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Spatial ecology of the giant burrowing frog (*Heleioporus australiacus*): implications for conservation prescriptions

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Keywords

frog, giant, ecology, heleioporus, burrowing, spatial, prescriptions, australiacus, implications, conservation

Disciplines

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Spatial ecology of the giant burrowing frog (*Heleioporus australiacus*): implications for conservation prescriptions

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Abstract. Management of threatened anurans requires an understanding of a species' behaviour and habitat requirements in both the breeding and non-breeding environments. The giant burrowing frog (*Heleioporus australiacus*) is a threatened species in south-eastern Australia. Little is known about its habitat requirements, creating difficulties in developing management strategies for the species. We radio-tracked 33 individual *H. australiacus* in order to determine their habitat use and behaviour. Data from 33 frogs followed for between 5 and 599 days show that individuals spend little time near (<15 m) their breeding sites (mean 4.7 days for males and 6.3 days for females annually). Most time is spent in distinct non-breeding activity areas 20–250 m from the breeding sites. Activity areas of females were further from the breeding site (mean 143 m) than those of males (mean 99 m), but were not significantly different in size (overall mean 500 m²; males 553 m²; females 307 m²). Within activity areas, each frog used 1–14 burrows repeatedly, which we term home burrows. Existing prescriptions are inappropriate for this species and we propose protection of key populations in the landscape as a more appropriate means of protecting this species.

Introduction

Many anuran species have distinct breeding and non-breeding habitats (e.g. Pearson 1955; Kelleher and Tester 1969; Schwarzkopf and Alford 2002; Schabetsberger *et al.* 2004), but most research on frog habitat use has examined the breeding habitat requirements of a species. Non-breeding habitat requirements of anurans have remained largely unstudied (Lemckert 2004), even though it is recognised that managing the complementary breeding and non-breeding habitats as a unit is an essential step in the conservation of species using multiple habitats throughout the year (e.g. Richter *et al.* 2001; Semlitsch and Bodie 2003).

Burrowing anuran species, as a group, have rarely been studied and little is known of their patterns of habitat use. Studies by Pearson (1955), Bamford (1992), Dodd (1996) and Jansen *et al.* (2001) suggest that most, if not all, burrowing frog species have complementary breeding and non-breeding habitat use patterns, and that burrowing anuran species may occupy non-breeding sites at greater distances from breeding sites (i.e. waterbodies) than non-burrowing species (e.g. Dodd 1996), and possibly for longer periods (e.g. Pearson 1955). Burrowing frog species may therefore present a greater challenge for conservation because they require larger areas of habitat to complete their life cycles.

The giant burrowing frog (*Heleioporus australiacus*) of south-eastern Australia is a listed threatened species under the Commonwealth *Environmental Protection and Biodiversity Conservation Act 1999* and corresponding state legislation in both states in which it occurs, making its management a high

priority. However, the lack of knowledge about its ecology (Tyler 1997; Lunney *et al.* 2000) and hence its management remains a difficult challenge. Individuals breed in intermittently flowing streams running through areas of native vegetation (Penman *et al.* 2006a). In the southern portion of its range the species is considered to be associated with a variety of dry forest communities (Littlejohn and Martin 1967; Gillespie 1990; Webb 1991; Lemckert *et al.* 1998; Penman *et al.* 2005a), whereas in the northern portion it is considered to be more commonly associated with heath communities (Mahony 1993; Daly 1996). Data from a small number of frogs followed for a short time suggest that individuals spend most of their time in forest areas away from riparian zones (Lemckert and Brassil 2003), following the patterns of the other burrowing species studied. The frog has not been recorded in areas cleared of native vegetation throughout its range (Penman *et al.* 2004). This information suggests that management of this species needs to be based on managing breeding and non-breeding habitat as a unit.

In this paper, we examine the movements and habitat use of a population of *H. australiacus* and compare information on microhabitat between 'used' and random points to try to determine what may be valuable site attributes for this species. We then use these data to assess the efficacy of the various conservation management prescriptions established for this species.

