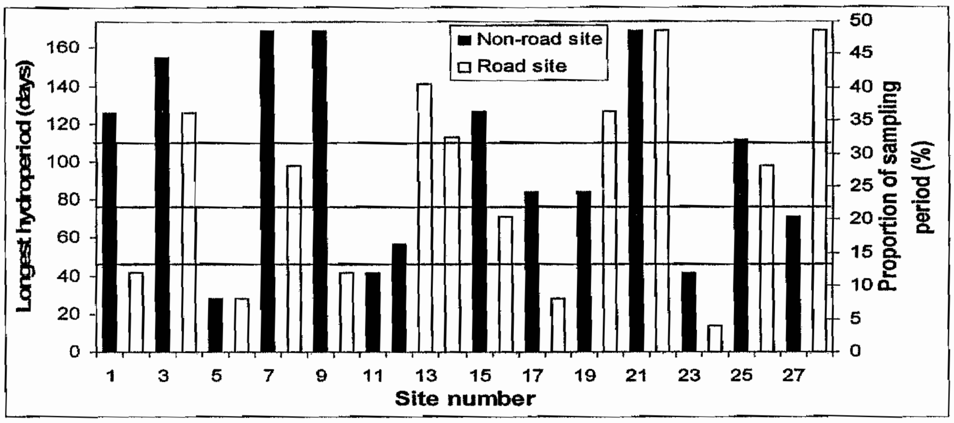

Figure 23 The maximum hydroperiod of each *P. australis* breeding pool (track and non-track environment) sampled over twelve months. The horizontal lines indicate minimum, mean and maximum larval periods reported for *P. australis* by Thumm & Mahony (2006).

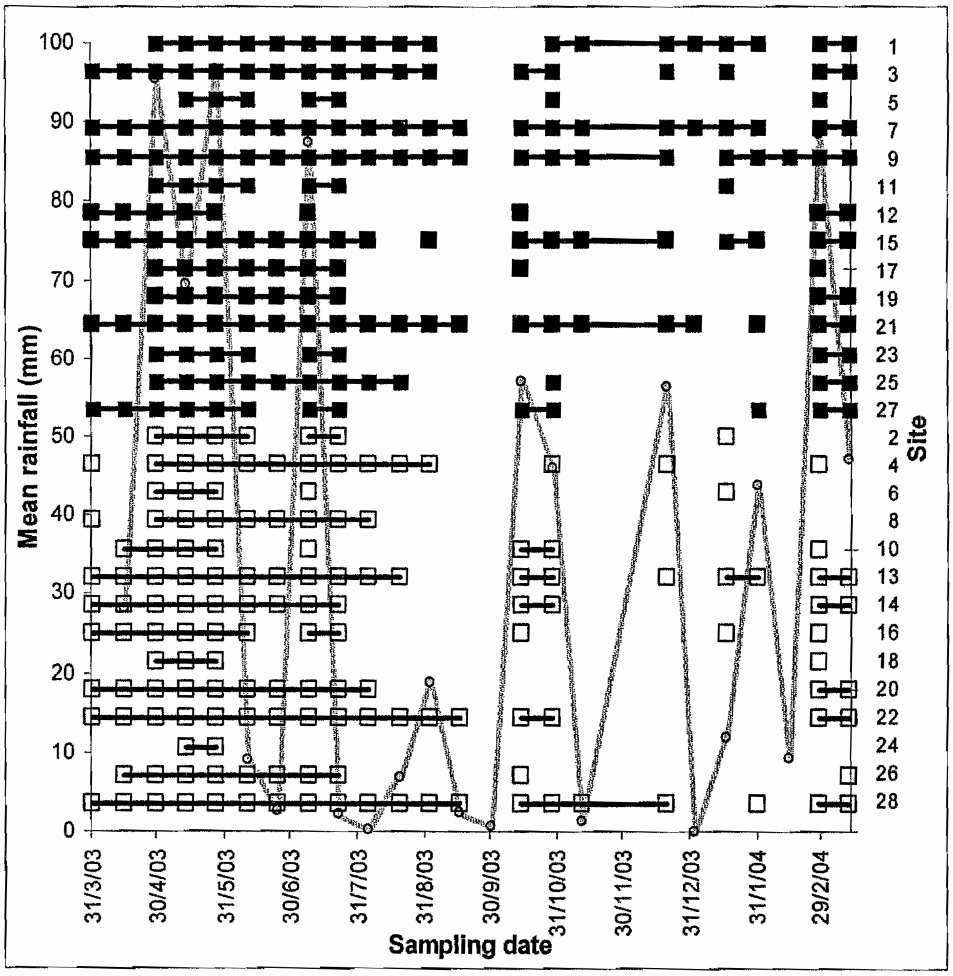

Figure 24 Hydroperiods of 14 track (hollow symbols) and 14 non-track (solid symbols) *P. australis* breeding pools. Broken lines and absent symbols indicate periods when pools had dried up. The dots along the grey line represent the rainfall from the period leading up to the sampling day taken as the mean from a gauge in each of seven study areas (maximum measurable rainfall per period was 97 mm). The time line (independent axis) is on a linear scale and printed dates do not necessarily state actual sampling dates.

3.2 Other habitat characteristics of *Pseudophryne australis* breeding pools

Water temperatures varied seasonally from a minimum of 9°C to a maximum of 30°C (Figure 25). Temperatures did not vary significantly among site types (the lowest M-W P value was 0.05 for one out of 18 tests), but temperature variations were significantly higher in track sites (Z = -3.44; P = 0.001). In 17 out of 20 comparisons did track sites have higher coefficients of variation than non-track sites (median values: 14.7%$_{(\text{ track})}$; 8.2%$_{(\text{non-track})}$). The temperature profile of non-track sites was 10.5 – 24.5°C; the same range was measured across all eligible pools while they contained tadpoles.

P. australis breeding pools were rarely deeper than 30 cm with high variations among different sites (Figure 26). All the deepest pools were non-track sites (mean depths: 8 cm$_{(\text{track})}$; 15 cm$_{(\text{non-track})}$). Surface area estimates (±SD) were generally less than 3 m^2 (mean areas: 2.7±0.9 m$^2_{(\text{track})}$; 4.4±2.5 m$^2_{(\text{non-track})}$).

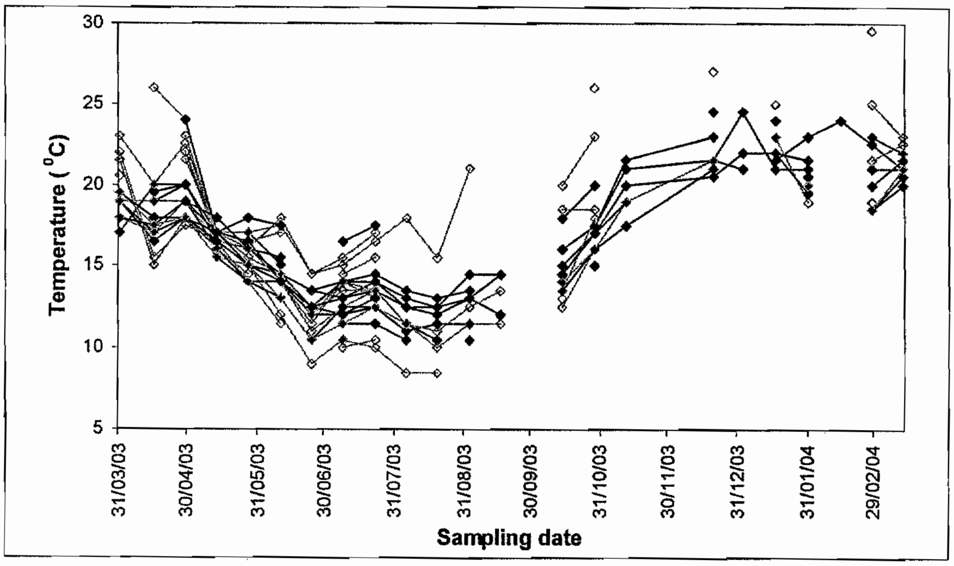

Figure 25 Twelve-month water temperature profiles of 28 *P. australis* track (hollow symbols, grey lines) and non-track (solid symbols, black lines) breeding pools. Water was not present at all times.

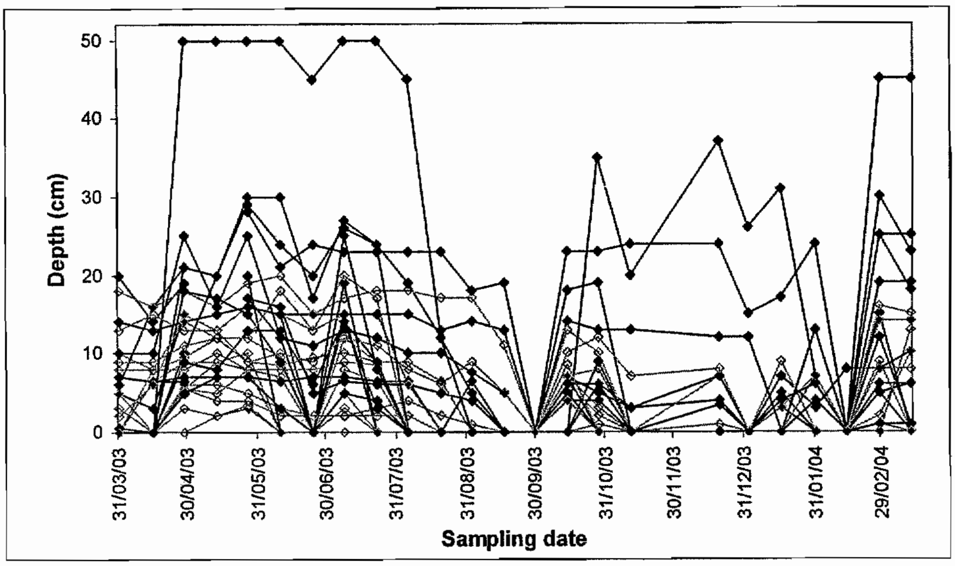

Figure 26 Depths of 28 *P. australis* breeding pools monitored over 12 months. Hollow symbols and grey lines are track sites, filled black symbols and lines represent non-track sites.

Non-track sites had more vegetation at ground level and leaf litter cover and shading than track sites, but only shading was significantly different among site types (Table 28). There were no differences in these attributes based on sites where tadpoles were present or absent, however shading was marginally significant (Table 28).

Table 28 Median physical attributes of monitored *P. australis* hydroperiod sites in track and non-track environment, and tadpole presence and absence comparisons. Minima and maxima of mode values are given in brackets. Cover was classed as :none (0); 1 - 33%; 34 - 66%; 67 - 100%; for simplicity upper values of applicable categories are stated.

	Vegetation cover	Leaf litter cover	Shade
Median value track site (n=14) in %	0 (0-66)	0 (0-66)	0 (0-100)
Median value non-track site (n=14) in %	33 (0-100)	33 (0-100)	66 (0-100)
Mann-Whitney U	73	69	57
P	0.22	0.14	0.05
Median value for tadpole presence (n=15) in %	33 (0-66)	0 (0-66)	33 (0-100)
Median value for tadpole absence (n=13) in %	33 (0-100)	0 (0-100)	0 (0-66)
Mann-Whitney U	94	89	62
P	0.86	0.67	0.09

3.3 Traffic and track works

Tadpoles were observed in three out of 13 track breeding sites where the track surface was unsealed. These three sites each recorded combined traffic scores of less than 11 for the 12-month sampling period (Table 29), which is in stark contrast to the maximum value of 33 recorded for a site where tadpoles were not observed. For example, a score of 11 is the equivalent of 11 14-day periods out of 24 during which 1 to 5 vehicles (either bikes, or cars, but not both) were recorded to have used the track. Most sites (71%) experienced some track works, ranging from the slashing of vegetation, to heavy topscrapes. One site (#8) was totally filled on 19/8/2003 during track works (Table 29). Site 28 was subjected to track works while it held tadpoles. No tadpoles could be found there afterwards. The track at site 20 was subjected to a heavy topscrape, but the table drain was left undisturbed. Tadpoles were observed there two weeks after the maintenance operation was completed. Site 4 was observed to fill up with silt which was later stirred up by dogs walking through.

Not a single worked site produced metamorphs during the study period!

The track sites that were not worked during the study period were graded within six months after. In addition, incidental observations were made on two other track breeding sites which were completely destroyed by track works. The first unmonitored site, a table drain, was dug out to solid base during a wet period when breeding activity was indicated by a large number of calling male *P. australis*. This was most likely the first reproductive effort in twelve months during which very little rain had fallen. That table drain was re-built six weeks later after a vehicle had driven through its entire length. The second unmonitored site, a depression in natural bushland about 1 m from the edge of the track, was used as a permanent dump for excess track fill. That depression is now a mound about 2 m long and 1 m high.

Table 29 Scores for motor bike and car traffic, their sums and tadpole presence for 13 *P. australis* track sites, ordered by the sum of traffic scores. Details of track works are also presented. The monitoring period was 12 months. See page 151 for how traffic scores were calculated. Track site 26 was excluded because its bitumen surface did not allow the calculation of traffic scores.

Site	Motor bike	Car	Total	Tadpoles	Track works
2	1	1	2	present	none
24	4	2	6	absent	light topscrape
20	5	3	8	present	heavy topscrape, not table drain
22	6	3	9	absent	light topscrape, slashing
28	5	6	11	present	light topscrape, slashing
18	7	4	11	absent	none
4	9	3	12	absent	heavy topscrape
16	8	5	13	absent	none
13	9	6	15	absent	none
8	0	15	15	absent	filling
6	6	21	27	absent	light topscrape incl. table drain
10	21	9	30	absent	slashing
14	23	10	33	absent	slashing

3.4 Hydroperiods of *Heleioporus australiacus* breeding pools

During no sampling session was there a significant difference between the track and non-track environment in the number of sites holding water (Goodness-of-fit Chi square tests, $\alpha = 0.05$), except at session 14 for which a test statistic could not be calculated because all track sites had dried up ($n_{(track)} = 0$; $n_{(non\text{-}track)} = 4$). The total number of dry episodes did not vary among site types ($\chi^2_{(1)} = 0.53$, $P = 0.47$) ($n_{(track)} = 10$; $n_{(non\text{-}track)} = 7$)(Table 27), however all permanent sites were non-track sites (Figure 27, Figure 28). As a result, maximum hydroperiods were shorter in track sites than non-track sites (M-W $U_{(n=11)} = 4.5$; $P = 0.044$ $_{\text{2-tailed, adjusted for ties}}$)(Table 27, Figure 27). Nevertheless, the total number of dry days did not vary significantly among track and non- track sites (M-W $U_{(n=11)} = 5$; $P = 0.082$ $_{\text{2-tailed, adjusted for ties}}$)(Table 27).

Minimum larval periods of *H. australiacus* ranged from 33 to 47 weeks (Table 30). Tadpoles were observed at all 11 sites but only six sites ($n_{(track)} = 2$; $n_{(non\text{-}track)} = 4$) had hydroperiods long enough to allow tadpoles to metamorphose (Table 30, Figure 28). Both track sites had dried up once (absence of water recorded for one sampling session) in

October when no tadpoles were seen. Tadpoles of the same size class as observed everywhere else were again found during the subsequent session when both pools had refilled. A lack of upstream sites suggested that these tadpoles could not have been swept into the study pools from upstream, nor would they have been able to travel from downstream because of rock shelves immediately below. The sites however provided underground shelters in the form of crayfish burrows and a cavity under a rock slab that presumably held water permanently in which the tadpoles may have sought refuge during the dry episode. Identical observations were recorded at the site with the rock cavity in September one year earlier (A. Stauber, pers. obs.).

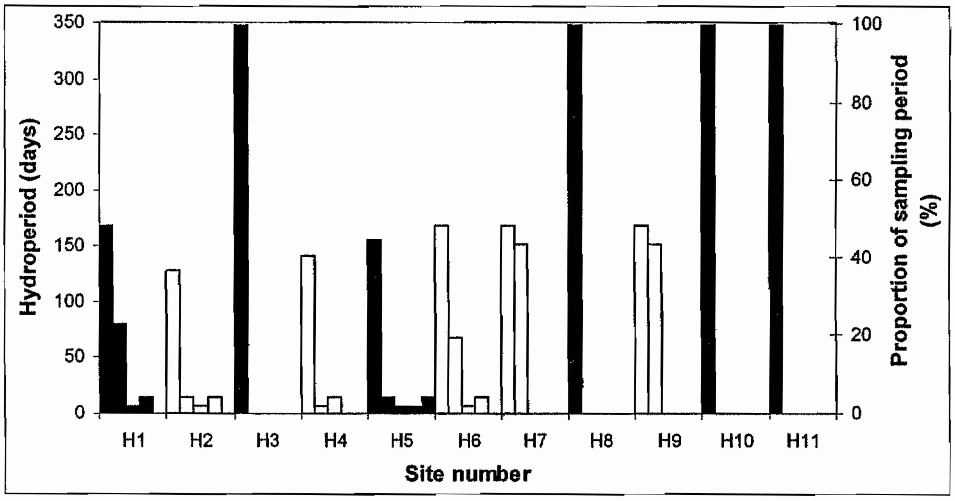

Figure 27 Chronologically ordered hydroperiods of each *H. australiacus* breeding pool in the track (white bars) and non-track (black bars) environment sampled over twelve months.

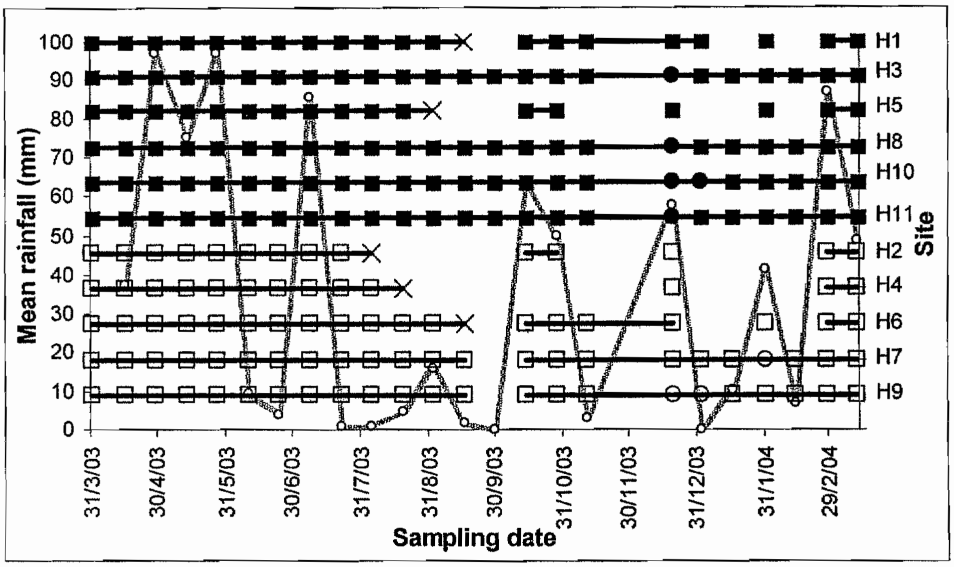

Figure 28 Hydroperiods of 5 track (hollow symbols) and 6 non-track (solid symbols) *H. australiacus* breeding pools. Broken lines and absent symbols indicate periods when pools had dried up. The dots along the grey line represent the rainfall from the period leading up to the sampling day taken as the mean from a gauge in each of three study areas (maximum measurable rainfall per period was 97 mm). Crosses represent days when tadpoles were last seen alive. Circles indicate sampling sessions when metamorphs were observed. The time line (independent axis) is on a linear scale and printed dates do not necessarily state actual sampling dates.

