

Population ecology of a cryptic arboreal snake (*Hoplocephalus bitorquatus*)

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Abstract. Biologists have traditionally been reluctant to study arboreal snakes due to low rates of capture. Overlooking such taxa can mislead interpretations of population trends for data-deficient species. We used regularly spaced transect searches and standard capture–mark–recapture techniques to describe population structure, growth rates, survival and capture probability in a population of the pale-headed snake (*Hoplocephalus bitorquatus*) in southern Queensland. We obtained data from 194 captures of 113 individual snakes between 2009 and 2015. Using the Cormack–Jolly–Seber method, we estimated apparent annual survival in subadult snakes at 0.23 ± 0.01 (s.e.) and 0.81 ± 0.08 for adults. Capture probability was estimated at 0.16 ± 0.14 per session in subadult snakes and 0.33 ± 0.06 for adults. Within the red gum forests of our study site, we estimate pale-headed snake density at $\sim 13 \pm 7 \text{ ha}^{-1}$. Using von Bertalanffy growth modelling, we predict that snakes reach sexual maturity after about four years and may live for up to 20. Our results suggest that the species is a ‘*k*’ strategist, characterised by slow maturation and low fecundity. These traits suggest that populations will recover slowly following decline, exacerbating the risk of local extinction.

Additional keywords: capture–mark–recapture, Cormack–Jolly–Seber, Elapidae, population estimate, von Bertalanffy growth modelling.

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Introduction

Demographic information is fundamental to understanding a species’ life-history strategy and conservation requirements. Arboreal snakes pose a particular challenge in documenting such information, due to the difficulty of collecting sufficient data for detailed analysis (e.g. Fitzgerald *et al.* 2004). Most species that have been studied tend to spend considerable periods on the ground, permitting comparatively higher capture rates (e.g. Slip and Shine 1988; Webb and Shine 1998a). When capture rates are low, data have poor statistical power and the distinction between true rarity and inadequate sampling can become obscured (Durso *et al.* 2011). Given that habitat specialisation is a significant correlate with extinction risk in reptiles (Böhm *et al.* 2016), data deficiencies in arboreal species are of concern. Identifying taxa that possess extinction-promoting traits allows conservation efforts to be implemented before precipitous declines occur (Böhm *et al.* 2016). Such analyses have been well documented in several vertebrate groups, with the notable exception of reptiles (Böhm *et al.* 2016).

The pale-headed snake (*Hoplocephalus bitorquatus*) is a mostly arboreal, nocturnal elapid inhabiting parts of eastern Australia (Fig. 1), between Sydney in New South Wales and Cairns in far north Queensland (a distance of ~ 2000 km) (UBCBBM 2016). The pale-headed snake is not listed as

threatened under international (IUCN), federal or state legislation in Queensland, but is recognised as vulnerable to extinction in New South Wales (*Biodiversity Conservation Act 2016*). The species appears to be uncommon and subject to threatening processes such as habitat clearing, which warrant concern about its conservation status (Fitzgerald *et al.* 2010). Additionally, the species shows a dietary preference for frogs, which has raised concerns over its ability to persist in areas occupied by the highly toxic, introduced cane toad (*Rhinella marina*) (Fitzgerald *et al.* 2010). The extent to which pale-head snakes feed on terrestrial prey is largely unknown; however, Shine (1983) recorded ground-dwelling frogs of the genus *Limnodynastes* within the stomach content of museum specimens. If this trophic relationship between ground frogs and pale-headed snakes is significant, this may leave them vulnerable to rapid population decline as cane toads expand their extent of occurrence. On the basis of conservative climate-change models, Phillips *et al.* (2003) estimate that cane toads will occupy $\sim 94\%$ of the pale-headed snakes’ known distribution by 2030.