Materials and methods

The study was conducted in a 200-ha area of Nullica State Forest in the south-east of Australia (37°2'S, 149°54'E) ~10 km

north of the township of Eden. Most of the site is classified as lowland dry shrub forest and the gully areas are classed as hinterland wet shrub forest (Keith and Bedward 1999). These forests are open sclerophyllous coastal forests with the dominant canopy species being red bloodwood (*Corimbya gummifera*), blackbutt (*Eucalyptus pilularis*) and blue stringybark (*E. agglomerata*). These areas have a heath understorey dominated by *Acacia longifolia*, *Hakea sericea* and *Pteridium esculentum*.

We used radio-telemetry to examine the behaviour and habitat use of individual *H. australiacus*. Frogs were initially located using nocturnal road transects and pitfall trapping (Penman 2005). Individuals were implanted with single-stage 2-g transmitters supplied by Sirtrack, New Zealand. The animals were anaesthetised with MS-222 (tricaine methane-sulfonate) (Ruth Consolidated Industries, Annandale, Australia) and then the transmitters were surgically implanted (Penman *et al.* 2006b). Frogs were located using a Titley Regal 2000 receiver in conjunction with a Yagi-style antenna to identify the general location of the frog and a loop wand antenna to identify the exact location of the burrow site. All tracking gear was supplied by Titley Electronics, Australia.

Thirty-three frogs (19 male, 13 female, one subadult male) were tracked between February 2002 and April 2004. Individuals were followed for periods of between 5 and 599 days, with a median tracking period of 108 days per frog, and between three and nine frogs were tracked simultaneously. Locations were obtained daily for the majority of the study with measurements being taken on 518 days, resulting in a total of 3303 location records from 256 unique non-breeding sites and eight breeding sites. Tracking effort was consistent throughout each season across the 26 months of the study. Each separate frog location was plotted by measuring the bearings and distances from known points. These points were transferred to ArcView Geographic Information System (ESRI, USA) for analyses. At each point we also recorded whether the frog was active or sheltering and, if so, whether it was in a burrow or above ground.

Movement patterns and activity areas were analysed using the Animal Movement Extension (Hooge and Eichenlaub 1997). Activity areas were defined using the minimum convex polygon (MCP) method. Bootstrapping with replacement was used to determine the number of sites required for an activity area to reach a relatively stable size. Animals tracked for only a short time (<30 days) were excluded from the analyses.

The data suggested that we were observing non-overlapping ranges. To test this we used ArcView GIS to estimate the probability that the exclusivity of activity areas could occur by random chance. To do this we used ArcView GIS to randomly place the activity areas (size and shape) of all frogs found within Areas 1 and 2 separately (Fig. 1). We then recorded the number of activity areas that overlapped another in each of 100 replicates.

A series of habitat measurements were taken at each of the 256 distinct non-breeding record sites and 100 random sites to determine whether there was an association between the characteristics of the burrow sites. Random sites were selected from areas within the study area where frogs were not observed. Measurements were taken for an area of 1 m² centred on the frog site or a random point. The measurements taken were: the

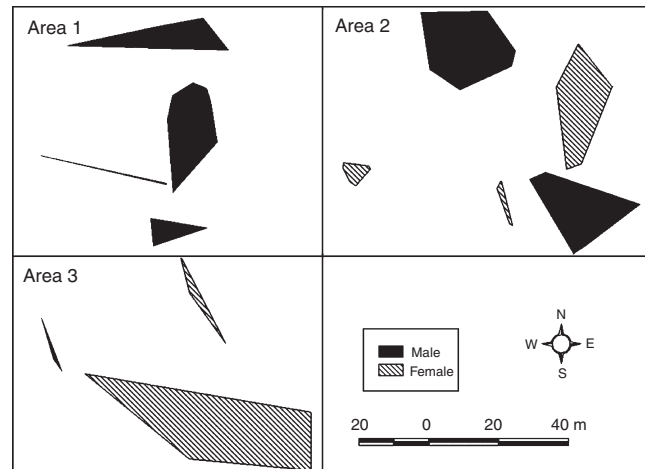


Fig. 1. Examples of the non-overlapping activity areas of *Heleioporus australiacus* for three clusters of frogs within the study area.