3.5 Other habitat characteristics of *Heleioporus australiacus* breeding pools

Water temperatures varied seasonally from a minimum of 9°C to a maximum of 31°C (Figure 29). Temperature variations were significantly higher in track sites ($Z = -2.59$; $P = 0.010$). In 18 out of 23 comparisons had track sites higher coefficients of variation than non-track sites (median values: 12.7%$_{(\text{ track})}$; 8.6%$_{(\text{non-track})}$).

The deepest *H. australiacus* breeding pool had a depth of 85 cm. There were considerable variations among different sites (Figure 30). Pools were generally deeper in non-track sites (mean depths: 22 $\mathrm{cm}_{(\mathrm{track})}$; 50 $\mathrm{cm}_{(\mathrm{non\text{-}track})}$). Mean surface area estimates (± SD) are 7.1±4.4 m^2 for track sites and 11.8±7.7 m^2 for non-track sites.

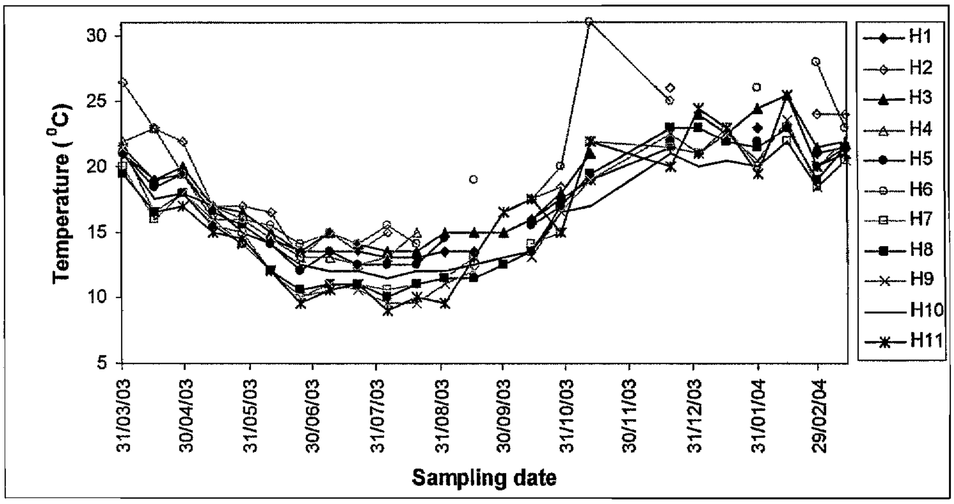

Figure 29 Twelve month water temperature profiles of 11 *H. australiacus* track (grey symbols and lines) and non-track (black symbols and lines) breeding pools. Water was not present at all times

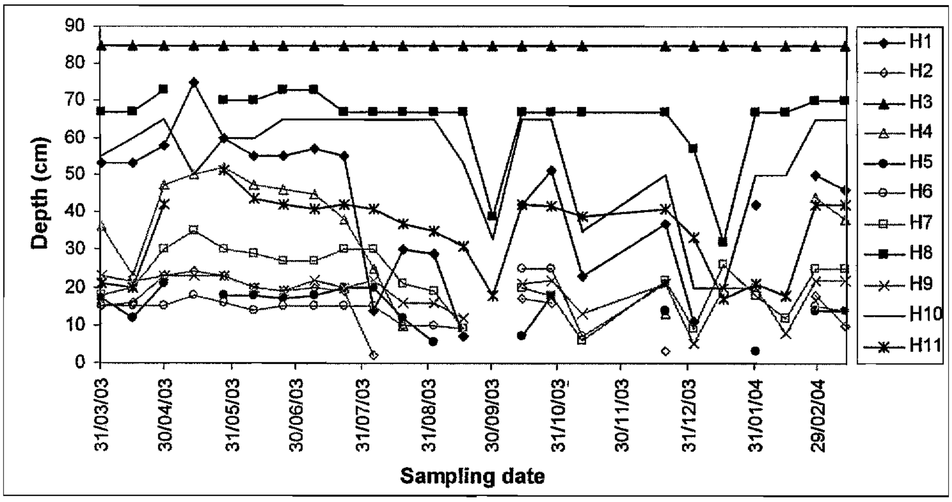

Figure 30 Depths of 11 *H. australiacus* breeding pools monitored over 12 months. Grey lines and symbols are track sites, black lines and symbols represent non-track sites.

Table 30 Larval periods and fate of individuals from 11 monitored *H. australiacus* breeding pools. Sampling resolution 14 days (exception: 39 days for one period in November - December, possible overestimates resulting from that period are indicated with *). Hatching date was estimated to be 24 days before sampling commenced.

Site	**Type**	**Larval period in weeks (days)**	**Fate**	**Comments**
H1	non-track	29 (206)	Desiccation	
H2	track	23 (164)	Desiccation	
H3	non-track	33 (234)	Metamorphosis	
H4	track	25 (178)	Desiccation	
H5	non-track	27 (192)	Desiccation	
H6	track	29 (206)	Desiccation	
H7	track	47 (329)	Metamorphosis	Pool completely dry in October
H8	non-track	34 (235)	Metamorphosis	
H9	track	39 (273)	Metamorphosis	Pool completely dry in October
H10	non-track	41 (287)*	Metamorphosis	
H11	non-track	41 (287)*	Metamorphosis	

Non-track breeding sites usually had more vegetation cover at ground level and were more shaded than track sites (Table 31).

Table 31 Median physical attributes of monitored hydroperiod sites for *H. australiacus* in track and non-track environments. Minima and maxima of mode values are given in brackets. Cover was classed as: none (0); 1 - 33%; 34 - 66%; 67 - 100%; for simplicity upper values of the relevant categories are stated.

	Vegetation cover	**Leaf litter cover**	**Shade**
Median value and range for track sites (n=5) in %	0 (0-33)	0 (0)	0 (0)
Median value and range for non-track sites (n=6) in %	33 (0-33)	0 (0-33)	33 (0-66)

3.6 Traffic and track works

The extent of track works varied greatly among *H. australiacus* sites (Table 32). Two sites along one track were not exposed to any maintenance work during the sampling period (vegetation was mowed and sawn within the following 12 months). Two had the vegetation slashed. Site H2, a pooling mitre drain on the lower track side of a low-level creek crossing continuously accumulated silt from the track run-off. During the study, the washed out ruts were filled with light-weight crushed concrete and building rubble, much of which was washed into the mitre during the following two rain events. After the monitoring period (October 2004), cement was mixed into the track topping. The hardened layer has since been crumbling away into the mitre. Site H6, a pool in a low-lying track section was filled with natural material from nearby, resulting in a much smaller pool which at the same time was shifted to the lower side of the track.

None of the worked sites produced any metamorphs during the study period!

Table 32 Scores for motor bike and car traffic and their sums and maintenance work details for 5 *H. australiacus* track sites. The monitoring period was 12 months. See page 151 for how traffic scores were calculated.

Site	Motor bike	Car	Total	Track works
H2	25	7	32	filled with crushed concrete, rebuilt
H4	24	8	32	slashing
H6	26	10	36	slashing; filling and rebuilding of track resulted in pool being shifted
H7	7	5	12	none
H9	8	6	14	none

4 Discussion

This study suggests that reproductive success of *Pseudophryne australis* and *Heleioporus australiacus* is higher in the non-track environment in comparison to breeding sites associated with the track drainage system. Differences were recorded in pool duration and the number of sites producing metamorphs.

4.1 *Pseudophryne australis* breeding sites

All *P. australis* breeding pools frequently dry out. Some were dry as often as five times during the 12 month sampling period. Although track sites were dry for 44% of the year, as opposed to 33% for non-track sites, no significant differences in hydroperiods were reported among track and non-track sites.

There were differences however during the warmer and drier half of the year in spring – summer when non-track sites held water for longer. Breeding activity as measured by the number of egg masses does not appear to differ between months and seasons (Thumm & Mahony, 2002b). Non-track sites are therefore likely to contribute more to population persistence than track sites because of the increased possibility of also producing metamorphs during the warmer half-year.

Non-track pools were deeper and in more heavily shaded locations, two factors that presumably combined to prolong the hydroperiod during warm weather. Vegetation cover may also better protect non-track sites from drying winds. Furthermore, possible differences in the hydrology between site types may also influence hydroperiod. Track drainage structures in many cases are designed to intercept surface run-off, whereas natural breeding sites may benefit from water that seeps out of the ground.

Water temperature ranged from 10.5 to 24.5^0C in non-track sites, and was more variable (9 to 30^0C) in track sites. Temperature fluctuations are greater in shallow and unshaded pools (Brady & Griffiths, 2000; Tejedo & Reques, 1994; Williams, 1987). Within physiological limits (Levins, 1968), temperature influences differentiation rates and is rate limiting in anuran metamorphic development (Smith-Gill & Berven, 1979) (see Chapter 3 for more details). The critical thermal maxima are not known for *P. australis*, but tadpoles of the species were only found in pools that matched the temperature range measured for non-track sites. Upper temperature limits vary substantially among anuran species and can be subject to acclimation (Duellman & Trueb, 1994). It is not clear if track sites can get too hot for normal development of *P. australis* tadpoles, a possibility which would need to be established experimentally. Such an experiment however is ethically questionable.

Of all the study sites, 20 (71%) had at least one hydroperiod in 12 months of sufficient duration to allow at least some *P. australis* tadpoles to complete the aquatic larval stage and metamorphose before the drying of their larval habitat. Tadpoles were indeed observed in 15 sites, but not all of these held water long enough to allow metamorphosis. Tadpoles died due to pond drying in five sites, but metamorphs were observed at five other sites. Of the 15 pools that contained tadpoles, only three were in the track environment and one of these produced metamorphs. Why is there such a big difference in tadpole presence among site types, keeping in mind that all sites had calling male *P. australis* recorded at some stage prior to the study? Hydroperiods did not vary among site types, and the presence of tadpoles in the majority of sites confirms that climatic conditions suited breeding requirements at some stages during the study period. One plausible explanation for the lack of tadpoles in track sites may be increased pre-hatching mortality in the terrestrial nest sites. These sites were less shaded and were exposed to greater desiccation risk. Thumm & Mahony (2002b) emphasized that desiccation of egg masses prior to hatching is a main cause of mortality in *P. australis*. In addition, vehicular traffic may also have been a contributing factor: motor bikes were often being ridden through shallow table drains. Eggs and their fates were not monitored for this study.

An alternative explanation may be found in the drought. The hydroperiod study was started at the first opportunity following a reasonable rainfall event after a prolonged drought (Bureau of Meteorology, 2005b). Lack of rain may have caused *P. australis* populations to shrink and retract toward natural sites. It is not uncommon to find males of the species calling from places with little chance of recruitment success during very wet weather. Track sites perhaps offer marginal breeding habitat at best and are mainly favoured during very wet times.

For many sites calling activity in the past was assumed to indicate breeding activity. Unfortunately it was not possible to test this assumption for each site. I noticed however that the physical characteristics of track sites can change substantially over a short period. Bare track surfaces contribute sediments (Austroads, 2001; Bennett, 1991; Department of Conservation and Land Management, 1994) that lead to the siltation of potential breeding pools (Carr & Fahrig, 2001). During this study it was also observed that wheel tracks can create new sites and drain existing ones. Such changes to breeding sites may also have contributed to the lack of tadpoles in the track environment simply because some of the sites may have become unsuitable in the meantime. Thumm (1997a) had never observed the species to recolonise silted sites.

Despite access to each monitored track being limited to authorised vehicles only, a great and highly variable range of vehicle movements were recorded among the sites. For one track in Brisbane Water NP at least one vehicle movement recorded (mostly motorbikes) for each sampling period. Tadpoles were never observed in these high traffic areas, despite the presence of calling males (calling males were recorded there repeatedly during *H. australiacus* transect work (Chapter 4)). Overall *P. australis* tadpoles tended to be absent from breeding pools in high-traffic areas.

This study demonstrates that tracks in the Reserve System are subjected to regular and frequent maintenance works. Track maintenance works were undertaken during the study period on all but one track where breeding pools were monitored. The remaining track was exposed to maintenance works six months after the monitoring period. Two unmonitored and two monitored breeding sites were completely destroyed as a result of the track works. The first unmonitored site, a table drain, was dug out to solid base during a wet period when breeding activity was indicated by a large number of calling male *P. australis*. This was most likely the first reproductive effort in twelve months during which very little rain had fallen. That table drain was re-built six weeks later after a vehicle had driven through its entire length. The second unmonitored site, a depression in natural bushland about 1 m from the edge of the track, was used as a permanent dump for excess track fill clearly contravening Austroads (2001) guidelines. That depression is now a mound about 2 m long and 1 m high. A monitored site, a rut in the middle of the track, was completely filled with crushed sandstone and was thus eliminated. No ameliorative measures were evident. The fourth site was damaged and drained by a truck that had driven through. It is somewhat unfortunate that these four events took place in a Nature Reserve in locations that are recorded in the *Atlas of NSW Wildlife*.

Records of track work activities directly altering *P. australis* breeding sites are by no means new or a rare occurrence. An unsealed track in Royal NP was resurfaced with ground bitumen in early 2001. A pool in the table drain where *P. australis* used to breed regularly was graded and drained. A visit in late March 2001 failed to locate any *P. australis* in or near the site which had become silted up (A. Stauber, pers. obs.). Regular maintenance works of the major tracks in the State Forests of the Watagan Mountains account for major disturbances in at least two *P. australis* breeding sites. A 40 cm deep table drain at the bottom of which *P. australis* used to call from under the leaf litter and in cavities was levelled with road spoil (A. Stauber, pers. obs.). The mitre drain nearby was converted to a dam in spring 2004. At the same time, another breeding site was bulldozed and diverted to a newly constructed dam (A. Stauber, pers. obs.). Madden (pers. comm.) attributed the extinction of a population in a drainage ditch in the Woronora catchment to grading of the site, rather than a recent fire. Track works during a fire in a bushland reserve on the Central Coast in October 2002 completely filled a depression in the track where previously *P. australis* were regularly heard calling. No *P. australis* were heard there for the following 17 months during which the species was heard in other known locations nearby (A. Stauber, pers. obs.) Dramatic reductions in the numbers of calling males were still recorded 12 months after the cleaning out of table drains elsewhere (Thumm, 1997a). Single maintenance operations can impact on multiple breeding sites as was demonstrated during "upgrading" works of a track when six breeding sites were backhoed (Thumm, 1997b).

The impact of track works on track-side breeding *P. australis* populations must not be underestimated. During this study, not a single worked site produced metamorphs of this species, whereas a non-worked site did.

4.2 *Heleioporus australiacus* breeding sites

Hydroperiods of *H. australiacus* breeding sites varied from ephemeral to permanent. The permanent sites were all non-track sites. Thus non-track sites held water for significantly longer periods than track sites. Not all non-track sites however were permanent and as a result only half of all monitored sites, which all had held tadpoles, produced metamorphs.

In the track environment, dying tadpoles were observed in the same mitre drain for two years in a row. At some stage masses of wriggling tadpoles were concentrated in the footprints of a large dog where the pool's remaining moisture had accumulated. This site is part of a small watercourse which offers several deep, natural breeding pools, which occasionally, but not always, were occupied by *H. australiacus* tadpoles. The mitre drain can be classified as an ecological trap because it is a habitat "low in quality for reproduction and survival that cannot sustain a population, yet is preferred over other available high-quality habitats" (Donovan & Thompson, 2001). At present it is not known whether this type of ecological trap is an isolated case, or a more widespread phenomenon.

Larval periods of *H. australiacus* are considerably longer than those of *P. australis* and despite their ability to accelerate larval development in a drying environment (see Chapter 3), losses were high due to early pond drying. The importance of crayfish burrows and crevices that provide access to the watertable below dry ponds was evident. These shelters allowed tadpoles to survive short dry spells and complete metamorphosis in replenished pools. This possibility was also raised by Daly (1996b). There is a strong association between *H. australiacus* breeding pools and the presence of crayfish burrows (Chapter 2), a relationship that appears to convey benefits to the frog. Male *H. australiacus* often call from such burrows and egg masses may get deposited there (A. Stauber, pers. obs; see also Hoser, 1989). It is not known if the crustacean preys on tadpoles. While crayfish appear as inefficient predators on free-swimming tadpoles (Lefcort, 1996; but see Nyström & Åbjörnsson, 2000), they would benefit as a predator when tadpole densities increase as a result of pool drying. An investigation into the nature of the relationship between crustacean and amphibian and its implications for both taxa is recommended.

Maximum water temperatures in non-track sites reached 25.5^0C. In track sites temperatures were considerably more variable and reached a maximum of 31^0C. As for *P. australis*, the physiological implications of the higher temperatures are not known for *H. australiacus*. The increased thermal stability of non-track sites can be explained by the fact that the pools are deeper, more shaded with higher amounts of vegetation cover around the edges, than track sites.

All track sites were subjected to track works within 2 years of the commencement of the hydroperiod study. On tracks that had experienced little traffic, this work was focussed on vegetation control by slashing track edges and the trimming of trees and shrubs with chainsaws. More heavily used tracks were re-worked with bulldozers, graders and rollers. Work with heavy machinery caused increased siltation of track breeding sites, an observation also reported from Marramarra NP (Recsei, 1996). Sites were also filled in directly. Site H2 on the track with the highest amount of mostly illegal traffic was within 12 months, re-worked twice with heavy machinery including a bulldozer and a roller.

This site (H2) is of particular concern because for two consecutive years short hydroperiods caused the failure of all reproductive efforts there in that time frame. At this site, an ephemeral creek flows across the track surface into a scooped out mitre drain, from where it follows its natural course. There are a number of deeply eroded pools in the clayey soil along the creek on both sides of the track where the gradient is gentle. These pools are under natural vegetation and well clear of the track edge and are suitable as *H. australiacus* breeding pools, and have been utilised as such. When flowing, the creek erodes the track surface, creating ruts and moving the material into the mitre below, which then becomes a shallower pool. It is possible that the very high number of vehicular movements recorded on this track may also contribute to the erosion at this particular track curve site. Originally, the track surface was crushed sandstone and other natural materials obtained from nearby. Later, crushed building rubble (mostly a light concrete with electrical and plumbing plastics) was used to fill in the ruts and to form a new surface, which was compacted with heavy machinery. The artificial material readily dislodged when the creek started flowing again and was collected in the mitre drain, filling it up with solid material. Later, cement was mixed into the surface material to harden it. Erosive forces and possibly vehicles are continuing to deteriorate this hardened surface which slowly crumbles into the mitre drain.

Managers must take note that none of the monitored worked sites produced metamorphs in the year when works were undertaken.

4.3 How important are track breeding sites to *P. australis* and *H. australiacus*?

Do track sites constitute a significant proportion of available breeding habitat in the landscape? It is not clear what proportion of all *Pseudophryne australis* and *Heleioporus australiacus* breeding sites are located in the track environment because of sampling bias associated with site access. The majority of track sites have most likely been recorded, whereas the accuracy of an estimate of the number of all sites away from tracks is very unlikely to be evaluated within the near future. What can be said however is that tracks, due to their continuity and linearity, can dissect a large number of adjacent drainage lines. This can be observed in many situations (including the study area) where maintenance tracks follow contours below the ridge top. In such situations (in elevated locations where slopes are gentle), tracks come in contact with every potential breeding site on hill sides, which may add up to a series of considerable and continuous areas of potential impact in certain regions. At this stage of knowledge, the precautionary principle should be applied and the impacts of track works taken into consideration.

A track site may be an ecological trap (*sensu* Donovan & Thompson, 2001). Alternatively, track sites may boost the number of breeding sites where breeding sites are limited. Which of these predominantly applies certainly needs further investigation.

4.4 Limitations

Considerable effort was put into this sampling program (24 full days, 600 km walked). Undoubtedly it could have been improved by increasing the sampling frequency and geographic area covered in order to record more changes to the states of breeding pools. The state of pools can change very rapidly as was observed in the field when a pool was completely filled 30 minutes after it had been recorded as being dry. Automated sampling would be necessary to record each change. Unrecorded interruptions to the hydroperiods in *P. australis* breeding sites may have contributed to the lack of observed tadpoles in those locations. Sampling frequency was well suited to the much longer and less variable larval periods of *H. australiacus* and ensured reliability of field observations on metamorphosis.

The larval periods of *P. australis* used (Thumm & Mahony, 2006) are considered representative. The data were obtained from captive tadpoles derived from field collected eggs from throughout the sampling area. Thumm & Mahony's experiment started at about the same time of the year that this sampling program commenced. This experiment also coincided with the period when pool duration was most stable (see Figure 24). The experiment took place outdoors in the south of my study area. Thumm & Mahony's water temperatures would therefore have been similar to the ones reported here for that period. In view of the observation that under constant temperature conditions at 18°C, *P. australis* metamorphs were reported to leave the water as early as 28 days after hatching (Jacobson, 1963b), my use of Thumm & Mahony's data is realistic for over-wintering tadpoles and perhaps conservative when applied to the warmer months.

The study period overlapped with drought conditions (Bureau of Meteorology, 2005b). It is expected that hydroperiods of individual sites would increase with increasing rainfall amounts and regularity. It remains unknown how such climatic conditions would translate into differences, if any, in the reproductive successes of track and non-track sites.

Sites were visited in the same order on sampling days. As a result, some sites sampled early in the day regularly recorded lower temperatures than those sampled in the afternoon. The design incorporated this variation by making sure that the sampling sequence approximately alternated between track and non-track sites for both species.

4.5 Recommendations

Given the legal status of both frog species and the conflicting situation between frog presence in track sites and the necessity for regular maintenance works there, recommendations are needed to reduce the impact of track management on frog populations. Mitigation strategies need to be adequately based on the species' ecology or life-history requirements. Particularly the early life-history of both frogs can be put at an increased risk in the track environment. This study demonstrated that track works carried out at sites containing tadpoles of *P. australis* or *H. australiacus* relate to reproductive failure of these sites.

Ideally, tracks, including their drainage systems, should be constructed in such a way that they and their run-off do not impact on existing breeding sites during and after construction. The ideal drainage system will not allow water to pool and therefore will not offer artificial breeding habitat. As a result there is no change in the number of breeding sites or their qualities. Practicalities however impose changes on such an ideal situation.

At the moment, these frogs are known to breed in numerous track sites which are recorded in the *Atlas of NSW Wildlife*. Data presented above strongly suggest that this database is not always utilised to identify sites where impending track works potentially impact the frogs. Time should be allocated to identify and mark known and potential breeding sites in order to eliminate accidental impacts and to reduce the impacts of necessary works. Accidental impacts include vehicle movements through the site while works are in progress nearby, and the temporary or permanent placement of road material stock piles. Unlike the track works example in the Nature Reserve given above for *P. australis*, maintenance works should be timed so that they do not coincide with breeding activity of the species. *P. australis* breed throughout the year after rain (Harrison, 1922; Thumm & Mahony, 2002b), which makes it impossible to find an off-season. A reduction in the impact should be expected if track works there were undertaken sufficient time after the last substantial rainfall event, to allow the ground to dry out and adults to move to more suitable shelters. If works at *H. australiacus* breeding sites were restricted to January and February, impacts on the larval stage of this species would be mitigated because the majority of tadpoles have metamorphosed and new eggs have not been laid by then.

A seemingly successful solution to the problem of threatened frog presence in the track environment is a dug-out table drain that runs parallel to the track in bushland on the high track side. This intercepts seepage and surface run-off from the hill above and channels the water to a permanent culvert under the track, effectively removing water before it enters the track environment. These table drains may be two to three meters from the edge of the track where they are not driven through or constantly trampled by walkers. Once revegetated naturally, these table drains are stable and maintenance free. Examples of such table drains can be found in many reserves including Royal, Ku-ring-gai, Brisbane Water and Bouddi National Parks where they are utilised as breeding habitat by one or both frogs.

The major advantage of this system is that the artificial habitat is placed away from the direct impacts of vehicular movements and maintenance works. It also offers accessible shelter to animals that exploit pools which may form on the track itself. This system reduces track run-off and a potential reduction in erosion lowers maintenance needs. The system could also be used advantageously during hazard reduction burning to minimise potential threats to vulnerable track-side plants and animals. The main disadvantages are the initially high costs to install the system. These however would be offset by likely savings in ongoing maintenance costs. Topography, soil type or potentially negative impacts on the hydrology may rule out the construction of the table drains in some areas.

The use of blue metal or crushed building rubble as road material should be avoided in the sandstone areas until their impacts on egg masses and tadpoles are better understood. Local materials should be used for track construction (Morse McVey & Associates, 1993), and Recsei (1996) and Thumm (1996) have advised in their papers against the use of blue metal because of its potential to alter soil acidity. Buchanan (1996) recorded pH increases in naturally acidic soils, such as those found on sandstone, near areas that are covered in blue metal.

The presence of *H. australiacus* and the recorded breeding activity (and repeated failure) at site H2 warrant investigation into a more permanent engineering solution of this creek crossing. There are likely to be similar situations in other areas. Placement of a culvert under the track would be a sensible approach in this case and would also make the mitre drain redundant. At present, this drain offers egg-laying opportunities, but no opportunity for tadpoles to reach metamorphosis. This drain is not essential to the species' persistence because there are at least four natural pools available as breeding habitat nearby in the same creek line.

Activities to reduce the number of illegal vehicles entering the park are also strongly encouraged because of their potential to directly impact on the species and their habitat, and the damage they cause to unsealed tracks. Areas of concentrated vehicular movement have been identified to pose a very high erosion hazard (Morse McVey & Associates, 1993).

Chapter 6

HELEIOPORUS AUSTRALIACUS MOVEMENT AND HABITAT USE IN THE TRACK ENVIRONMENT

Abstract

The vulnerable *Heleioporus australiacus* is a burrowing species that frequently associates with tracks. Five individuals known to utilise track habitat were tracked weekly for up to three months using radio-telemetry to primarily investigate whether this frog burrows in the track environment. One animal burrowed in the soft mud at the track edge once and twice separately at the outer edge of a table drain. None of the other animals sheltered within the existing track system, but two individuals exclusively burrowed in previously disturbed areas (an old disused track and an old quarry). Cumulatively, 30 burrowing locations were recorded. Ten of these were within 3 m of the track edge, and 15 within 10 m. Weekly distances moved between burrows ranged up to 80 m, with movements in the 41 to 50 m range class occurring most frequently. The home ranges of two individuals were estimated as minimum convex polygons of 1480 m^2 and 2210 m^2. Burrowing depths of 5 to 15 cm and the potential of individuals to be located near the track places them at risk of being dug up and possibly injured during track maintenance works. A number of recommendations are made designed to minimise potential negative impacts of such operations on population persistence.

1 Introduction

The habitat of *Heleioporus australiacus* is often traversed by tracks, on which individuals may sit or forage (Gillespie, 1990; Hoser, 2002; Recsei, 1996). The presence of tracks in *H. australiacus* habitat may offer advantages to this species. For example, it is possible that the open space facilitates foraging and plays a role in thermo-regulation. The track drainage system may offer breeding habitat (Chapter 5). The species' use of tracks has a well recorded disadvantage: individuals have been found run over by vehicles (Mahony, 1994; Recsei, 1996). Other potentially negative impacts remain the subject of speculation. One of the questions frequently asked is whether individuals of this species burrow within the track environment where they may be impacted by maintenance works.

The substrate on the edges of unsealed tracks is frequently loose sand or soft mud. A number of factors presumably contribute to this situation. Track edges are rarely as well compacted as the track itself during construction and maintenance work and re-working of the track surface with a grader also often results in the build-up of loose material along the track edge. Traffic continuously compacts the track as it is being used (Trombulak & Frissell, 2000) while simultaneously working loose surface material toward the edges. Run-off water may also deposit loose material there.

Similarly, the drainage system of tracks, particularly mitre and table drains, contain large areas of soft substrate. These drains accumulate considerable amounts of silt over time. Furthermore, the soil in such infrastructure is rarely compacted during construction and maintenance.

H. australiacus burrow vertically into the soil to shelter for the day and for prolonged dry periods. First the hind legs are pushed into the top of the soil with short back and forward movements and once a foothold is gained, the hind legs keep working the soil while the animal slowly rotates into the cavity thus created. It took one animal half a turn to completely bury itself in soft soil up to the top of the head with only the eyes still visible (A. Stauber, pers. obs. May 2004). It is expected that soft mud facilitates burrowing, and that *H. australiacus* may utilise track edges and drains for sheltering. As an added potential attraction, track edges and drains also frequently support higher soil moisture levels, because rainwater run-off is diverted there (Bennett, 1991; Megahan, 1976; Trombulak & Frissell, 2000). Should *H. australiacus* indeed shelter in the track or associated drainage system, individuals run the risk of being dug up and injured during routine track maintenance operations. Such a risk would need to be addressed in impact assessments required under the *NSW Threatened Species Conservation Act 1995.*

Based on previous observations, I hypothesised that at least some individuals occasionally burrow in the track environment. Five adult *Heleioporus australiacus* were equipped internally with radio transmitters in late spring 2003 and were tracked weekly for up to 14 weeks in their natural habitat. The main aim was to establish whether any burrow locations, and hence sheltering positions, are associated with tracks or the track drainage system. This study also provided an insight into the micro-habitat of burrowing locations and home range size. Such values have never been reported previously for this species and add considerably to our understanding of the basic biology of this frog and its spatial requirements.

This chapter reports observations on dispersal behaviour with respect to tracks by this frog. These observations build on our current knowledge of the species and are undoubtedly of great interest to ecologists and managers alike. A number of recommendations have been made to minimise potential negative impacts of track maintenance operations on population persistence.

2 Materials and methods

Radio-tracking work was carried out along Thommo's Loop (340000m E; 6294000m N), a track in Brisbane Water National Park near Woy Woy, NSW. The Thommo's Loop transect was intensively studied (see Chapter 4). The area was chosen because the track drainage system included a large number of both culverts and mitre drains.

Five adult *H. australiacus* were captured by hand during spot-lighting walks between 20/10/2003 and 31/10/03 (5 sessions). These were the first five animals encountered on the track during the stated period and included 2 males and 3 females (Table 33). The sample was therefore made up of animals that showed an association with the track. Two of the animals had been previously marked and recaptured several times (Table 33) and previous locality data were available for these.

The animals were taken to the University of Newcastle on 3/11/03 for surgical implantation of single-stage radio transmitters (Sirtrack, New Zealand). Each frog was anaesthetised by placing it in 2 cm of 0.4% MS222 solution (3-ethyl-m-aminobenzoate, buffered with Na_4PO), until the frog stopped responding to gentle pressure above the eye. The transmitter was inserted into the abdominal cavity through a single 15 – 20 mm incision on the lower left side, which was then closed with three sutures. Following surgery, the animals were placed under running water until they had recovered from the anaesthetic. Animals were kept under observation for another five days in individual cooler boxes containing 10 cm of moist sand, before being released at their exact location of capture on the night of 8/11/03 following a rain event. On that night, three other adult *H. australiacus* were encountered on the track which suggests that climatic conditions were suitable for the release of the transmitter-equipped frogs.

Each transmitter unit was powered by an E386 battery with an expected life of 4.5 months at 40 pulses per minute. The whole unit including the wrap-around aerial was supplied encased in polymer and weighed 3.8 g, well below the maximum recommended 10% of animal body weight (Kenward, 1987; Richards *et al.*, 1994; White & Garrott, 1990).

Animals were located using a Regal 2000 receiver with a 3-element yagi-style and a loop antenna (Titley Electronics, Australia). Burrow locations were marked and labelled with flagging tape. Maps were produced based on the following field measurements: distance from previous burrow and distance from the closest track edge measured to the nearest half metre with a tape measure; and bearing from previous burrow to nearest 10 degrees with a hand-held magnetic compass. Animals were generally not dug up in order to minimise disturbance, which might have affected their behaviour. However, burrowing depth was occasionally checked by careful removal of soil by hand until the back of the animal was felt. The distance between the top of the animal and the substrate surface was measured with a tape measure to the nearest cm before replacing the soil. Habitat descriptions follow the methodologies outlined in Chapter 2.

Table 33 *Heleioporus australiacus* identification numbers, gender, recapture histories (number of times previously captured) and AMG positions (m) of the locations of their capture and release prior to commencement of the radio-tracking study.

Animal ID	Gender	Recapture history	AMG Easting	AMG Northing
#43	Female	6	339120	6293950
#62	Male	4	339880	6294230
#160	Male	0	340590	6294530
#161	Female	0	340480	6294480
#162	Female	0	340000	6293630

All animals were located 3 days after their release and again 4 days later on the 14/11/03. After that, sampling was undertaken at weekly intervals. On two occasions, that interval was a fortnight. Data obtained prior to 14/11/03 are shown on the maps (Results). However these data were not included in the analyses to prevent possible influences to movement by the temporary removal of animals from their home ranges. The frogs were given one week to orient themselves, and their movement patterns were assumed to be normal after that time.

Animals were removed from the field three months later on the 7/2/04, with approximately 20% of expected transmitter battery life remaining in accordance with NPWS licensing conditions. One animal was found by chance on the 5/4/04 although its transmitter had failed. Transmitters were removed surgically under anaesthetic as outlined above. Animals were returned on the 7/3/04 and the 16/5/04 to their location of capture after a brief period in captivity during which their health was monitored.

Minimum convex polygon areas (White & Garrott, 1990) were calculated to estimate the home range of individuals during the study period based on sheltering locations. Burrow locations were mapped at a scale of 1 : 500. The outer locations were connected to form a convex polygon. The area within was calculated by summing the areas of the minimum number of individual triangles contained within the polygon.

Means (± 1 SE), modes, minima and maxima were calculated for distances between consecutive burrows (displacements) and distances of burrows from track structures. Weekly rainfall amounts were measured at nearby Umina (6.5 km from study area) using a standard rain gauge.

3 Results

3.1 Distances between burrows and movement patterns

Maps showing the point of release, burrow locations, direction of movement, and the location of track and other features are given for each tracked frog in Figures 31 – 37. Animal #43 was detected in two closely spaced burrows within a cleared area adjacent to the track (Figure 31), before radio contact was lost. The burrows of individual #62 (Figure 32, Figure 33) were all within the area where the animal had been previously caught. This frog revisited two burrows (A, C) several times and occasionally sheltered in the track edge (B, C). The habitat occupied included a track and a creek. Frog #160 moved away from the track, following a drainage line into a swampy creek (Figure 34). Animal #161 (Figure 35) sheltered exclusively (3 burrows) within an old, disused track, before it was taken by a predator. Female #162 occupied a home range within about 20 m of a creek (Figure 36,

Figure 37). Burrows were located on both sides of the track. Two of these (C, F) were associated with the track edge and the edge of a drain. Burrows A and D were utilised more than once.

Summary statistics of weekly distance displacements of each animal are shown in Table 34. The maximum distance recorded was 80 m. Home ranges were calculated only for those animals that were recovered alive at the end of the study period (#62, #162). The only remaining animal that provided data on more than 2 burrowing locations (#160, Table 36) moved in a linear fashion (Figure 34) and was thus excluded from home range calculation. Weekly displacements are also shown in relation to sampling period for two animals (Figure 33 and Figure 37). Male #62 sheltered the longest in burrow A which it had visited several times during the study period (Figure 32). Female #162 (Figure 36, Figure 37) had relocated in each sampling interval, except the last, regularly revisiting the same areas, but not necessarily using the same burrows. Net displacements between burrows by this individual occurred in a clockwise fashion.

Collectively, weekly net displacements of zero metres were recorded eight times (i.e., individuals were in the same burrow where they were last recorded). Weekly distance displacements in the 41 - 50 m class occurred most frequently (Figure 38).

Table 34 Summary statistics of weekly* distance displacements and estimated home range size^ (minimum convex polygon method) of five radio-tracked *Heleioporus australiacus*, based on burrow locations (* on two occasions the interval was two weeks; ^ not all animals provided enough data points to warrant home range size estimates). n = number of sampling sessions.