proportion of ground cover that comprised leaves or bare ground (i.e. 'burrowable' area), rocks, woody debris and vegetation, the soil type, average leaf litter depth (within 1 m²), leaf litter depth above burrow, distance to the road, vegetative cover provided by the canopy, understorey or subcanopy (3–15 m), shrub layer (0.5–3 m) and ground cover (0–0.5 m), distance to the nearest small tree (diameter at breast height (dbh) <100 mm), distance to the nearest large tree (dbh >100 mm) and distance to the nearest known or potential breeding site.

A comparison was made between the habitat selectivity of the two sexes using a multivariate analysis of variance (ANOVA). All factors were initially included and then non-significant factors were removed in a stepwise manner (Rosenthal and Rosnow 1985). The number of sites was not consistent between individuals, therefore to fulfil the assumptions of ANOVA (Sokal and Rohlf 1995) we used an average of the habitat conditions for all of the sites used by a frog. Frogs for which fewer than three non-breeding site records were available were removed from the dataset, resulting in mean non-breeding habitat conditions for a total of 17 males and 11 females.

Habitat associations were examined using a forwards continuation-ratio model (Guisan and Harrell 2000) in SAS ver. 8.2 (SAS Institute Inc., USA). These models are used for ordinal data and model the ratio of the two probabilities $\Pr(Y=j|x)$ and $\Pr(Y>j|x)$ (Ananth and Kleinbaum 1997); that is, the model predicts the probability of being in a group (j) given that the sample is taken for those data that are either in group j or higher on the ordinal scale. The ordinal factor used in this analysis was based on site usage. Random sites were assigned a value of 0, sites where an individual sat on the surface were assigned a value of 1, burrows that were only visited once (single-use burrows) were assigned a value of 2 and burrows that were visited more than once (multiple-use burrows) were assigned a value of 3. Continuation ratio models allow us to simultaneously model the probability of being a random site when all sites were considered (i.e. values of 0, 1, 2 or 3), the probability of an animal sitting on the surface when all frog sites were considered (i.e. values of 1, 2 or 3) and the probability of a frog using a burrow once when all burrow sites

were considered (i.e. values of 2 or 3). We used extended continuation-ratio models, which allow for different slopes for all of the x values (Guisan and Harrell 2000). Continuation ratio models were run using Generalised Estimating Equations (Liang and Zeger 1986) to remove any potential effects of pseudoreplication by repeatedly measuring the habitat of an individual. Variables were tested individually and those significant at the 0.05 level were used to build the final model. The area under the curve (AUC) value from the receiver operating characteristic (ROC) curve with the traditional academic point system (Swets 1988) was used to measure the fit of the model (Thuiller *et al.* 2003). The ROC curve represents the relationship between the true positive (sensitivity) and the false positive fraction (1-specificity) of the model over a range of threshold values (Woodward 1999). A good model maximises the true positive values and minimises false positive values.

Results

Breeding activity

Frogs were recorded moving to breeding sites only rarely during our study. Frogs undertook breeding migrations between February and April (Fig. 2), and once in October 2002. Only 4 of the 13 adult females and 10 of the 19 adult males were observed entering a breeding site during the period when they were tracked. Migrations to breeding sites were always associated with rainfall events, moving on the night of, or within 10 days of, rainfall of more than 20 mm.

Six discrete breeding sites were used by the frogs tracked in this study. Four of the sites were situated in semipermanent pools in first- and second-order streams and the other two sites were roadside ponds (for more details see Penman *et al.* 2006a). Individual frogs spent only 1–12 days at a breeding site, with a mean of 5.00 ± 0.89 days. There was no significant difference between males and females in the time spent in the breeding site (males mean 4.6 day and females 6.3 days; $t = -0.837$, d.f. = 4, $P = 0.450$). When at a breeding site, individuals either burrowed into the ground or sheltered under vegetation or woody debris. The points where frogs sheltered

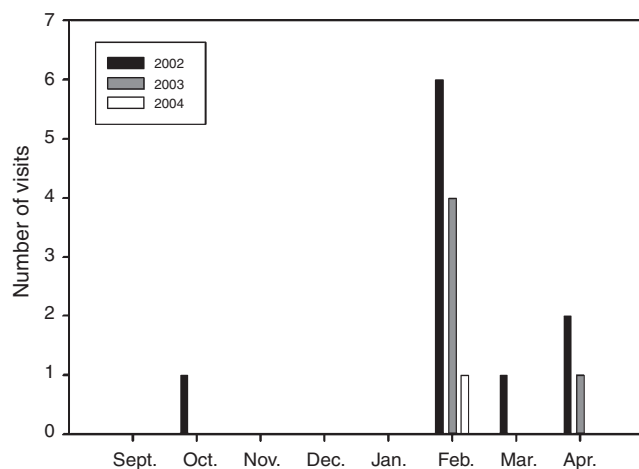


Fig. 2. The number of individual frogs visiting the breeding sites by month throughout the entire study period.

when breeding were 1–17 m from the breeding site with an average distance of 9.2 m ($n = 13$).

Non-breeding activity

All tracked individuals used a limited number of burrows located within a discrete forest area during their non-breeding activities, which we refer to hereafter as their 'activity area'. The burrows used by this species were not structured burrows and could rarely be recognised from the surface. On each visit to a burrow an individual frog must dig through the soil surface. The Loop wand allowed the location of the burrow to be determined to within 2 cm and therefore repeated use of a burrow could be determined precisely.

Bootstrapping with a MCP indicated that the size of individual activity areas stabilised after ~110 records; datasets of this size were available for only 14 frogs (8 males, 6 females). Therefore, we compared the activity of frogs for which more than 110 records were available to that of frogs for which 30–110 records were available (mean 56 records; 5 males, 5 females, 1 subadult). We refer to these frogs as having a stable activity area and an expanding activity area respectively. There was no significant difference in the size of the non-breeding activity areas between the sexes for both frogs with stable activity areas ($t = -1.67$, d.f. = 11, $P = 0.12$) and those with expanding activity areas ($t = -0.56$, d.f. = 8, $P = 0.59$) and so we combined the data for the sexes for further analyses. Mean activity areas for frogs with stable estimates for activity areas were 498.1 ± 79.1 m² compared with 200.2 ± 39.1 m² for those frogs with expanding activity areas (as determined by bootstrapping analysis).

Figure 1 demonstrates the locations of activity areas for three different clusters of frogs at the study site, using the MCPs generated for each individual to demarcate their non-breeding activity areas. Each cluster is separated by a minimum of 100 m and therefore is presented separately. Of particular note is that there is no evidence of overlap between any of the activity areas generated at any of the three locations, regardless of sex.