Animal ID (n)	**Mean (±SE) (m)**	**Mode (m)**	**Range (m)**	**Home Range (m^2)**
#43 (1)	1.5	1.5	-	-
#62 (11)	32 (9.1)	0	0-80	2210
#160 (4)	16 (12.4)	0	0-52	Not calculated
#161 (1)	33	33	-	-
#162 (11)	35 (5.3)	43	0-55	1480

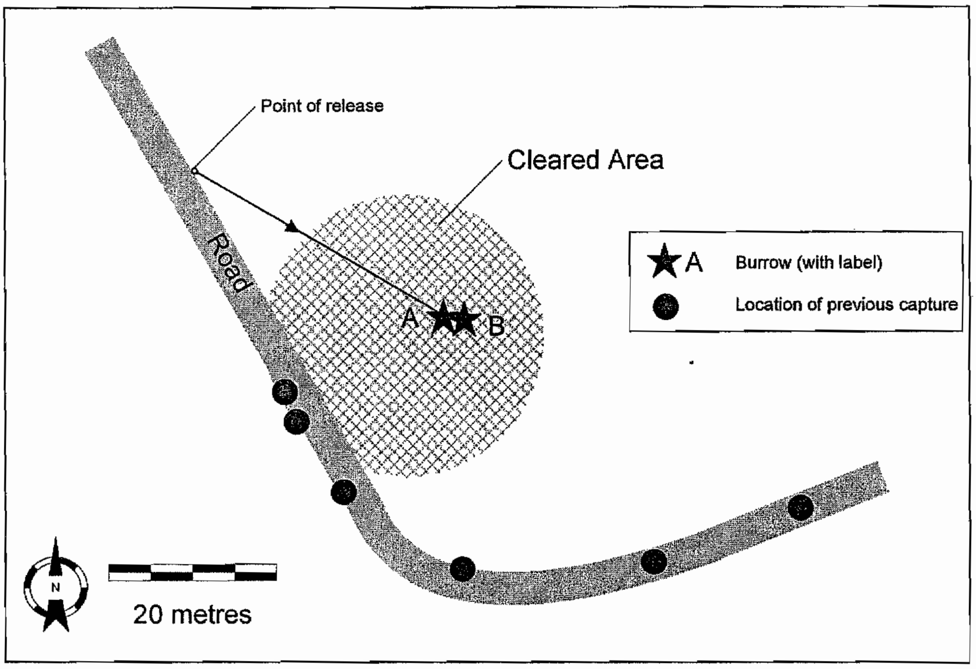

Figure 31 Burrow locations in relation to the point of release and habitat features of radio-tracked *H. australiacus* #43. The line and arrow indicate movement and direction.

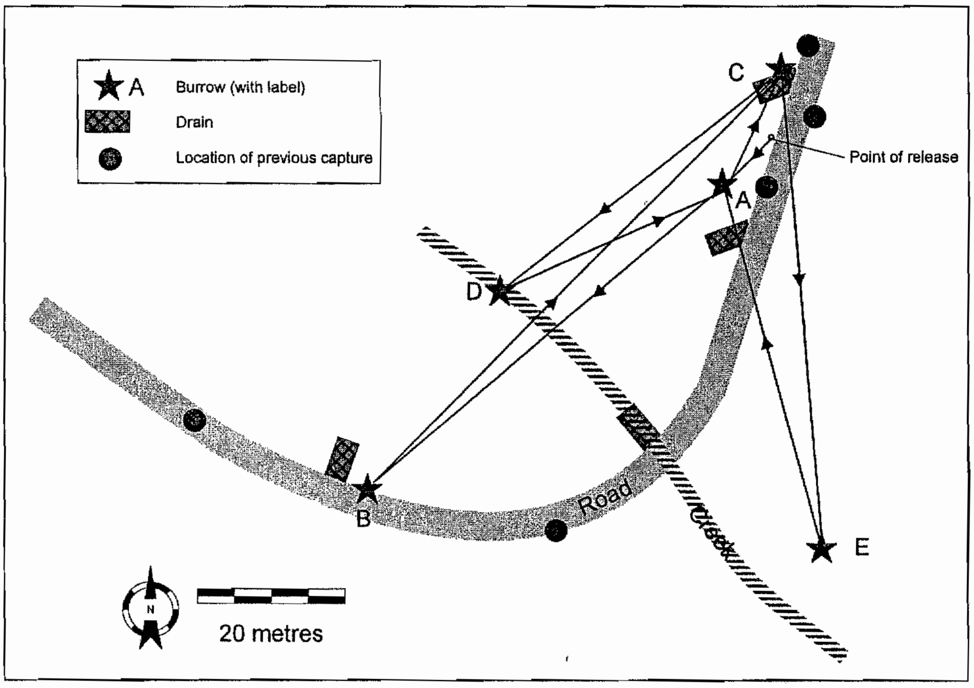

Figure 32 Burrow locations in relation to the point of release and habitat features of radio-tracked *H. australiacus* #62. The lines and arrows indicate movement and direction.

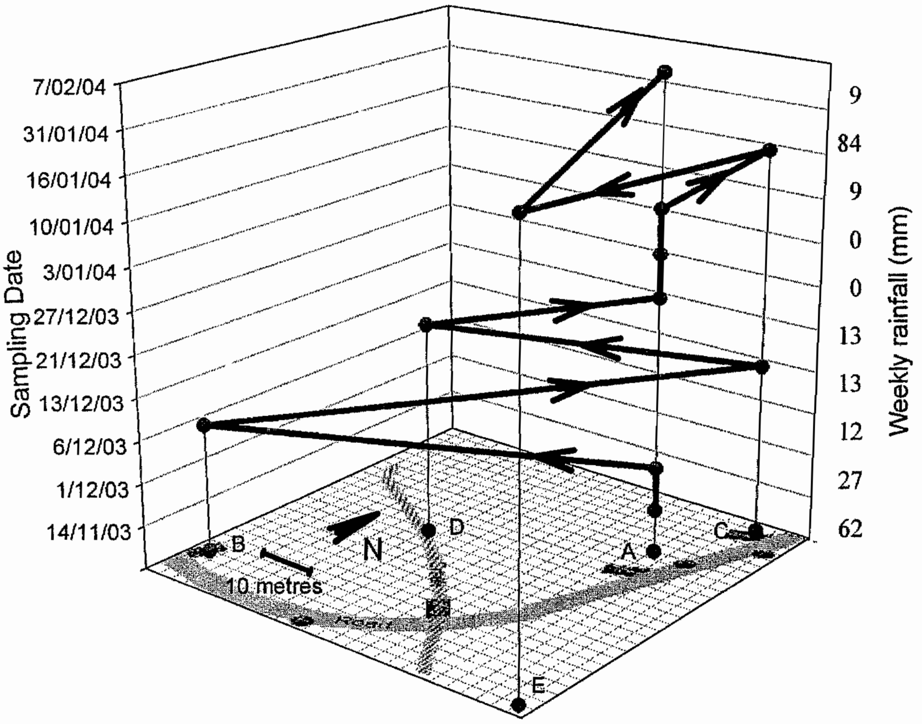

Figure 33 Three dimensional plot of weekly displacements and direction of movement based on the burrow locations of *H. australiacus* #62. Rainfall amounts are also shown.

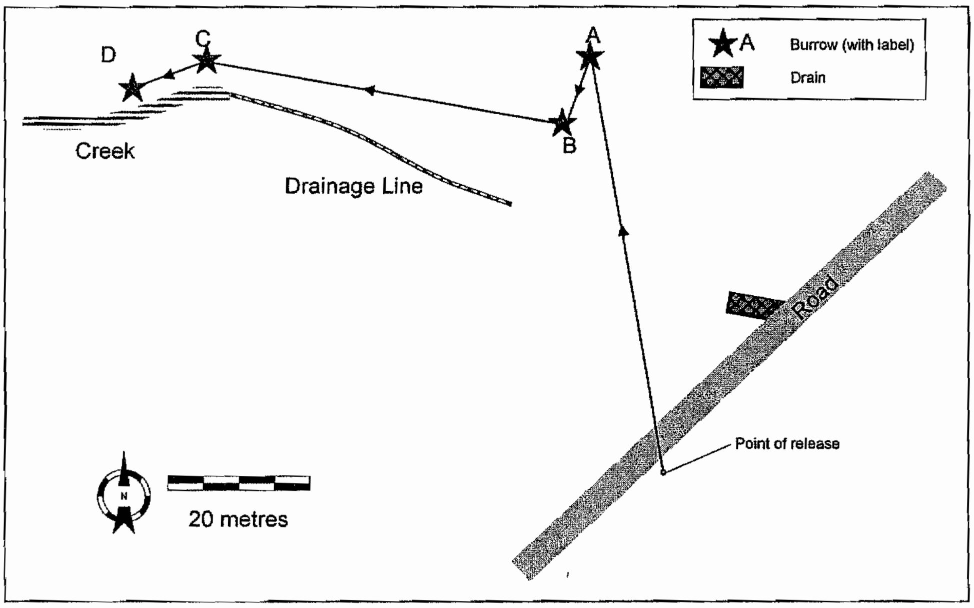

Figure 34 Burrow locations in relation to the point of release and habitat features of radio-tracked *H. australiacus* #160. The lines and arrows indicate movement and direction.

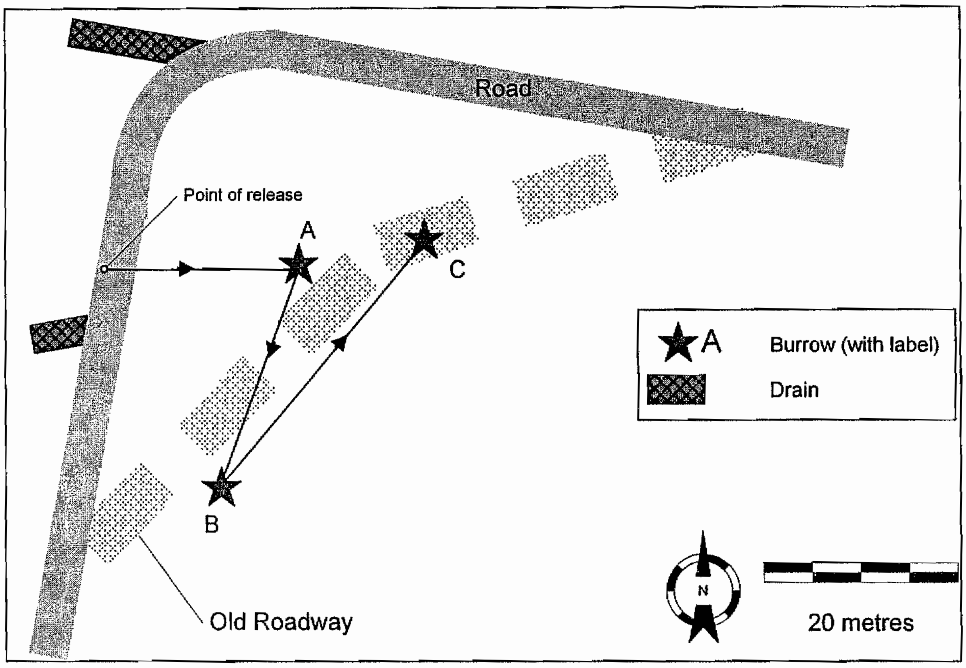

Figure 35 Burrow locations in relation to the point of release and habitat features of radio-tracked *H. australiacus* #161. The lines and arrows indicate movement and direction.

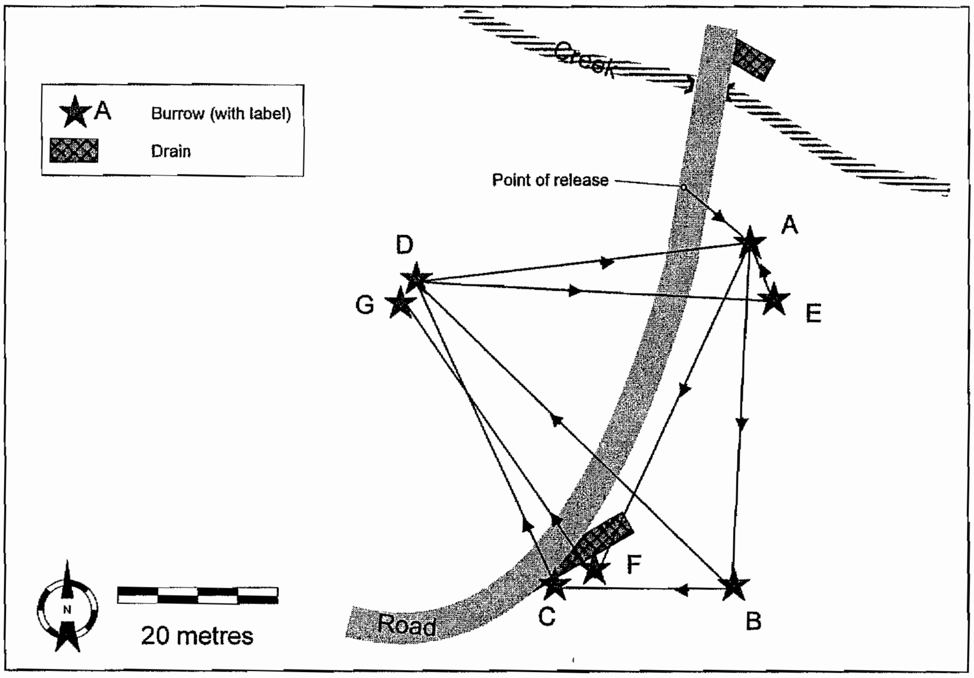

Figure 36 Burrow locations in relation to the point of release and habitat features of radio-tracked *H. australiacus* #162. The lines and arrows indicate movement and direction.

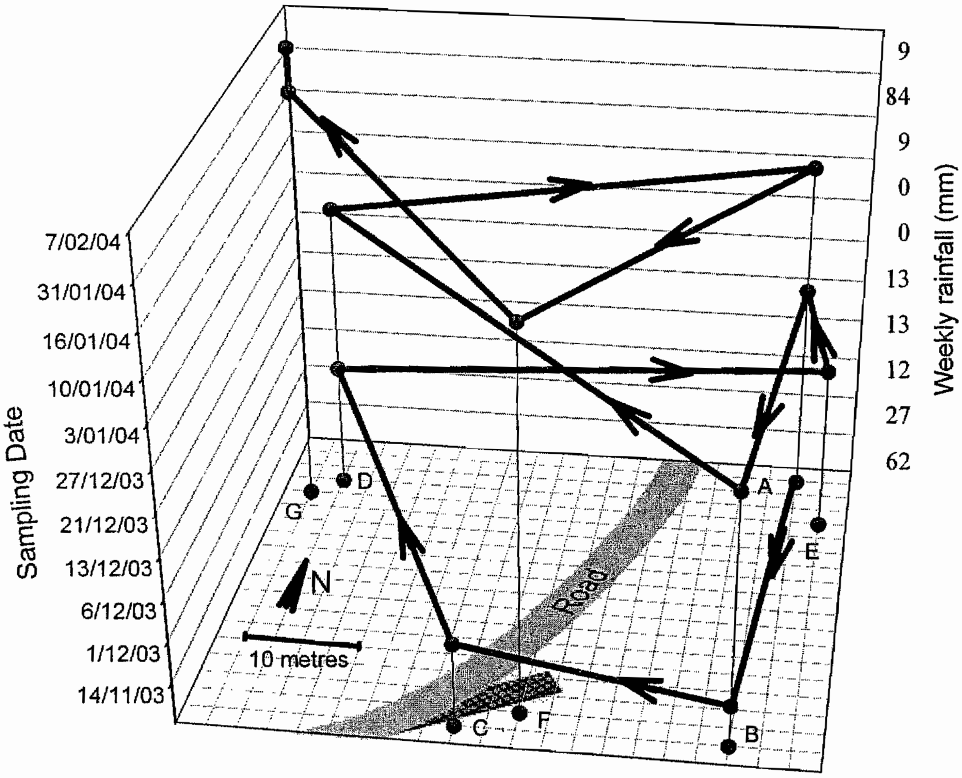

Figure 37 Three dimensional plot of weekly displacements and direction of movement based on the burrow locations of *H. australiacus* #162. Rainfall amounts are also shown.

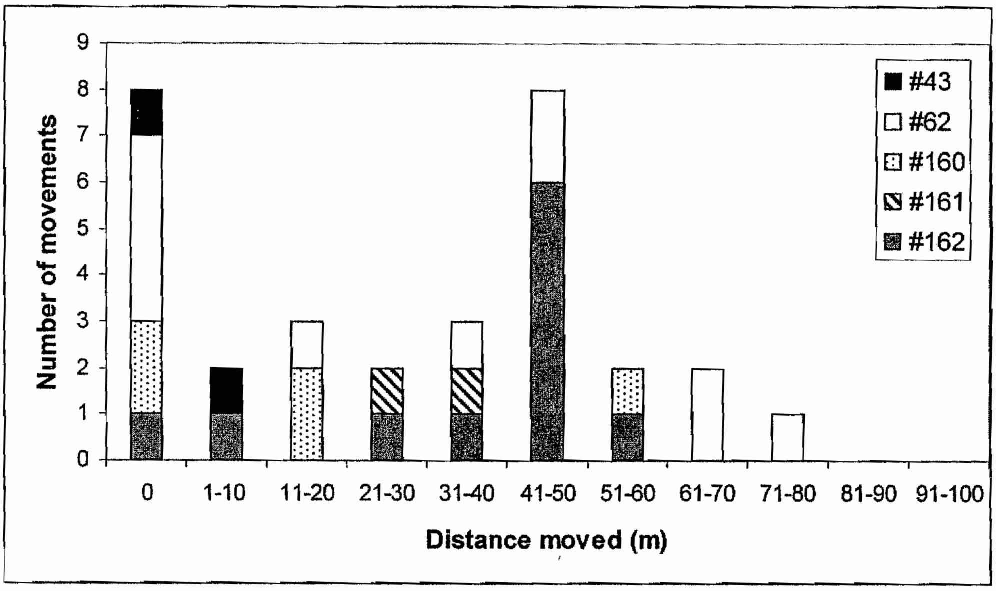

Figure 38 Frequency distribution of weekly displacements based on burrowing locations for each of five radio-tracked *H. australiacus*.

3.2 Distance of burrows from track structures (including drains)

The burrows (n = 20) of the five radio tracked animals ranged in distance from tracks or artificial drains along track sides from 0 to 91 metres (Table 12), with a median distance of

14 m (mean±SE = 18.5±4.7 m). Animal #62 was detected burrowed in the soft mud at the very edge of the track once (burrow B) and in a similar situation on the outer edge of a table drain twice non-consecutively (burrow C). None of the other animals burrowed within the existing track system or associated drainage. However, animal #161 sheltered exclusively within an old and disused, lightly revegetated, now by-passed section of track (2 burrows); and #43 burrowed exclusively within a previously cleared and disturbed area, which was probably used for the supply of road fill (1 burrow).