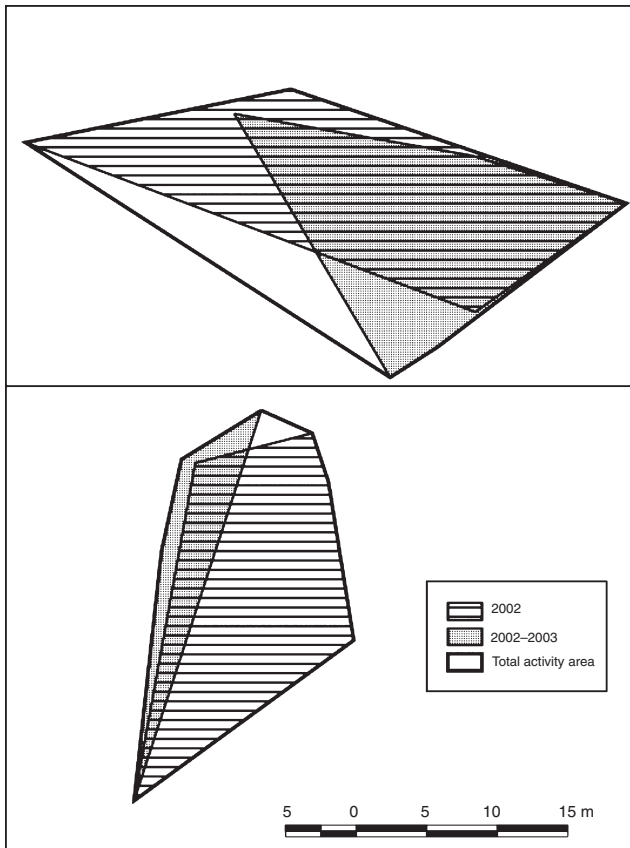
We used a simulation technique to determine whether the non-overlapping home ranges could occur randomly for two clusters of frogs observed in the study. For Area 1, only 9 of the 100 attempts exhibited exclusive activity areas for all frogs and in Area 2 this was reduced to 3 (Table 1). There is thus an overall probability of 0.0027 (0.09×0.03) that the activity areas in both Area 1 and Area 2 are exclusive for all frogs considered. It is therefore unlikely that the observed exclusivity of activity areas occurred by chance alone.

Seven frogs (5 males, 2 females) were radio-tracked for more than one season. One male established a new activity area 500 m from his original area. The remaining six animals used several home burrows between years and portions of the same activity area for two (4 males, 1 female) or three (1 female) consecutive seasons (see Fig. 3 for two examples).

All recorded activity areas had central points located 20–250 m from the breeding streams (Fig. 4). Although activity areas for each sex were found across all distances from the streams, those of males were significantly closer (mean 99 m) than for females (mean 143 m) ($F = 4.78$, d.f. = 1,27, $P = 0.038$). The distance from the central point of the activity area to the breeding site was not related to the body size (snout–vent length) for males

Table 1. Number of overlapping home ranges in 100 random placements of activity areas

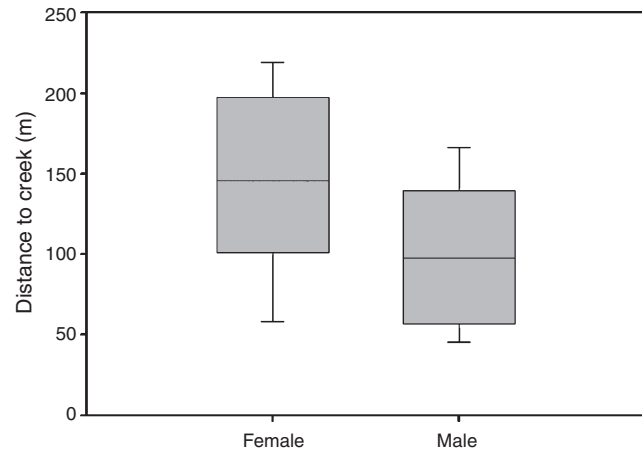
No. of frogs with exclusive ranges	Area 1	Area 2
All	9	3
3	24	12
2	30	28
1	25	40
0	12	17

**Fig. 3.** Seasonal variation in yearly activity areas for two frogs for which data are available.

($F=0.246$, d.f. = 1,7, $P=0.638$), females ($F=0.625$, d.f. = 1,5, $P=0.474$) or both sexes combined ($F=0.060$, d.f. = 1,13, $P=0.810$).

Burrowing

Individuals in the non-breeding area primarily sheltered diurnally by burrowing into the soil (1791 records for males, 98.2%; 1279 records for females, 99.1%). We also recorded frogs sitting on the substrate on 32 occasions, partially burrowed in leaf litter 12 times and twice perched within the foliage of grass trees (*Xanthorrhoea australis*) ~0.4 m above the soil surface. The

**Fig. 4.** Average distance of male and female activity areas from known breeding sites.

choice of diurnal shelter sites did not differ by sex ($\chi^2=4.96$, d.f. = 2, $P=0.084$).

Each frog occupied single-use burrows and multiple-use burrows (which we term home burrows). We defined a home burrow as a site that was used on two or more separate occasions for periods longer than one night. Males used 3 to 12 (mean 6.78) burrows in each area, whereas females used 3–24 (mean 8.72) burrows. Males used 1–7 home burrows (mean 3.5) and females used 1–14 (mean 4.2). With the data corrected for the number of records per frog, there was no significant difference between the sexes for the number of burrows used ($t=2.06$, d.f. = 23, $P=0.78$) or the number of home burrows ($t=2.07$, d.f. = 23, $P=0.53$).

Across all visits, the number of days spent in a home burrow during a single visit ranged from 1 to 156 for males with a mean of 13.2 ± 1.7 (mean \pm s.e.) days and from 1 to 95 days with a mean of 11.2 ± 1.3 (mean \pm s.e.) for females. Two frogs (1 male, 1 female) used the same burrow for a period of three months and were observed to be active during this period. The time between the reuse of a burrow ranged from 2 to 379 days for males (mean 34.62 ± 4.59 days) and 2 to 335 days (mean 36.1 ± 5.2 days) for females. The mean distance between home burrows was 7.63 ± 0.91 m (mean \pm s.e.) and the maximum 40 m. The greatest distance travelled between home burrows on any one night was 40 m.

Non-breeding habitat characteristics

There were no significant differences between the habitat features of the burrows occupied by males and females. Points at which the species burrowed had low levels of coverage by ground vegetation with the square metre surrounding the site having a mean of $7.84 \pm 1.01\%$ ground cover. Bare ground or leaf litter (both of which are suitable for frogs to burrow in) constituted a mean of $79.78 \pm 1.34\%$ of the ground coverage, with the remainder being either woody debris ($10.74 \pm 1.00\%$) or rocks ($1.64 \pm 0.60\%$). Litter depth above the burrow was a mean of 2.76 ± 0.15 cm. Records of the frogs were from 15 m through to 240 m from a breeding site, representing the lower slope through to the ridgeline.

The final habitat model, developed using a forward continuation ratio model, is presented in Table 2. Model fit was considered good, with an AUC value of 0.802. There were no detectable differences in any of the habitat characteristics of single-use ($n=131$) and multiple-use burrows ($n=98$). A quadratic relationship between the location of frog sites and the distance to the breeding site was found ($P<0.001$). This relationship suggests that two clusters of frog locations exist in the dataset: one ~60–80 m from the breeding site and another ~150 m from the breeding site. Frogs selected sites with more understorey cover ($P=0.0009$) than was recorded at the random sites. If a frog was found at a site, the probability of the individual sitting on the surface increased as the proportion of 'burrowable' ground (i.e. leaf litter + bare ground) decreased ($P=0.0003$).

Mortality

No mortality was recorded from the implanting procedure and all frogs appeared healthy (i.e. no wounds and maintaining body condition) when observed throughout the study. Five radio-tracked frogs were preyed upon during the course of the study: four due to red-bellied black snakes (*Pseudechis porphyriacus*) and one by a kookaburra (*Dacelo novaeguineae*). Predation of a further two frogs not implanted with radio-transmitters was recorded during the study period (Penman and Lemckert 2007).

Discussion

In this study, 33 individual *H. australiacus* were radio-tracked for extended periods and over successive seasons. This unique dataset has provided us with an improved understanding of this species' habitat use and behaviour, particularly in the non-breeding habitats. Broadly, forest habitats used in this study are consistent with the reports from the other south-east New South Wales sites (Lemckert *et al.* 1998; Lemckert and Brassil 2003; Penman *et al.* 2005a), Victoria (Gillespie 1990) and from the north of its range (Mahony 1993; Daly 1996). Data from this study has enabled us to develop recommendations about the most appropriate approaches for the management of this species.