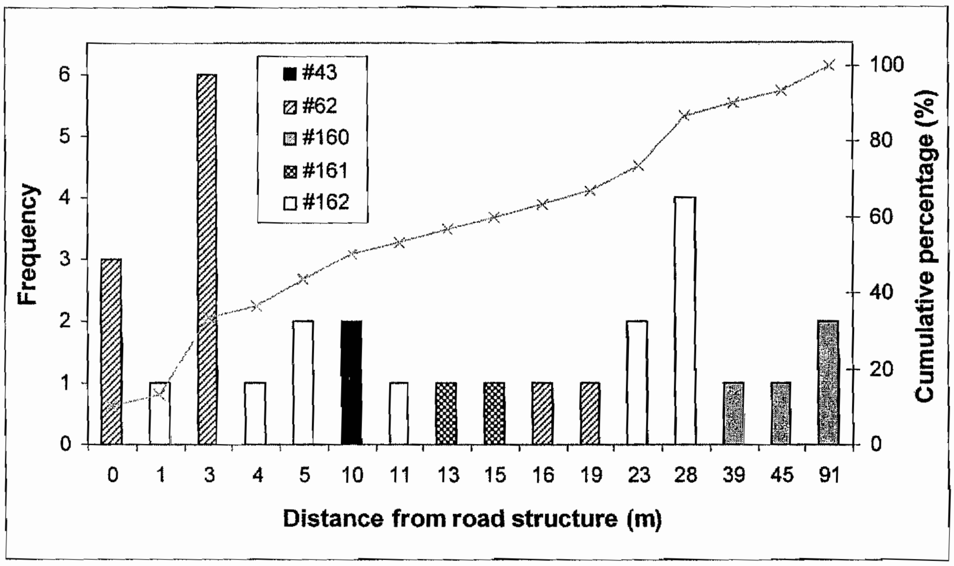

Figure 39 Frequency of burrowing locations of 5 individual radio-tracked *H. australiacus* as a function of their proximity to tracks or artificial track drains. The x-axis is not on a linear scale.

3.3 Number of times burrows were used

Some animals revisited burrows after sheltering elsewhere. Male #62 used burrow A three times, sometimes staying for prolonged periods, particularly during a two-week interval when no rain fell (Figure 33). Burrow C was visited twice by this animal (Figure 32, Figure 33). Female #162 utilised each of two burrows (B, D) twice (Figure 36, Figure 37). Location A was visited 3 times, but different burrows all within 1 m^2 were used each time. The 7 burrows utilised by this female can be grouped into four areas regularly visited: A+E, B, C+F and D+G. This female recorded weekly movements regardless of whether rain fell or not (Figure (37).

Figure 39 illustrates the frequency of burrows used in relation to the distance from track structures. Animal #62 was detected to shelter 82% of sampling time within 3 m from the track. Cumulatively, 30 burrowing locations were recorded. Ten of these were within 3 m from the track edge, and 15 (50%) within 10 m.

3.4 Micro-habitat descriptions of burrow locations

Micro-habitat descriptions are detailed in Chapter 2. Three burrowing locations were associated with crayfish tunnels, one was in sand under leaf litter, and the remaining locations (80%) were in bare sand (Table 12). Even these unconcealed burrows were difficult to see because the burrow was always filled flush with the ground surface.

Burrowing depth during this generally dry and warm period ranged from 5 to 15 cm.

Table 35 Surface substrate, depth and distance from track structure of individual *H. australiacus* burrows, including those occupied immediately prior to the study period. Burrow identifications are preceded by the animal identification number.

Burrow ID	**Substrate / Cover**	**Depth (cm)**	**Distance from track structure (m)**
#43-A	Bare sand	-	9
#43-B	Bare sand	8	10
#62-A	Bare sand	9-15	3
#62-B	Track edge, soft clayey sand		0
#62-C	Outer edge of table drain, soft clayey sand		0
#62-D	Cray burrows, sparse sedge cover		19
#62-E	Bare sand in elevated position on cliff shelf		16
#160-A	Bare sand	5	45
#160-B	Bare sand		39
#160-C	Network of cray burrows near creek line		91
#161-A	Sand, old track		15
#161-B	Sand, old track		15
#161-C	Sand, old track		13
#162-A	Bare sand, next to burnt branch		5.5
#162-B	Cray burrows	10	23
#162-C	Bare sand in burnt heath thicket		0.5
#162-D	Bare sand, under burnt branch		28
#162-E	Soft bare sand next to active ant nest		11
#162-F	Bare sand in burnt heath thicket		4.5
#162-G	Sand under leaf litter	10	28

3.5 Fate of individuals

The radio-tracking study period included 11 sampling sessions. However, only two animals were recovered alive at the end of the study. A third animal was recovered by chance well after completion of the study (see below). For the other two only the transmitters were located. Table 36 details the fate of each individual, the number of times it was located, and the number of burrows each was observed to use.

For four months animal #43 was not detected. Considerable search effort (three hours on each of two separate occasions) was put into trying to relocate the individual without success. However, two months after completion of the study, the animal was recaptured by chance during routine transect work. It appeared to be in good health and was temporarily held for the removal of the failed transmitter.

The final location of the transmitter of animal #160 was recorded in an extensive network of crayfish burrows amongst clumps of *Ghania* sp. next to a creek. The animal was never observed burrowed there but was assumed to be within the tunnel system, or buried under the dense vegetation. A thorough search for this individual involving digging up the burrow system was conducted at the end of the study period. The transmitter was eventually recovered without any trace of the animal. The frog may have perished and decomposed there. Alternatively, a predator may have removed it from its previous location and deposited the transmitter where it was eventually found. Apart from inclusion on the map, the last burrow was excluded from all analyses because the presence of the live animal at that site could not be confirmed.

The transmitter of animal #161 was recovered on the ground 1.2 m from an excavated burrow. There were no traces of the frog. Previous rain had erased tracks and altered the excavation. Fox tracks were regularly seen in the area, even after the completion of a baiting program conducted by NPWS in September 03. It is possible that the frog had fallen prey to a fox.

Table 36 Summary of tracking success for *Heleioporus australiacus*. The number of times individuals were located out of 11 sampling sessions and the number of burrows utilised are given for each animal. The fate of individuals shows that only two animals were recovered alive at the end of the study period, and a third much later.

Animal ID	Number of times located	Tracking period (days)	Number of burrows utilised	Fate
#43	2	17	1	No signal detected after session 2, previous burrow vacant. Recovered alive 5/4/04 by chance with failed transmitter.
#62	11	85	5	Recovered alive 7/2/04.
#160	5 (11)	≥ 37	4	Animal never observed at burrow where last signal was detected. Signal detected each session. Transmitter recovered 7/2/04.
#161	2	17	2	Transmitter recovered 1/12/03, 1.2 m from an excavated burrow.
#162	11	85	7	Recovered alive 7/2/04.

4 Discussion

4.1 *Heleioporus australiacus* and the track habitat

Tracks featured strongly in the habitat of at least two of the tracked animals. One male's burrows were mostly located near the track which suggests that the track served as a corridor for movement. Frequent observations of this particular animal on the track while active (Chapter 4) support this suggestion. A female regularly sheltered on both sides of the track. The home range of that animal was dissected by the track.

Not only do *H. australiacus* individuals shelter within the track or associated drainage system, others use other previously disturbed areas. One of the five animals relocated and burrowed into the soft substrate at the track and drain edges three times out of eight recorded moves. One of these burrows was visited more than once. At least for a short time, two other animals exclusively sheltered within a disused track and a disused quarry. Another frog never burrowed within the track system, but regularly sheltered in two areas near the track and a drain, and utilised habitat on both sides of the track. Only one of the five tracked animals never associated with any track structure apart from its original location of capture.

In addition to the frogs observed during the radio-tracking study, a male (#106) was observed sheltering in the top of an 80 cm high mound of road spoil (loamy sand) that was deposited in bushland about a metre from the track edge some years earlier. This animal was observed on the mound next to its burrow (50-55 mm diameter, 80 mm deep) during routine transect work. Seven days later, the burrow was found filled in and the frog was found buried 14 cm below the surface. On another occasion, a female (#72) was observed in the centre of a table drain on top of a burrow of similar size as the one mentioned above. The back of this frog was still covered in sand. While this frog was never observed in the burrow, it appears likely that the drain was utilised for shelter. A third animal, female #60 was observed as she emerged from a burrow 30 cm from the track edge.

4.2 Distance of burrows from the track

One study animal sheltered for a disproportionately high amount of time (82%) within 3 m of the track, including two burrows in the track. The burrow it used most regularly falls into that zone. This animal showed no temporal shift in burrowing locations away from the track. Another individual spent 36% of sheltering time in burrows within 5 m from the track. Its closest burrow was 0.5 m from the track edge.

While some frogs sheltered at least 10 m from maintained track structures, others are at risk of getting injured during track works. The consequences such an impact may have on population persistence are unknown. The use by *H. australiacus* of previously disturbed areas as sheltering locations may also pose a risk to individuals if these areas are again made operational as quarries, turning bays or track by-passes.

4.3 Movement patterns and home range

The observed mean weekly displacements of the study animals are similar to those recorded for *H. australiacus* at Olney SF and Yambulla SF (Lemckert & Brassil, 2003). Such measures have to be assumed to be underestimates of unknown magnitude of the actual distances moved because they do not record deviations to a straight-line movement between both burrows, nor do they consider activity patterns for the week. The number of nights on which the individual was active, the number of areas visited during the week, the frequency of visits and the geometry of displacements all influence actual distances moved. It is therefore unknown just how far individuals really moved between their burrowing locations.

Home range estimates for *H. australiacus* have not previously been reported. The 2210 m^2 minimum convex polygon estimate for the male is possibly inflated because the animal moved in a star-like pattern, rather than following the perimeter of the calculated shape. The 1480 m^2 estimate based on burrow locations much more accurately describes the area regularly used by the female.

Clearly, the estimates only apply to the 14 week period covered by the study which coincided with late spring and summer, incidentally ending just at the onset of the breeding season. No generalisations can be made about the actual area used by an animal throughout its life, or whether there are seasonal shifts in home range sizes or locations (e.g., Matthews & Pope, 1999).

My tracking results in combination with mark and recapture data (Chapter 4) for two radio-tracked animals however demonstrate strong site fidelity (*sensu* White & Garrott, 1990) and show no signs of seasonal range shifts. In addition to the tracking period (Spring-Summer 03-04), these animals were present within their respective areas in Autumn 02, Spring 02, Summer 02-03, Autumn 03, Winter 03 and Autumn 04. There is strong agreement between these observations and the mapped ranges (Figure 31, Figure 32). This suggests that *H. australiacus* adults remain within their home ranges for years and possible absences would be of only short duration. Many frog species show site fidelity to at least some components of their habitats (see Sinsch, 1990 and references therein), but generally this is not for the length of time observed in *H. australiacus*.

It is quite clear, however, that adult animals of this species must move to a watercourse in order to breed. The female's calculated home range for instance did not include a suitable water course, and it would have to be assumed that she needs to move outside her home range in order to breed. Many other individuals (Chapter 4) were repeatedly observed considerable distances away from suitable breeding sites. All these would need to leave their home range, or would considerably increase their home range in order to breed. Home range size would presumably become a function of the distance from the closest breeding site.

I argue that an annual excursion or migration of *H. australiacus* to the breeding site, while undoubtedly of great importance, falls outside the normal activities based on the low frequency of occurrences and should not be included in home range estimates. Burt (1943) defined home range as the area used by an animal in its normal activities and Sinsch (1990) divided up the space utilised annually by individual toads, *Bufo* spp., into several home ranges based on the resources each provided, terming movements between migration. The complement of an individuals home ranges and migration paths was described as the activity area by Spieler (1998). Regardless of whether home ranges include breeding sites or not, it is important that conservation management includes the complete activity area utilised by populations.

Home range size for *H. australiacus* is comparable to that estimated for *Bufo bufo* (1901±312 m^2; Sinsch, 1987), but much larger than those estimated for *Atelopus oxyrhynchus* (56 m^2; Dole & Durant, 1974), *Atelopus varius* (3 m^2; Crump, 1986), two other *Bufo* spp. (*B. japonicus*: 220 m^2; Kusano *et al.*, 1995; *B. marinus*: 160 m^2; Zug & Zug, 1979), *Hoplobatrachus occipitalis* at the onset of the rainy season (142 m^2; Spieler & Linsenmair, 1998), and three ranids (*R. sylvatica*: 60 m^2; Bellis, 1962; *R. pipiens*: 400 m^2; Dole, 1965; *R. calamitans*: 60 m^2; Martof, 1953). The recorded home range for *Bufo americanus* (28 000m^2; Grubb, 1970) is much larger than that of *H. australiacus*.

4.4 The number of burrows used

All of the tracked animals used several burrows and some of these provided shelter on more than just one occasion. Why does *H. australiacus* not use a single ideally placed shelter and forage from this location? Such behaviour would allow it to return to a known, presumably safe, and partially prepared burrow. At this stage the reasons for multiple burrows remain unknown. *H. australiacus* may spend considerable time underground and the use of several burrows potentially reduces exposure to pathogens and parasites associated with the subterranean habitat. It is not clear if this behaviour has evolved as a way of avoiding predators. Home ranges can be increased if several sheltering locations are used, which should result in greater food availability, and an increased likelihood of finding a mate. Alternatively, the tracked frogs may still be looking for the ideal shelter.

4.5 Borrowing locations

During the study period, each animal exclusively sheltered buried in the soil and no observations were made of alternative shelters on the surface under logs or vegetation as was observed by Lemckert & Brassil (2003). Eight burrows were concealed by natural cover such as both live and dead vegetation, or logs. Twelve locations were in relatively open and bare ground. Individuals that were tracked to more than three burrows sheltered in both concealed and open locations, thus showing no preference for any particular habit. Even the unconcealed burrows were difficult to see because the burrow was always filled flush with the ground surface. Burrows were shallow (generally less than 15 cm deep) which may place individuals at risk of being dug up during track works. It appears that *H. australiacus* does not burrow as deep as other *Heleioporus* spp. do: *H. albopunctatus* was reported from depths of around 80 cm (Bentley *et al.*, 1958).

4.6 Limitations

The sample size of this study was reduced through presumed predation as well as transmitter failure. Logistical and ethical constraints also limited an expansion of the study. Tracking studies obviously can be revealing with their potential to provide information on the fate of individuals at times beyond their deaths. At least one of the study animals had fallen prey. *H. australiacus* are potential food to lace monitors *Varanus varius* and red-bellied black snakes *Pseudechis porphyriacus* (Towerton & Lemckert, 2001). Both predators were detected during the course of radio-tracking work in Yambulla SF because they had ingested transmitters that were earlier implanted in *H. australiacus* (Towerton & Lemckert, 2001) Both predators presumably swallowed their prey whole. I suspect that it is more likely that at least one of my study animals had fallen prey to a fox. Foxes chew their prey and are able to spit out a transmitter before swallowing the frog. Fox tracks were regularly observed in the area including at the time of the radio-tracking study, despite a recently completed baiting program. Foxes are also listed by the IUCN as "potentially a major threatening process" to the species (Lemckert *et al.*, 2001b). Spotted-tailed quolls *Dasyurus maculatus* are present in the area (A. Stauber, pers. obs.) but are less likely to have preyed on that animal (G. Körtner, pers. comm.).

5 Conclusions and Recommendations

Heleioporus australiacus occasionally shelter in structures that are part of unsealed tracks, including track edges and the drainage system. Individuals may also inhabit areas that had been previously disturbed and created through the construction or maintenance of such tracks. This species relies on its ability to burrow for shelter, and may utilise such unnatural sites because the soft substrate facilitates digging and perhaps for the relatively higher soil moisture content.

Generally, these frogs shelter within the top 15 cm of the soil. This potentially places them at an increased risk of being dug up and injured during track maintenance work. The impacts this might have on population persistence are unknown, but since many individuals have been found to associate with track habitat (Chapter 4), they could be threatened by track works even in the reserve system including national parks and nature reserves. Sound management of any threatened species should consider all potential threatening processes in order to improve the status of that taxon.

H. australiacus is a highly cryptic species and targeted surveys often fail to detect the frog even in areas where populations are known to exist (Chapter 4). In addition, burrowing locations cannot be predicted, and occupied burrows are virtually undetectable unless tracking devices are used. Pre-track work surveys therefore would only be of limited use in detecting the presence of the species, unless considerable effort is invested. Breeding sites can be identified by the presence of tadpoles during winter and spring, but these sites are often long distances from individual home ranges (Chapter 4). It is essential that the *Atlas of NSW Wildlife* is consulted to identify areas where the species potentially occurs.

The timing of the track works would be of little consequence. *H. australiacus* are nocturnal and leave their burrows only at night during periods of activity. At all other times they shelter in the soil. Track maintenance works are carried out in the day time and always have the potential to unearth and mutilate a buried frog.

A sound management approach embraces a reduction in the frequency of necessary maintenance work and suggests that tracks should not be topped up or even sealed with materials that are foreign to the site (blue metal, demolition waste, bitumen). Such materials are known to change chemical and physical properties of the soil and run off water (Buchanan, 1996; Trombulak & Frissell, 2000) and their use is discouraged in NSW (Morse McVey & Associates, 1993).

Some flood ways of the ephemeral watercourses in *H. australiacus* habitat may need to be replaced initially with permanent culverts to eliminate gully erosion of the track at these crossings and sedimentation of the waterway downstream. Maintenance of the track surface in combination with its linear nature facilitates the transport of suspended sediments, particularly because vegetation is absent. In addition, the compacted track surface has a comparatively lower infiltration rate which leads to increased sedimentation (Krause *et al.*, 2003). A more important issue however appears to be the erosion caused by traffic (Anderson, *et al.*, 1976; Coker *et al.*, 1993). Many tracks that dissect *H. australiacus* habitat in the reserve system experience frequent and regular illegal use by motorcycles and 4WD vehicles. Law enforcement may be a solution in this situation because the elimination of such vehicular movements would inevitably lead to a reduction in track damage (Morse McVey & Associates, 1993; see also Reid & Dunne, 1984), and hence a reduction in the frequency and severity of required maintenance work.

I recommend that continuously eroding causeways are replaced by culverts, and that active measures are undertaken to kerb illegal vehicular traffic.

Chapter 7

GENERAL DISCUSSION

In this study I investigated the habitat requirements and habitat use in two threatened frogs from the greater Sydney region, Australia: the red-crowned toadlet *Pseudophryne australis* and the giant burrowing frog *Heleioporus australiacus.* Both frogs have had declines reported in some populations (Gillespie & Hines, 1999; Mahony, 1996) and were identified by the Action Plan for Australian Frogs (Tyler, 1997) as frogs "that may be of [conservation] concern but which are poorly understood."

Urban expansion continues to encroach on the habitat of both frogs. Nevertheless, only limited information is available on the habitat requirements and habitat use of both species. This situation presents difficulties to managers charged with the conservation of these species. Furthermore, ecologists are interested in knowing how these frogs, and their habitat, are affected by encroaching urbanisation. Many ecological studies ignore the fact that human influences are present in the habitat of just about every species on Earth. This study does not. And even in the absence of urbanisation, wildlife biologists are keen to learn more about organisms and their interactions with others and their environment. As was shown in Chapter 1, there are large gaps in our knowledge of these two truly remarkable frogs despite them being the first two Myobatrachids that were ever described (Littlejohn *et al.*, 1993). Ecological research on species such as these not only serves us to better understand the organisms, but also to teach us what sets them apart from others.

Much of the work reported here deliberately focussed on the track environment. Tracks are utilised by both species and are also the interface of ongoing anthropogenic activity. Even in the Reserve System of national parks and other protected lands, frog meets machine quite frequently.