Habitat use

Heleioporus australiacus spends at least 97% of its time in the non-breeding habitat. To our knowledge, this is longer than has been demonstrated for other amphibian species. This may reflect that most detailed research has either focussed on breeding behaviour (e.g. Fukuyama *et al.* 1988; Lemckert and Brassil 2000) or on post-breeding migrations (e.g. Lamoureux and Madison 1999; Richter *et al.* 2001) rather than the non-breeding habitat use itself. Some other frog species use forest areas only during primarily wet periods. For example, Bulger *et al.* (2003) found that *Rana aurora draytonii* used terrestrial sites for short periods (median of 4–6 days) only after summer rains or during the winter wet season. Other burrowing frog species have been found to spend extended periods of the year in non-breeding activity areas (e.g. Pearson 1955; Pilliod *et al.* 2002). The ability to burrow to obtain shelter seems the most likely reason for *H. australiacus* to occupy dry forest areas away from breeding sites throughout the year rather than just during wetter times.

Activity areas estimated for *H. australiacus* were similar between the sexes and were within the ranges reported for other species. In a review, Lemckert (2004) found a mean home range of 1773 m² (range 6.3–5099 m²) for anurans based on 18 studies. In this study, we estimated the activity area for *H. australiacus* as 498.1 ± 79.1 m². However, this considered only sheltering ranges in the non-breeding habitat and the estimates would have been significantly higher if we included nocturnal movements and breeding migrations.

The non-breeding activity areas appear to be based strongly around a series of home burrow sites that are used repeatedly and are well known to the individual. Individuals are able to home directly to these sites, even after many months of non-use and in the absence of a structured burrow. This indicates that these home burrow sites must have features that are highly preferred by individuals, but what factors drive this selection are not yet clear. Sites for the activity areas appear to be selected mainly on the basis of increased shade from the shrub and understorey layers. Increased shading over a burrow site would reduce the range of temperatures experienced, resulting in a reduction in the rate of moisture loss from the soil hence from burrowed individuals. Notably, records of frogs remaining on the surface were associated with wet conditions, suggesting that they did not need

Table 2. Results from the continuation ratio model examining habitat associations for random surface, single use and home burrow sites

Parameter	Estimate	s.e.	Wald χ^2	$P > \chi^2$
Level 0 – Random				
Intercept Level 0	-9.37030	1.92000	23.8174	<0.0001
Distance to creek	0.10340	0.02390	18.6859	<0.0001
Distance to creek ²	-0.00027	0.00007	13.5625	0.0002
Understorey cover	-0.01960	0.00720	7.3902	0.0066
Shrub cover	-0.01440	0.00775	3.4555	0.063
Level 1 – Surface				
Intercept Level 1	8.69190	2.00140	18.8609	<0.0001
Percentage of ground 'burrowable'	-0.02000	0.00767	6.7830	0.0092
Level 2 – Single-use burrows				
Intercept Level 2	9.66050	1.92470	25.1937	<0.0001

to burrow to avoid desiccation. Alternatively burrowing may have been avoided at this time owing to reduced oxygen availability in the saturated soils.

Homing behaviour to sites has been observed in other frog species, with animals returning to breeding ponds (e.g. Gill 1979), over-wintering burrows (e.g. Kelleher and Tester 1969) and structured shelter sites (e.g. Seebacher and Alford 1999). However, such specific site fidelity after long periods of absence has not been reported. Pearson (1955) studied the behaviour of spadefoot toads (*Scaphiopus holbrooki holbrooki*) and found animals using 2–5 structured burrows in the non-breeding area, indicating that other burrowing frog species may have similar habits. How they find these burrows again so specifically is uncertain, although chemical cues are likely.

The finding that the activity areas of individual *H. australiacus* do not appear to overlap with those of conspecifics was unexpected. There may possibly be some overlap of activity at times that frogs were not observed, but we never located a frog sheltering within the known activity area of another individual and individuals were never observed to cross into an activity area during periods of nocturnal activity (>30 observations), adding weight to the belief that they do not share activity areas. The fact that individual activity areas never overlap suggests an active avoidance or exclusion from activity areas by individuals and so they are exhibiting non-breeding territoriality. Many anurans are well known to be strongly territorial during times of reproduction, but there is little evidence of non-breeding territoriality. Mathis *et al.* (1995) reviewed territoriality in anurans and urodeles and concluded that anurans regularly undertake territorial defence of breeding sites, but rarely show any evidence of aggressive behaviour during non-breeding periods. Pearson (1955) observed some spatial and temporal separation of *S. h. holbrooki* in the non-breeding environment, which may have been a result of territoriality, but he had no specific evidence to confirm this. There are no obvious reasons why more anurans would not exhibit non-breeding territoriality if there was a resource that was limited and worth defending. However, we do not yet know what resources would be limited for these species, and further investigation is required. In particular, the abundance of prey within forests occupied by *H. australiacus* should be assessed to determine whether they could form the limiting resource that is being defended.

Implications for conservation

The patterns of habitat use and behaviour of *H. australiacus* creates challenges for the conservation of this species where multiple-use of forests is the desired outcome. This species occupies activity areas of ~500 m² in dry forest areas, with only rare movement into the breeding sites. They burrow in relatively shallow unstructured burrows that support the notion that fire and commercial timber harvesting are considered the main threats for this species (Penman *et al.* 2004, 2005b, 2006c).

Prescriptions have been developed for this species that incorporate either stream-side buffer zones or broad-scale exclusion areas in which fire and logging are excluded, depending on the region in which the frog is found (e.g. Anon. 1999). In the central coast region of New South Wales, stream buffer zones of 30 m are established around all drainage lines within 200 m of a

known locality for the species. Along the south coast a disturbance exclusion zone with a 500-m radius (78 ha) is established around the record. In far southern New South Wales a 200-ha exclusion zone is established around any record site for this frog within which no logging is allowed and there are restrictions placed on conducting prescribed burns. Within Victoria, where individuals are detected on smaller streams or away from streams a 50-ha disturbance exclusion zone is established. For records on larger streams a linear buffer of 100 m is established around the stream for 1 km upstream and downstream of the record.

The results of this study indicate that implementing stream-side buffer zones can probably not be applied effectively if both timber production and species conservation are the management aims. Males are more likely to be found closer to the breeding site than females and so narrower buffer zones will protect a disproportionate number of males relative to females, leading to a decline in the size of the population of breeding females and almost certain serious reductions in overall population size and genetic diversity. A larger 300-m buffer zone, as suggested by Semlitsch and Bodie (2003), will very likely protect most of a *H. australiacus* population and so be effective for conservation, but would not be practical if timber production was to continue. In areas occupied by *H. australiacus*, more than 95% of a catchment falls within 300 m of a potential breeding site, therefore for all intents and purposes 300-m buffer zones would function essentially as complete exclusion zones.

The use of buffer zones around known locations of this frog also has its limitations. Individual burrowing frogs have average non-breeding activity areas of ~0.05 ha. A 200-ha exclusion zone is therefore ~4000 times larger than an individuals' activity area and covers a significantly larger area than is used by the populations in this study. Where point records have occurred scattered over forests, large areas have been removed from forestry operations and most of this will have no significance to the species being protected.

A more suitable approach to managing this species, where timber production is also required, is the specific reservation of several known populations rather than attempts to buffer key habitat features within these areas. Specific reservation zones should be based on biologically meaningful areas that encompass several known breeding sites as well as the associated non-breeding habitat areas and not just an exclusion zone of a predetermined area, therefore the size of the zone needed to be protected will vary between areas. For most populations needing reservation, this would mean that additional surveys are required to adequately design the protection zones as this information is not currently available. The remaining populations would be protected with standard prescriptions designed to protect water quality and stream-side habitat, but recognising that most individuals will be subject to disturbances. The use of such an approach weighs up the desire of society to have a timber resource whilst trying to maintain the long-term conservation of these populations.

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