The habitat is arguably an organism's greatest asset. The information presented within this thesis was drawn from both animal locality records and from movement patterns of individuals in their habitats in the Sydney Basin Bioregion (NSW National Parks and Wildlife Service, 2003) with a view to making a valuable contribution to a better understanding of the ecology of two unusual frogs, and to improve their conservation management.

This discussion draws together the key findings of the work presented in the previous chapters into a general picture of the habitat of both frogs. The findings are synthesised at the level of the three general research questions (page 9; also restated with the next three section headings). Areas of future research are also highlighted and the recommendations identified in individual chapters that relate to the conservation management for both frogs are restated.

This is one of very few studies of Australian amphibians that address conservation at a landscape scale (but see Parris, 2001) and may well be the most detailed quantitative analysis to date of the habitat requirements of any Australian frog.

1 How are the habitats of *P. australis* and *H. australiacus* best described?

This question clearly relates to the frog's habitat requirements. The aim was to provide wildlife managers and ecologists with the information required to accurately model the distribution of both frogs. This will allow the identification of potential habitat where the species have not (yet) been observed, and will facilitate assessment of the overall impact of disturbances and habitat destruction on the species. The information can also be used in reserve design, habitat ranking, allows comparisons with the habitat requirements of other species, whether sympatric or allopatric, and is essential in understanding the complex nature of the spatial distribution of both related and unrelated organisms and their links to specific environments. I hypothesised that animal locations were not randomly distributed throughout the landscape within their ranges, but were linked to some specific, but then unknown, environmental attributes of these sites.

Within the Sydney Basin, the distribution of both *Pseudophryne australis* and *Heleioporus australiacus* is limited to specific habitats, that is, these species are not randomly distributed throughout the landscape within their ranges. I found that both frogs utilise very specific habitats and therefore label them as habitat specialists. Their habitats are best described as follows.

Both frogs are found in places where the climate is milder with reduced temperature variation and higher rainfall relative to other places within the Sydney Basin. Both species are restricted to Hawkesbury Sandstone in elevated parts of the topography, such as the upper slopes and mid slopes where gradients are gentle. Watercourses in their habitat are ephemeral, and breeding sites frequently dry out. *H. australiacus* are slightly less restricted topographically compared to *P. australis*. The consequence is that *H. australiacus* also access more permanent breeding habitat, an advantage in light of their relatively long larval period. There, the breeding habitat often supports crayfish. Crayfish burrows are utilised by *H. australiacus* for breeding and also provide temporary refuges to tadpoles in drying ponds. The elevated, well drained positions of animal locations with soils of poor water-holding capacities and the unpredictability of rainfall render this habitat as marginal habitat for most frogs in the region.

The habitat occupied by both *P. australis* and *H. australiacus* is unusual in that only one other frog, the wide-ranging *Crinia signifera*, is known to breed in the ephemeral water bodies found there. Each of the three frogs has its own reproductive adaptations that allow it to persist in its own way in this marginal environment away from permanent water courses. Other frogs found there, including *Litoria citropa, Lit. freycineti, Limnodynastes peronii, Lim. dumerelii,* and *Uperoleia* spp., are not confined to the ephemeral breeding sites in sandstone habitats of the Sydney Basin.

Both frogs are dependent on vegetation with a complex structure (as defined by growth form and crown separation of woody plants; Walker & Hopkins, 1998) and are absent from cleared land. Within native bushland with a well developed vegetation structure, *H. australiacus* at least, shows no preference among heath, woodland or forest. Furthermore, *P. australis* frequently associate with cliffs, whereas *H. australiacus* do not.

P. australis are heavily dependent on leaf litter, hollow logs, soil cavities under logs or rocks, rock crevices and holes and cracks in soil. These resources offer shelter, breeding and foraging sites where *P. australis* form small groups of very closely spaced individuals. It is likely that bush rock is also an important resource for sheltering, but was not identified as such possibly because the availability of such rocks may have become too scarce through their removal by collectors for use in suburban garden landscaping.

H. australiacus are capable of phenotypically responding to decreasing water levels by shortening their larval periods. This response is interpreted as an adaptation to its ephemeral habitat and allows them to move metamorphosis forward in deteriorating ponds. However, losses in the field can be high due to early pond drying, despite their ability to accelerate larval development. Hydroperiods of 33 weeks were recorded to be the minimum required for successful metamorphosis in the field. Crayfish burrows can offer important refuges to tadpoles during short episodes in dry ponds. The acceleration in larval development is at the expense of size at metamorphosis, which may affect fitness in terrestrial life. It was also shown that the larval periods of *H. australiacus* vary considerably under different sets of environmental conditions.

The modelling of potential habitat should not solely be based on GIS derived values but should include data collected in the field. For example the results indicate that modelled habitat based on slope could be quite different in location and area between GIS derived slopes and slopes measured in the field.

2 How do *P. australis* and *H. australiacus* use their habitats?

This question addresses habitat use. It also investigates associations with a set of habitat features. The aim was to provide wildlife managers and ecologists with information they need to decide on the spatial requirements of populations, and to provide additional information that helps with the identification of likely sites of animal presence in the field. This information also pertains to habitat connectivity and potential migration paths. Links to habitat attributes as well as the spatial arrangement at the intra-specific level are identified. Such information provides insights into interactions among individuals as well as links of individuals and populations to certain habitat features.

Around breeding areas, *Pseudophryne australis* form small groups of very closely spaced individuals. This clustering behaviour is strongly linked to resources necessary for breeding, and possibly sheltering and foraging, such as leaf litter piles. The strong link to leaf litter piles is further supported by the observations repeatedly made in drainage lines where water action and birds regularly rearranged and moved leaf litter piles: *P. australis* moved with these piles and resettled in relocated ones. Clearly, *P. australis* demonstrated resource selection (Johnson, 1980) for cover provided by leaf litter piles, logs, rocks and dense low vegetation. It is possible that such resources are limiting factors on population numbers and sizes.

Heleioporus australiacus populations on the other hand are made up of widely and sparsely, but randomly distributed individuals, many of which must migrate hundreds of metres to suitable breeding sites in order to reproduce. Males may be more common near culverts, but the species does not show associations with track drainage structures or natural drainage lines.

Individuals of both species show site fidelity and generally only move short distances. *P. australis* may stay with a single leaf litter pile, even if that pile is relocated or rearranged by flood water. The full spatial requirements of populations however remain uncertain but are expected to be larger than a single drainage line, because of the species' need for dry-weather refuges and additional foraging sites. The spatial arrangement of *H. australiacus* individuals suggests that they may avoid each other. Individual home ranges are relatively large and apparently rarely overlap with neighbouring home ranges, which suggests that self-sustaining populations of this species require large areas of suitable habitat. Considering that microhabitat is discontinuous and that there are edge effects, the spatial requirements of a viable population is likely to measure one hundred or more hectares.

3 Is track-side habitat beneficial to *P. australis* and *H. australiacus*?

The third question relates to both species' associations with roads. The aim was to determine the value of artificial road drainage structures including table drains and mitre drains to recruitment, and to evaluate potential impacts of road maintenance works. This aspect of the study focused on the interface where frog habitat and human infrastructure, as well as ongoing human activity, meet. Frog presence on road sites obviously pose management problems, particularly those associated with the maintenance of these roads, but also the potential of traffic induced mortality. Ecologists also find interest in studying organisms that incorporate artificial habitat features into their natural habitat. Such studies allow assessment of the potential value of novel habitat features, their relative importance to the organism in question, and may contribute to a better understanding of the distributional limits imposed on this organism.

Tracks feature in the habitat of both frogs and both species breed in artificial track drainage structures, but reproductive success, being affected by hydroperiod, is higher in the non-track environment. For *Pseudophryne australis*, some table drains offer suitable breeding habitat. However, non-track breeding sites hold water for longer and are therefore likely to produce more metamorphs annually compared to track breeding sites. *P. australis* tadpoles tend to be absent from track-side pools with high traffic volumes, even in places where males regularly call. It remains to be investigated whether traffic inhibits breeding (calling males do not necessarily indicate that breeding takes place), or whether it has adverse effects on the egg masses or hatchlings.

Only half of the monitored *Heleioporus australiacus* sites held water long enough to allow tadpoles to metamorphose. As a result, many tadpoles died despite their ability to accelerate larval development in response to pond drying. Natural sites included some permanent pools and therefore held water considerably longer than those in the track environment. As a result, reproductive success was higher away from tracks.

At the terrestrial life stage, some *H. australiacus* do burrow in the track environment and other previously disturbed areas such as quarries, and are at risk of being dug up and injured during maintenance operations.

For *P. australis* and *H. australiacus* alike, all worked sites failed to produce any metamorphs. Further research is required to determine whether tracks act as ecological traps (*sensu* Donovan & Thompson, 2001) for either frog. At present, the effects of ecological traps on long-term conservation efforts are unclear, but their dire implications for population persistence means that they should not be ignored in the management and conservation of animal populations (Battin, 2004).

4 Future research

This research identified a number of unanswered questions that relate in some way or another to the habitat or its use by *Pseudophryne australis* and *Heleioporus australiacus*. These are restated here and may serve as the basis for future research on these species.

Both frogs are strongly associated with Hawkesbury Sandstone and to a much lesser degree the Narrabeen group. Whether the habitat of the frogs is linked to transition zones (as may perhaps have been indicated by the presence of clay lenses at some sites studied) between geological strata remains to be further investigated. Habitat models could then be tailored to identify areas near such transition zones, rather than include the total area of Hawkesbury Sandstone.

The frogs studied were never observed to utilise watercourses dominated by weeds including privet (*Ligustrum* spp.) or lantana (*Lantana camara*). Clements (1983) found elevated phosphorus levels in the soils of watercourses with weeds. The topographical position and underlying geology suggest that phosphorus levels in *P. australis* and *H. australiacus* habitat are lower in comparison to those found in valleys or on shale derived soils (see Clements, 1983). Soil phosphorus levels are one responsible factor determining the make-up of vegetation communities at least in the northern part of the Sydney Basin, also influencing the abundance of exotic plants and other weeds (Clements, 1983). The actual influences of soil and water nutrient levels and the vegetation itself on the small-scale distribution of the frogs remain an area to be investigated further.

The spatial requirements of *P. australis* individuals and populations are most likely to be much higher than the space and resources offered by breeding sites alone. Extensive search efforts through the leaf litter did not produce any frogs during prolonged dry weather conditions. Unfortunately, the fossorial habit and small body size make it extremely difficult to track individuals to their retreats during unfavourable climatic conditions. It has been reported however, that these frogs may retreat to lower clay layers or into crevices in cliffs (Thumm & Mahony, 1999). It can only be speculated that frogs seek such refuges as close to breeding sites as possible. The closeness of an individual to a potential breeding site can affect the time required to acquire and defend a high-value egg deposition site when weather conditions turn favourable. High-quality habitat is usually occupied very quickly in other animals (e.g., Orians & Wittenberger, 1991). Proximity to breeding sites is likely to be an important factor influencing individual reproductive success in species such as *P. australis* because the timing of reproduction in this frog is independent of season but strongly linked to prevailing weather conditions (Thumm & Mahony, 2002b). Also, little information is available in relation to the foraging behaviour of *P. australis*. Foraging may indeed further increase the spatial requirements of individual *P. australis*. Ross (1908) described *P. australis* as "a great wanderer" with individuals found half a mile (approx. 800 m) from any water. On several occasions, *P. australis* females were observed considerable distances (Watagans: 100 m; Stauber, pers. obs., Hornsby: 72 m; Thumm, unpubl. data) away from the nearest breeding sites feeding on termites at the base or even on top of their mounds. Perhaps females range further than males to seek out high quality food items for egg production. Such foraging behaviour further increases the spatial requirements of a species. Further advances in the miniaturisation of tracking devices are necessary to follow individuals in the quest to determine their true spatial requirements, and to identify all habitat components used by this species.

A new *P. australis* population was observed to be formed 120 m away from a declining one. The origin of the founders of the new population remains a puzzle because none of the individuals were members of the two neighbouring populations. This leaves open many questions that relate to dispersal of this species, which of course also relates to the spatial requirements of populations.

Dispersal is an important area that remains to be investigated in both *P. australis* and *H. australiacus* because it fundamentally influences gene flow and the genetic structure of populations (Berry, 2001; Driscoll, 1998; Ibrahim *et al*, 1996; Lacy & Lindenmayer, 1995; McCauley *et al*, 1995; Neigel & Avise, 1993; Peterson & Denno, 1997), their spatial arrangement through colonisation and recolonisation (Hengeveld, 1994; Shaw, 1995), and population demography and persistence (Hansson, 1991). In amphibians, a reliance on dispersal seems highly likely because of the patchy distribution of breeding sites (Hughes, 1990). For amphibians, dispersal is generally thought to be primarily achieved by juveniles (Berven & Grudzien, 1990; Breden, 1987; Gill, 1978). No juvenile *P. australis* and only very few *H. australiacus* (no recaptures) were encountered during this study. Juveniles do not call and would only be detected by chance. Given the longevity of *P. australis,* and possibly *H. australiacus,* and the low recapture rate of adults, it is highly likely that adult dispersal is an important element in these species ecologies and population demographics. Dispersing individuals had a very low probability of being recaptured in the present study, unless they dispersed to a neighbouring population which was monitored, or along the transects. Some individuals were recorded to have moved distances greater than the lengths of some of the shorter study sites, which suggests that individuals were quite capable of moving out of the study sites.

The association of *H. australiacus* males with culverts was only observed at one transect – where the numbers of animals and culverts were highest – and not at the other two. The influence of sample size on the result is not known, it is therefore not clear whether this association applies to a few, or indeed all populations of this species. The aggregation indices based on nearest-neighbour distances for the three transects, however, do not support the finding that *H. australiacus* associate with culverts. Further work could clarify the situation.

The spacing of individuals within populations is not solely influenced by the location, quality and availability of resources. Behavioural interactions such as social interactions (Blaustein & Walls, 1995; Brown & Orians, 1970), including avoidance (e.g., Aberg *et al.*, 2000), also influence the spatial distribution of mobile organisms (Moody *et al.*, 1997). The effects of behaviour on spatial patterns were not investigated in this study, but would make an interesting subject of further research. The large values of the actual nearest-neighbour distances measured in the field do suggest that avoidance behaviour to conspecifics may be implicated in the spatial distribution of *H. australiacus.*

Whether site fidelity in *H. australiacus* translates to territoriality remains to be tested. If a territory is defined as a "defended space", the definition adopted by Noble (1939), then territoriality describes behaviour which includes the defence of the site and the exclusion of competitors (Gergits, 1982). Resource limitations linked to particular sites (a resource may be space itself or any biotic or abiotic feature (Begon *et al.*, 1996)) and resource defence by

H. australiacus remain to be investigated in order to demonstrate territoriality in the species. Male *H. australiacus* do possess prominent cone-shaped nuptial spines on their fingers (Moore, 1961), which could be used as weapons against each other to possibly defend resources. Captive juveniles were observed repeatedly head-butting each other when a limited number of prey items were made available (A. Stauber, unpubl. data). It is not clear how females would defend resources because they do not possess nuptial spines, nor do they call to advertise their presence. Perhaps they use head-butting or possibly even chemicals. Territoriality would explain the sparse distribution of individuals. At densities that are higher than those encountered during this study, territoriality would be expected to translate into a regular spatial distribution pattern. Territoriality in frogs is not uncommon (see references in Brown & Orians, 1970; Mathis *et al.*, 1995 and references therein; Roithmair, 1994; Thumm, 2004).

The interpretations of the data offered here assume that the number of "track avoiders" within the sampling areas was insignificant, and that tracks do not act as "magnets" to the species. However, roads may provide benefits to the species, such as open foraging ground, or a unique microclimate, or factors associated with the edge-effect. If such benefits influence the spatial distribution of *H. australiacus* by attracting them to roads, then the population density would be lower in natural bushland. This would influence the overall spatial requirements of *H. australiacus* populations. On the other hand, roads may also act as ecological traps (*sensu* Donovan & Thompson, 2001), by attracting individuals to places where they may get run over by vehicles or are easily taken by predators. This topic clearly needs more work.

Furthermore, tracks offer artificial breeding sites. While these sites have a lower potential to produce metamorphs, it remains unknown whether track breeding sites truly act as ecological sinks by attracting breeding adults away from natural (and possibly better) breeding sites. Alternatively, track sites may boost the number of breeding sites where breeding sites are limited. Which of these predominantly applies at the landscape scale certainly needs further investigation. *P. australis* it also remains to be investigated whether traffic inhibits breeding (calling males do not necessarily indicate that breeding takes place), or whether it has adverse effects on the egg masses or hatchlings.

Within-clutch variation in larval periods may be an additional strategy to phenotypic plasticity that allows *H. australiacus* to reduce the risk to reproductive effort associated with pond drying. Asynchrony in larval period, which did not obscure the plastic response to pond drying in *H. australiacus*, may possibly be a secondary survival strategy to phenotypic plasticity in larval period. While weight differences in *H. australiacus* tadpoles (Chapter 3) were not significant between treatments in the laboratory, the modest relationship with larval period suggests that an increase in the difference of the mean duration of the larval period among treatments (for instance possibly under lower temperatures) would from some point in time onward be expected to produce significant weight differences among treatments. Further experimentation is required to test how temperature affects the magnitude of the phenotypic response to pond drying in *H. australiacus*. Furthermore, it is not clear whether natural temperature differences among the hatching sites of the three studied populations and possible acclimatisation of hatchlings to these differences account for some of the differences in larval periods observed in the laboratory.

The importance of crayfish burrows and crevices that provide access to the watertable below dry ponds was evident. These shelters allowed tadpoles to survive short dry spells and complete metamorphosis in replenished pools. There is a strong association between *H. australiacus* breeding pools and the presence of crayfish burrows (Chapter 2), a relationship that appears to convey benefits to the frog. Male *H. australiacus* often call from such burrows and egg masses may get deposited there (A. Stauber, pers. obs; see also Hoser, 1989). It is not known if the crustacean preys on tadpoles. While crayfish appear as inefficient predators on free-swimming tadpoles (Lefcort, 1996; but see Nyström & Åbjörnsson, 2000), they would benefit as a predator when tadpole densities increase as a result of pool drying. An investigation into the nature of the relationship between crustacean and amphibian and its implications for both taxa is recommended.

An indirect effect fire hazard reduction burning is likely to be the temporary loss of leaf litter piles and logs, resources that are particularly important to *P. australis*. It has been stated that the congener *P. corroboree* may be more vulnerable to dehydration following fire (Osborne, 1991). Whether this also applies to *P. australis* remains to be tested, but it is highly likely that the temporary and perhaps even partial loss of sheltering, feeding and breeding habitat may negatively affect population size, which, in the worst case may also affect population persistence.

5 Management recommendations

The habitat occupied by both *Pseudophryne australis* and *Heleioporus australiacus* is unusual in that only one other frog, the wide-ranging species *Crinia signifera*, is known to utilise it. Each of the three frogs has its own reproductive adaptations that allow it to persist in its own way in this marginal environment away from permanent water courses. Habitat specialisation by *P. australis* and *H. australiacus* require that their unique habitat requirements are taken into consideration in the management of urban impacts. These include the management of tracks, wild fires and fire hazard reduction operations, the clearing of habitat and the collection of bush rock. Both *P. australis* and *H. australiacus* should benefit if conservation managers give consideration to the following issues and recommendations.

Both frogs breed in feeder creeks (not mapped on the 1:25000 topographic map series), natural and artificial gutters (including table drains), natural drains, soaks and depressions high up in the catchment where the hydroperiod is ephemeral. Importantly, this means that the creeks shown on the topographic map series are not very useful for identifying potential habitat of these frogs.

H. australiacus is a highly cryptic species and targeted surveys often fail to detect the frog even in areas where populations are known to exist (Chapter 4). In addition, burrowing locations cannot be predicted, and occupied burrows are virtually undetectable unless tracking devices are used. Pre-track work surveys therefore would only be of limited use in detecting the presence of the species, unless considerable effort is invested. Breeding sites can be identified by the presence of tadpoles during winter and spring, but these sites are often long distances from individual home ranges (Chapter 4). It is essential that the *Atlas of NSW Wildlife* is consulted to identify areas where the species potentially occurs.

5.1 Fire hazard reduction burning

Leaf litter piles and logs are clearly important to *P. australis* because they provide shelter, egg deposition sites and foraging opportunities. Once dry, they are also highly combustible.

Fire hazard reduction burning, and wild fires alike, potentially reduce population sizes (Thumm & Mahony, 1999; A. Stauber, pers. obs.). An indirect effect of such disturbances is likely to be the temporary loss of leaf litter piles and logs. It has been stated that the congener *P. corroboree* may be more vulnerable to dehydration following fire (Osborne, 1991). Whether this also applies to *P. australis* remains to be tested, but it is highly likely that the temporary and perhaps even partial loss of sheltering, feeding and breeding habitat negatively affects population size, which, in the worst case may also affect population persistence. Given the importance of these habitat features to the species, managers should aim at reducing fire impacts on natural drainage lines and table drains that are colonised by *P. australis*. High frequency fire has been listed as a key threatening process by the NSW Scientific Committee (*Threatened Species Conservation Act 1995*). Thumm & Mahony (1997b, 1999) recommended that fire hazard reduction burns should be implemented only after careful planning taking into consideration exclusion zones to protect the species, and that no more than one fire management activity (including burning, slashing, clearing) should be carried out at a single site within [about] 10 years. These recommendations are obviously designed to minimise the temporary loss of important microhabitat features and should be adopted across the species' range. Ideally, fire management activities within an area are carried out in small patches at different times to form a temporal mosaic pattern at a metapopulation scale.

5.2 The spatial requirements of *Pseudophryne australis* and *Heleioporus australiacus*

The spatial requirements of *P. australis* populations remain uncertain. Apart from breeding sites, the frogs also need access to shelters nearby that provide refuges during adverse climatic conditions. Additional foraging space seems to be another requirement. Habitat protection should therefore not be restricted to breeding sites alone, but also needs to incorporate shelter and foraging areas. Individuals demonstrated site fidelity and may not be able to relocate to nearby sites when conditions in their home ranges change.

While being dependent on natural bushland, *H. australiacus* do not show any preference for heath, woodland or forest. Vegetation structure based on growth form and crown separation of woody plants (*sensu* Walker & Hopkins, 1998) is therefore a poor predictor for species occurrence in bushland. Within their habitat, populations are made up of randomly, or possibly evenly, spaced individuals. Individual home ranges are located independently of their proximity to creeks, mitre drains and culverts, although males in one study area appeared to be more common near culverts. While the protection of breeding sites is important, it is also a necessity to consider the presence of individuals up to several hundreds of metres from potential breeding sites.

H. australiacus have demonstrated site fidelity and it appears that individuals do not share their space with conspecifics. Given that individual home ranges may exceed 2000 m^2 (Chapter 6) with little overlap, the minimum spatial requirements of a viable population is at least a hundred hectares. The reduction of habitat availability by several house block sized allotments may therefore negatively impact on population persistence, even if these developments are located considerable distances away from water courses.

5.3 Management of the track environment

This study suggests that reproductive success of *P. australis* and *H. australiacus* is higher in the non-track environment in comparison to breeding sites associated with the track drainage system. Differences were recorded in pool duration and the number of sites producing metamorphs.

This study also demonstrates that tracks in the Reserve System are subjected to regular and frequent maintenance works. Track maintenance works were undertaken during the study period on all but one track where breeding pools were monitored. The remaining track was exposed to maintenance works six months after the monitoring period.

Two unmonitored and two monitored breeding sites were completely destroyed as a result of the track works. The first unmonitored site, a table drain, was dug out to solid base during a wet period when breeding activity was indicated by a large number of calling male *P. australis*. This was most likely the first reproductive effort in twelve months during which very little rain had fallen. That table drain was re-built six weeks later after a vehicle had driven through its entire length. The second unmonitored site, a depression in natural bushland about 1 m from the edge of the track, was used as a permanent dump for excess track fill clearly contravening Austroads (2001) guidelines. That depression is now a mound about 2 m long and 1 m high. A monitored site, a rut in the middle of the track, was completely filled with crushed sandstone and was thus eliminated. No ameliorative measures were evident. The fourth site was damaged and drained by a truck that had driven through. These four events took place in a Nature Reserve in locations that are recorded in the *Atlas of NSW Wildlife*.

Records of track work activities directly altering *P. australis* breeding sites are by no means new or a rare occurrence. An unsealed track in Royal NP was resurfaced with ground bitumen in early 2001. A pool in the table drain where *P. australis* used to breed regularly was graded and drained. A visit in late March 2001 failed to locate any *P. australis* in or near the site which had become silted up (A. Stauber, pers. obs.). Regular maintenance works of the major tracks in the State Forests of the Watagan Mountains account for major disturbances in at least two *P. australis* breeding sites. A 40 cm deep table drain at the bottom of which *P. australis* used to call from under the leafl itter and in cavities was levelled with road spoil (A. Stauber, pers. obs.). The mitre drain nearby was converted to a dam in spring 2004. At the same time, another breeding site was bulldozed and diverted to a newly constructed dam (A. Stauber, pers. obs.). Madden (pers. comm.) attributed the extinction of a population in a drainage ditch in the Woronora catchment to grading of the site, rather than a recent fire. Track works during a fire in a bushland reserve on the Central Coast in October 2002 completely filled a depression in the track where previously *P. australis* were regularly heard calling. No *P. australis* were heard there for the following 17 months during which the species was heard in other known locations nearby (A. Stauber, pers. obs.) Dramatic reductions in the numbers of calling males were still recorded 12 months after the cleaning out of table drains elsewhere (Thumm, 1997a). Single maintenance operations can impact on multiple breeding sites as was demonstrated during "upgrading" works of a track when six breeding sites were backhoed (Thumm, 1997b).

The impact of track works on track-side breeding *P. australis* populations must not be underestimated. During this study, not a single worked site produced metamorphs of this species, whereas a non-worked site did.

In the track environment, dying *H. australiacus* tadpoles were observed in the same mitre drain for two years in a row. At some stage masses of wriggling tadpoles were concentrated in the footprints of a large dog where the pool's remaining moisture had accumulated. This site is part of a small watercourse which offers several deep, natural breeding pools, which occasionally, but not always, were occupied by *H. australiacus* tadpoles. That mitre drain can be classified as an ecological trap because it is a habitat "low in quality for reproduction and survival that cannot sustain a population, yet is preferred over other available high-quality habitats" (Donovan & Thompson, 2001). At present it is not known whether this type of ecological trap is an isolated case, or a more widespread phenomenon.

It is not clear what proportion of all *P. australis* and *H. australiacus* breeding sites are located in the track environment because of sampling bias associated with site access. What can be said however is that tracks, due to their continuity and linearity, can dissect a large number of adjacent drainage lines. This can be observed in many situations (including the study area) where maintenance tracks follow contours below the ridge top. In such situations (in elevated locations where slopes are gentle), tracks come in contact with every potential breeding site on hill sides, which may add up to a series of considerable and continuous areas of potential impact in certain regions. At this stage of knowledge, the precautionary principle should be applied and the impacts of track works taken into consideration.

Given the legal status of both frog species and the conflicting situation between frog presence in track sites and the necessity for regular maintenance works there, recommendations are needed to reduce the impact of track management on frog populations. Mitigation strategies need to be adequately based on the species' ecology or life-history requirements. Particularly the early life-history of both frogs can be put at an increased risk in the track environment. This study demonstrated that track works carried out at sites containing tadpoles of *P. australis* or *H. australiacus* relate to reproductive failure of these sites.

Ideally, tracks, including their drainage systems, should be constructed in such a way that they and their run-off does not impact on existing breeding sites during and after construction. The ideal drainage system will not allow water to pool and therefore will not offer artificial breeding habitat. As a result there is no change in the number of breeding sites or their qualities. Practicalities however impose changes on such an ideal situation.

At the moment, these frogs are known to breed in numerous track sites which are recorded in the *Atlas of NSW Wildlife*. Data presented above strongly suggest that this database is not always utilised to identify sites where impending track works potentially impact the frogs. Time should be allocated to identify and mark known and potential breeding sites in order to eliminate accidental impacts and to reduce the impacts of necessary works. Accidental impacts include vehicle movements through the site while works are in progress nearby, and the temporary or permanent placement of road material stock piles. Unlike the track works example in the Nature Reserve given above for *P. australis*, maintenance works should be timed so that they do not coincide with breeding activity of the species. *P. australis* breed throughout the year after rain (Harrison, 1922; Thumm & Mahony, 2002b), which makes it impossible to find an off-season. A reduction in the impact should be expected if track works there were undertaken sufficient time after the last substantial rainfall event, to allow the ground to dry out and adults to move to more suitable shelters. If works at *H. australiacus* breeding sites were restricted to January and February, impacts on the larval stage of this species would be mitigated because the majority of tadpoles have metamorphosed and new eggs have not been laid by then.

A seemingly successful solution to the problem of threatened frog presence in the track environment is a dug-out table drain that runs parallel to the track in bushland on the high track side. This intercepts seepage and surface run-off from the hill above and channels the water to a permanent culvert under the track, effectively removing water before it enters the track environment. These table drains may be two to three meters from the edge of the track where they are not driven through or constantly trampled by walkers. Once revegetated naturally, these table drains are stable and maintenance free. Examples of such table drains can be found in many reserves including Royal, Ku-ring-gai, Brisbane Water and Bouddi National Parks where they are utilised as breeding habitat by one or both frogs.

The major advantage of this system is that the artificial habitat is placed away from the direct impacts of vehicular movements and maintenance works. It also offers accessible shelter to animals that exploit pools which may form on the track itself. This system reduces track run-off and a potential reduction in erosion lowers maintenance needs. The system could also be used advantageously during hazard reduction burning to minimise potential threats to vulnerable track-side plants and animals. The main disadvantages are the initially high costs to install the system. These however would be offset by likely savings in ongoing maintenance costs. Topography, soil type or potentially negative impacts on the hydrology may rule out the construction of the table drains in some areas.

The use of blue metal or crushed building rubble as road material should be avoided in the sandstone areas until their impacts on egg masses and tadpoles are better understood. Local materials should be used for track construction (Morse McVey & Associates, 1993), and Recsei (1996) and Thumm (1996) have advised in their papers against the use of blue metal because of its potential to alter soil acidity. Buchanan (1996) recorded pH increases in naturally acidic soils, such as those found on sandstone, near areas that are covered in blue metal.

The presence of *H. australiacus* and the recorded breeding activity (and repeated failure) at one site warrant investigation into a more permanent engineering solution of this creek crossing. There are likely to be similar situations in other areas. Placement of a culvert under the track would be a sensible approach in this case and would also make the mitre drain redundant. At present, this drain offers egg-laying opportunities, but no opportunity for tadpoles to reach metamorphosis. This drain is not essential to the species' persistence because there are at least four natural pools available as breeding habitat nearby in the same creek line.

H. australiacus occasionally shelter in structures that are part of unsealed tracks, including track edges and the drainage system. Individuals may also inhabit areas that had been previously disturbed and created through the construction or maintenance of such tracks. This species relies on its ability to burrow for shelter, and may utilise such unnatural sites because the soft substrate facilitates digging and perhaps for the relatively higher soil moisture content. One male's burrows were mostly located near the track which suggests that the track served as a corridor for movement. Frequent observations of this particular animal on the track while active (Chapter 4) support this suggestion. A female regularly sheltered on both sides of the track. The home range of that animal was dissected by the track. One study animal sheltered for a disproportionately high amount of time (82%) within

3 m of the track, including two burrows in the track. The burrow it used most regularly falls into that zone. This animal showed no temporal shift in burrowing locations away from the track. Another individual spent 36% of sheltering time in burrows within 5 m from the track. Its closest burrow was 0.5 m from the track edge. Generally, these frogs shelter within the top 15 cm of the soil. This potentially places them at an increased risk of being dug up and injured during track maintenance work. The impacts this might have on population persistence are unknown, but since many individuals have been found to associate with track habitat (Chapter 4), they could be threatened by track works even in the reserve system including national parks and nature reserves. Sound management of any threatened species should consider all potential threatening processes in order to improve the status of that taxon.

The timing of the track works would be of little consequence in minimising impacts on adult *H. australiacus*. These animals are nocturnal and leave their burrows only at night during periods of activity. At all other times they shelter in the soil. Track maintenance works are carried out in the day time and always have the potential to unearth and mutilate a buried frog.

A sound management approach embraces a reduction in the frequency of necessary maintenance work and suggests that tracks should not be topped up or even sealed with materials that are foreign to the site (blue metal, demolition waste, bitumen). Such materials are known to change chemical and physical properties of the soil and run off water (Buchanan, 1996; Trombulak & Frissell, 2000) and their use is discouraged in NSW (Morse McVey & Associates, 1993).

Some flood ways of the ephemeral watercourses in *H. australiacus* habitat may need to be replaced initially with permanent culverts to eliminate gully erosion of the track at these crossings and sedimentation of the waterway downstream. Maintenance of the track surface in combination with its linear nature facilitates the transport of suspended sediments, particularly because vegetation is absent. In addition, the compacted track surface has a comparatively lower infiltration rate which leads to increased sedimentation (Krause *et al.*, 2003). A more important issue however appears to be the erosion caused by traffic

(Anderson, *et al.*, 1976; Coker *et al.*, 1993). Many tracks that dissect *H. australiacus* habitat in the reserve system experience frequent and regular illegal use by motorcycles and 4WD vehicles. Law enforcement may be a solution in this situation because the elimination of such vehicular movements would inevitably lead to a reduction in track damage (Morse McVey & Associates, 1993; see also Reid & Dunne, 1984), and hence a reduction in the frequency and severity of required maintenance work.

I strongly recommend that continuously eroding causeways are replaced by culverts, and that active measures are undertaken to kerb illegal vehicular traffic.

APPENDIX 1

Manuscript submitted to Wildlife Research

RELIABILITY OF VENTRAL PATTERN MAPPING AS AN IDENTIFICATION TECHNIQUE IN ANURAN RESEARCH

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Abstract. Pattern mapping is an advantageous marking technique, as long as patterns remain unchanged ontogenetically and allow reliable individual recognition. These pre-requisites were tested on ventral patterns of captive frogs *Pseudophryne australis*. Patterns of individuals ranging in age from 2 months to more than 10 years were drawn repeatedly over 4 years and compared for ontogenetic change and variability. We found that ventral patterns of *P. australis* do not change throughout the frog's terrestrial life and high variation among individuals allows unambiguous distinction. High variation in ventral patterns was also found in museum specimens of nine other frog species. Pattern mapping, suitable for long-term studies and allowing the inclusion of juveniles, has great potential for ecological work on many anurans.

Introduction

Mark-recapture studies are an integral part of ecological research and provide much ecological information ranging from population size and demographics, to habitat use and individual growth rates (Donnelly and Guyer 1994). The ideal marking technique does not alter an organism's behaviour and survival, is easily applied, and lasts throughout the study period (Ferner 1979).

Many study objectives rely on marks that uniquely identify individuals, as opposed to the recognition of cohorts. A wide range of marking techniques for individual recognition is available to amphibian researchers (Donnelly *et al.* 1994), varying greatly in cost, ease of application, durability and extent of distress caused to the organism. Toe-clipping is inexpensive, quick and has been in use for several decades, but evidence suggests that it can affect behaviour, survivorship and hence return rates (Clarke 1972; Humphries 1979; Parris and McCarthy 2001; McCarthy and Parris 2004). Ethical concerns over toe-clipping have also been raised (e.g. May 2004). Other techniques include tattooing (Joly and Miaud 1989-1990)), visual implant elastomer (VIE) tagging and dye injections (Brown 1997; Lampert and Linsenmair 2002), passive integrated transponder (PIT) tagging (Christy 1996), branding, and the use of jaw tags (Ferner 1979) or reflective tape (Robertson 1984). Each technique has its own limitations, and increasing awareness and enforcement of animal welfare issues potentially decreases the number of marking techniques available to researchers.

Several studies have made use of natural colour patterns to recognise individual amphibians (e.g. Summers 1989; Loafman 1991; Doody 1995; Barandun and Reyer 1998; Caldwell and Oliveira 1999; Buschmann 2002). For such patterns to be useful for individual identification, they must meet two conditions: patterns must not change ontogenetically, and they must be sufficiently different from each other to allow the observer to distinguish among patterns without ambiguity.

Duellman and Trueb (1994) point out that many recently metamorphosed amphibians have colour patterns unlike those of the adults. Juvenile patterns keep changing for the first three years in newts and salamanders (e.g. Smith 1969). Dramatic ontogenetic changes in colouration and patterning have been reported for some dart-poison frogs (e.g. Myers & Daly 1983), but to our knowledge, ontogenetic change of patterns has never been tested in any other groups of frogs.

Previously, dorsal pattern mapping had been applied for the identification of dendrobatid adults in short-term behavioural studies (e.g. Roithmair 1994; Caldwell and Oliveira 1999). Ventral patterns had also been used for the individual recognition of *Adelotus brevis* (Katsikaros and Shine 1997), *Pseudophryne australis* (Thumm and Mahony 2002), and *Bombina variegata* (e.g. Seidel 1993; Buschmann 2002), but exclusively for adult frogs. Besides Thumm and Mahony (2002), who reported that patterns did not change over an unspecified period, no other author reported on the constancy of patterns. Their results only suggest that the markings allowed recognition of individuals for the duration of their studies. The only indication to date that juvenile patterns may be useful for later recognition in frogs is given by Gollmann and Gollmann (2000). They recognised a few *Bombina variegata* individuals in the field after 3 years on the basis of ventral pattern photographs taken of 'relatively large metamorphs' (SUL not stated).

Here we investigate ontogenetic change of ventral colour patterns in a very small frog (adult mean snout-vent length: males = 22 mm; females = 26 mm (Thumm and Mahony 2002)) and evaluate the suitability of ventral patterns for individual recognition in several frog species. The model species is an Australian ground frog, the red-crowned toadlet *Pseudophryne australis* (Myobatrachidae). Red-crowned toadlet venters are black with bold white blotches (Fig. 1). This frog and several congeners are listed as threatened species in Australia (e.g. NSW NPWS 1995) and internationally (IUCN 2003), necessitating ecological research toward the formulation of management and recovery plans. Adult sizes are too small for PIT tagging (*sensu* Camper and Dixon 1988; Christy 1996) and permits for toe-clipping have been refused to us by licensing authorities on the grounds that this predominantly walking frog may be severely incapacitated by the loss of a phalange. Thumm and Mahony (1999; 2002) also showed the species' potential as a model for this study by successfully identifying adult *P. australis* using photographs and drawings.

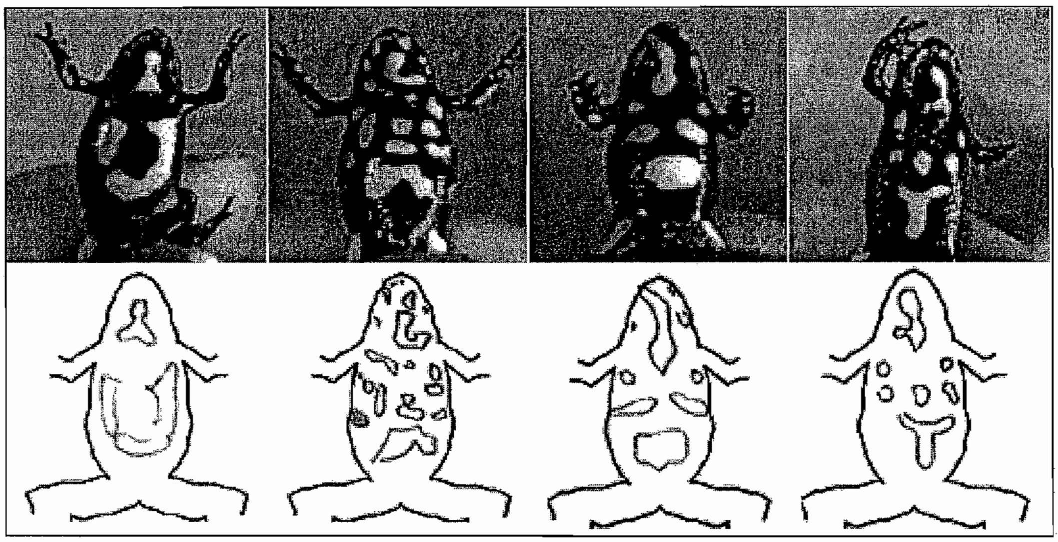

Figure 1 Examples of ventral patterns of red-crowned toadlets *Pseudophryne australis*. The lower half shows parts of a pre-printed marking sheet with pattern drawings made of juveniles three and a half years before the same animals were photographed as adults. Mean snout-urostyle length of these individuals increased from 14.1 mm to 24.3 mm over that period.

Materials and methods

Data were obtained from a collection of captive *Pseudophryne australis* (n = 68) unless stated otherwise. The collection was originally established for a series of experiments not related to this study. It included captive bred juveniles from five egg clutches (each from a different population), and wild collected adults from 11 populations spanning a geographic range of 85 km. Juveniles are defined as four-limbed individuals (post Gosner 1960: stage 42) that have not yet reached sexual maturity, hence include metamorphs and sub-adults. Age of juveniles was measured as the time since front limb emergence during early metamorphosis (Gosner 1960: stage 42). In captivity, *P. australis* will have reached sexual maturity by age 2.5 years (Thumm 1997). The animals were regularly fed termites and kept in 11 terraria that contained a thick layer of moist sandy soil and some leaf litter and woody debris. Animals were recovered for this study by systematically searching each terrarium. It was considered unnecessary to artificially mark the animals because of the wide-ranging variety of very dissimilar patterns previously observed in the field. Measurements taken of individuals were body mass using an electronic balance, and snout-urostyle length (SUL) using callipers.

Do ventral patterns change in growing juveniles?

Juvenile frogs (n = 43) were monitored to test whether ventral patterns change during the early terrestrial life stages from juvenile to adulthood, which is generally the period of fastest growth (e.g. Morey and Reznick 2001). Field observations confirmed that ventral patterns in *P. australis* first develop during metamorphosis (Gosner 1960: stages 42 - 46). The captive juveniles, initially ranging in age from two to seven months, all had clearly distinguishable ventral patterns. These animals were drawn and measured on four occasions (Table 1). Only a subset was redrawn in April 2002. Animals were restrained to expose the ventral surface, by holding the legs between thumb and middle finger with the index finger supporting the head. A pencil was used to draw the shapes of ventral blotches on printed forms containing a 40 mm x 55 mm outline of head, body, and location of the legs (Fig. 1). Drawings were completed within 30 to 60 seconds depending on the complexity of the patterns.

In order to evaluate ontogenetic change of the markings it was important that subsequent sets of ventral patterns were obtained free from the influence of the existing drawings. This was achieved by the drawer creating a new set of drawings without referring to the previous ones, until all animals were recorded for that session. Sets of new drawings were then compared and matched to the oldest ones by the drawer and two other observers independently. The drawer and both matchers were the same persons throughout the study.

Do ventral patterns change in adults?

The ventral patterns of adult frogs (n = 25), initially ranging in age from approximately three to six years, were drawn on three occasions at months 0, 22 and 48 (Table 2). Drawing and matching procedures were carried out as outlined above.

Do ventral patterns allow reliable recognition of individuals?

For ventral patterns to be useful for individual identification, they must be sufficiently different from each other. Each drawing of a captive individual was compared to all other drawings to assess the potential of ambiguity due to similarities between individuals.

Objective criteria used were the position, shape and direction of the larger and medium sized blotches and the patterns formed by smaller blotches and their numbers.

In addition, ventral drawings of 500 individuals from the field were compared individually using the same criteria. Two observers were asked to find matches within the set.

Comparison of drawn and digital images

To compare the efficacy of the drawing method above with digital images, we also used a Sony digital still camera Mavica MVC-FD7. For digital images to be of benefit, these had to be taken at night by one person because assistance was normally not available. The right hand held the camera together with a torch to illuminate the subject, which was held in the left hand. The frog was held ventral side up with its hind legs between thumb and middle finger. The torch was necessary to aim and focus the camera. Camera-to-subject distance was about 30 cm, rendering use of the built-in flash inappropriate. Images were checked in the field before the animal was released, and saved onto computer later. Images were compared to ventral pattern drawings made in the field, concentrating on the shape and position of individual blotches and their numbers.

Can ventral pattern identification be applied to other frogs?

In order to explore possibilities for the wider application of ventral pattern identification in Australian ground frogs, intraspecific pattern variability was evaluated in nine other myobatrachids. These were: *Adelotus brevis, Pseudophryne bibronii, P. coriacea, P. corroboree, P. dendyi, P. major, P. occidentalis, P. semimarmorata, P. pengilleyi.* Preserved specimens held by the Australian Museum, Sydney, were inspected. For each species, ten (exceptions: sample sizes for *P. major* = 6; *P. occidentalis* = 3) randomly chosen animals were laid out ventral side up. Strongly faded or dissected specimens were rejected. The ventral pattern of each individual was then compared to the others to check for individual differences as outlined above.

Results

Do ventral patterns change in growing juveniles?

The position, shape and direction of the blotches did not change over time in growing juveniles. Ontogenetic change in blotch size was judged to be isometric, the number of recorded blotches, however, increased during the first sampling period by one to three small blotches (< 4 mm long) in four animals (9%). These would have been considered too small and unimportant originally to be recorded and did not cause problems with identification. Examples of pattern drawings from December 2001 and photographs taken of matching individuals in June 2005 are shown in Fig. 1.

Ventral patterns were initially drawn for 43 juveniles (Table 1). These animals had a mean (± s.d.) body mass of 0.20 ± 0.07 g, and a mean SUL of 12.8 ± 1.35 mm. Each pattern map from a subsample drawn at Session 2, 4.5 months later, was easily matched with one of the original drawings. The results were consistent between all observers.

The 25 survivors (Table 1) located 13 months later measured 0.50 ± 0.15 g in mean body mass and 18.3 ±2.12 mm in mean SUL. The drawings obtained from 23 of these animals were easily matched with original drawings (each observer individually reported a matching rate of 92%). The two remaining new drawings and the animals themselves could not be matched with any of the older ventral pattern maps. It is quite possible that not all juveniles were originally drawn because they were overlooked in the terraria as a result of the gentle approach taken when removing the small individuals.

All animals had reached adulthood 12 months later (ages: 31 – 36 months; and males were heard vocalising). All 25 individuals alive in May 2003 were again drawn two years later (mean body mass: 0.83 ± 0.15 g; mean SUL: 22.6 ± 1.66 mm). Matching rates of this last set of drawings made 3.5 years after Session 1, including the two additions from the previous session, were 100% for all observers.

Table 1. Sample sizes and ventral pattern matching rates for juvenile Pseudophryne australis, and their ages since metamorphosis. Juvenile mortality reduced sample size during the first half of the experiment. Only a sub-sample was marked in Session 2 as a trial. * Two individuals could not be matched in Session 3 and may have been absent in Session 1.

Sampling session	Session 1 Dec 2001	Session 2 Apr 2002	Session 3 May 2003	Session 4 June 2005
Numbers marked in session 1 and matched in subsequent sessions	43	18	23	23
Numbers of presumed new additions marked in session 3 and matched in subsequent session			2*	2
Total marked	43	18	25	25
Total matched		18	23	25
Matching rate		100%	≥92%*	100%
Time since metamorphosis (months)	2-7	6-11	19-24	44-49

Do ventral patterns change in adults?

No pattern changes were observed in adult frogs. Twenty five adults were originally drawn (Table 2). Males (n = 15) measured 1.26 ± 0.2 g and 24.6 ± 1.5 mm in SUL, female (n = 10) measurements were 1.90 ± 0.4 g and 28.0 ± 1.7 mm. Six adults were known to have died before the second drawing session (these were readily identified through keeper's log book entries), the fate of another two remains unknown. Despite these losses, the captive collection had increased for Session 2 (Table 2) due to breeding activity and additional collection of specimens from the field. This collection was not set up with the identification of individuals being a main concern, thus identity data were not available for new individuals. Two unmatched drawings for Session 2 were further investigated. Several attempts to obtain a match failed, and it had to be assumed that these animals were recent additions to the collection. Males and females were easily matched in the last session with all matches being consistent among observers (matching rate = 100%).

Table 2. Sample sizes and ventral pattern matching rates for adult Pseudophryne australis, and their ages. * Six individuals were known to have died before Session 2, other number reductions are attributed to unrecorded losses.

Sampling session	Session 1	Session 2	Session 3
	Jun 1999	May 2001	Jun 2003
Numbers marked in session 1 and matched in subsequent sessions	10♀; 15♂	6♀; 11♂	5♀; 6♂
Numbers of new additions marked in session 2 and matched in subsequent session		7♀; 16♂	5♀; 11♂
Total marked	25	40	27
Total matched		17*	27
Matching rate		≥92%*	100%
Approximate time since metamorphosis (months)	36-72	60-96	84-120

Do ventral patterns allow reliable recognition of individuals?

Matching drawings very closely resembled each other. Drawing quality and the high variation among individual ventral patterns combined to allow easy and unambiguous identification with matching in 92% and 100% of all cases for both juveniles (Table 1) and adults (Table 2). Observers consistently matched the same pairs independently.

Each of the 500 drawings obtained from wild animals differed in number, size and shape of individual blotches and their arrangement. Only one (0.2%) was potentially ambiguous. The ventral markings of this animal were similar to a uniform, finely speckled pattern and could not be drawn, but were described as 'very spotty'. This may cause problems if the population contains other individuals with similar markings that cannot be drawn.

Comparison of drawn and digital images

Six individuals were photographed twice each. Each image was subject to one or two types of error. Animals frequently obscured parts of their ventral patterns with their arms, or by bending their heads forward. Secondly, the artificial lighting necessary produced reflections on the image introducing false blotches. It was impossible to distinguish between these reflections and the white ventral blotches. Only two of the twelve images clearly reproduced the true number and shapes of individual blotches (error rate = 83%).

Can ventral pattern identification be applied to other frogs?

All nine species allowed the observer to easily distinguish among individuals based on ventral patterns. Compared to the other species, *P. bibronii* patterns generally consisted of a larger number of smaller spots. These differed considerably however in shape and arrangement. Several *P. semimarmorata* specimens showed no ventral pigmentation. This is very likely to be an artefact of preservation (see Barker *et al.* 1995). In addition, *P. corroboree* and *P. pengilleyi* showed varied dorsal patterns.

Discussion

The striking ventral pattern in *Pseudophryne australis* does not undergo ontogenetic change throughout the terrestrial life stage. This was tested on captive frogs ranging in age from 2 months to more than 10 years post metamorphosis. Our results demonstrate that in *P. australis*, adult patterning of the ventral surface is attained within a few weeks of metamorphosis in both males and females.

Adult colour patterns in amphibians generally develop within a few days of morphological metamorphosis (Duellman and Trueb 1994), however notable exceptions occur. Research on some Caudata found that natural markings change ontogenetically. Ventral spots of the newts *Triturus cristatus cristatus* and *T. vulgaris vulgaris* change in number and size over the first three years post metamorphosis (Smith 1969). After that period, patterns remain constant in those species for at least 3 years (Hagström 1973). Dorsal spot patterns allowed life-long identification of adult *Notophthalmus viridescens* (Gill 1978), but apparently not recently matured juveniles. Amongst the frogs, *Phyllobates terribilis* juveniles differ both in colour and patterning from adults (Myers & Daly 1983). It is not clear just how widespread ontogenetic change in dorsal patterns is among the Dendrobatidae.

The only suggestion that ventral patterns may remain constant in developing temperate frogs was provided by Gollmann and Gollmann (2000), who successfully applied pattern mapping on a group of large *Bombina variegata* juveniles using photographs. Our long-term study provides the most comprehensive assessment to date of pattern change in a myobatrachid frog and included individuals of all ages, except the ones too small to handle.

Pseudophryne australis showed not only constancy in ventral patterns but also great variation among individuals. This intraspecific variation expressed itself in the complexity, shapes, sizes and numbers of bright blotches, as well as their arrangement, giving each individual an unambiguous identity. However, matching rates were not always 100%. While low-quality drawings or ontogenetic pattern change in a very small number of individuals may explain this, it is more likely that not all individuals were initially drawn for this study.

Ventral pattern identification has also great potential to be useful in mark-recapture studies of several other frogs, including the Australian *Adelotus brevis*, all *Pseudophryne* spp. and possibly *Crinia* spp.; all members of the Myobatrachidae. The wider applicability across other families remains to be investigated. For example, in Africa, ontogenetic change and intraspecific variation in ventral patterns could be tested on non-myobatrachid genera including *Phrynomantis, Breviceps* (Microhylidae) and *Cacosternum* (Ranidae). The amount of research carried out on the European *Bombina* has demonstrated the usefulness of ventral pattern identification in the Discoglossidae despite its apparent lack of verification. Ontogenetic change in colouration and patterning of the dorsum may need to be investigated separately in light of reported changes in a dendrobatid (Myers & Daly 1983).

Ventral pattern mapping is potentially applicable to juveniles and adult frogs alike of species with distinguishing marks. A major advantage is the absence of lower size limits, provided individuals are large enough for handling. Mark-recapture studies that include juveniles allow the construction of accurate growth curves and estimates of juvenile dispersal, habitat use and survivorship. Such information is useful for the sound management of declining frog populations by shedding light on the age structure of populations, their turn-over rates, as well as movement patterns and longevity of individuals. Chance encounters of juvenile frogs of some species may be rare in the field, but sampling techniques are available that should produce representatives of that life stage. Other advantages of pattern mapping are that individuals are not injured; it distinguishes individuals rather than cohorts; and is inexpensive, permanent and requires only basic skills. We have successfully applied the technique to 500 individuals in the field. Drawbacks are the time required for pattern recording (approximately 30-60 s) and matching (time dependent on pattern complexity and number of records available), and that identification requires handling of the animals that may alter their behaviour. Observations of many of these species, however, cannot be carried out without interference because of the required removal of leaf litter or vegetation under which the animals live.

None of the study animals were artificially marked nor could they be housed separately to allow individual recognition independent of natural patterns. This was not thought to be a problem in our study because of the high intraspecific variation in ventral patterns. For ontogenetic changes in patterning to remain undetected, these would have needed to occur in synchrony and reciprocally among pairs or larger groups. It was assumed that this was highly unlikely.

Pattern mapping has all the desirable features, both practical and ethical, of a marking system for population level work on anurans. This advantageous technique is valuable in conservation biology because it is easily and readily applied to a number of juvenile and adult frogs, including some threatened Australian species that are in need of management.

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APPENDIX 2

Heleioporus australiacus voucher specimens lodged with the Australian Museum, Sydney.

Table 37 Registration numbers of *Heleioporus australiacus* metamorphs lodged with the Australian Museum, Sydney (AM). These animals took part in the drying treatment (Chapter 3). Populations and experimental treatment are also stated (see Chapter 3 for details). Lodgement dates are 5/5/2003 and 4/6/2003.

AM Number	Population	Treatment
R162834	Kariong	-
R162835	Kariong	-
R162836	Kariong	-
R162837	Hornsby Heights	Control
R162838	Hornsby Heights	Control
R163274	Hornsby Heights	Drying
R163275	Hornsby Heights	Drying
R163276	Hornsby Heights	Control
R163277	Hornsby Heights	Control
R163278	Pearl Beach	Control
R163279	Hornsby Heights	Drying
R163280	Kariong	Control
R163281	Hornsby Heights	Control
R163282	Hornsby Heights	Drying
R163283	Hornsby Heights	Drying
R163284	Kariong	Control
R163285	Kariong	Drying
R163286	Hornsby Heights	Control
R163287	Hornsby Heights	Control
R163288	Hornsby Heights	Control
R163289	Kariong	Drying
R163290	Hornsby Heights	Drying
R163291	Hornsby Heights	Drying
R163292	Hornsby Heights	Drying
R163293	Hornsby Heights	Control
R163294	Kariong	Control
R163295	Hornsby Heights	Drying
R163296	Kariong	Control
R163297	Hornsby Heights	Control
R163298	Kariong	Control
R163299	Hornsby Heights	Drying

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