Our study was conducted in part of the species’ geographic range where (until early 2016) cane toads had not been recorded. We describe demographic characteristics of a pale-headed snake (PHS) population from southern Queensland and estimate density using standard capture–mark–recapture (CMR)



Fig. 1. Typical defensive posture of *Hoplocephalus bitorquatus*.

procedures. The ecology of the two PHS congeners – broad-headed snake (*H. bungaroides*) and Stephen's banded snake (*H. stephensi*) – has been well documented in the scientific literature and both species exhibit ‘slow’ life-history traits that predispose them to extinction (Webb and Shine 1998b; Fitzgerald *et al.* 2004). We use our data to extend the comparison by Fitzgerald *et al.* (2010) between the life-history traits of the PHS and that of its congeners.

Methods

Study area

Our study area was located near Dalby (27.1944°S, 151.2660°E) in the western Darling Downs region of southern Queensland. The climate is characterised by hot summers (mean January temperature range = 18.7–32.4°C) and mild winters (mean July temperature range = 4.0–19.6°C) (Bureau of Meteorology 2016). Rainfall predominantly occurs over summer months, averaging 607 mm annually (Bureau of Meteorology 2016). The landscape is flat with underlying geology primarily comprising Quaternary alluvial deposits. Four regional ecosystems, as defined by Sattler and Williams (1999), occur in the study area: cypress pine forest (dominated by *Callitris glaucophylla*), brigalow woodland (dominated by pilliga grey box, *Eucalyptus piligera*), open woodland (dominated by bimble box, *E. populnea*) and red gum forest (dominated by *E. tereticornis*). Most of the study area is considered remnant vegetation;

however, the site was extensively grazed before being protected in 1978. The surrounding district is principally cleared and continues to be used for agricultural purposes and gas exploration.

Survey design

The study area was overlain by a 500 m × 500 m grid, with resulting grid-cell intersections used to locate a set of potential sampling units. Vegetation boundaries were identified from aerial photography and confirmed in the field. Our preliminary surveys for PHS (before this study) resulted in difficulty detecting the species outside red gum forest. Thus, for the purpose of a CMR study, only grid-cell intersections that represented this regional ecosystem were selected. These resulted in eight grid intersections being identified for sampling, each transect measuring 250 m × 40 m and orientated to align with topographical contours.

Visual encounter surveys were conducted at night using head torches, attempting to sight snakes in any component of the forest structure. Transects were traversed on foot and surveyed for the equivalent of one person-hour. Factors considered likely to influence snake activity were standardised by starting 30 min after sunset and conducting surveys only during the warmer months (when ambient air temperatures were ≥15°C). We captured all PHS that were observed wherever possible (either in transects or opportunistically encountered whilst traversing between transects).

Capture data

Upon capture we recorded the sex, tail length and snout–vent length (SVL) of each snake. At first capture each snake was uniquely identified by implanting a PIT tag (Trovan Electronic Identification Devices Ltd) under a ventral scale (~20 scales anterior to the cloaca). The tags measured 11 mm × 2.2 mm in the first year of our study and 7 mm × 1.25 mm thereafter. The insertion site was swabbed with ethanol, followed by a topical application of Lignocaine (allowing at least five minutes for anaesthesia to take effect). Incision areas were sealed with surgical adhesive (3M Vetbond) to minimise secondary infection and prevent tag loss. All procedures were performed the morning after capture and snakes were thereafter released as near as possible to their original capture location (i.e. closest suitable tree cavity).

Growth rates

We used the von Bertalanffy growth model (von Bertalanffy 1957) to estimate the relationship between age and SVL of PHS. The von Bertalanffy growth model follows the following equation:

$$L(t) = A(1 - \exp(-k(t - t_0)))$$

where L is the length in metres, A is the asymptotic length (length at an infinite age), k is the intrinsic growth rate and t is time in years. L at birth (t_0) was estimated at 0.2 m, equating to the size of the smallest snake captured during this study. This is consistent with the SVL at birth reported for captive specimens (Lazell 2000) and the smallest museum specimens (Shine 1983). Length at birth was assumed to be the same for both sexes,

while A was determined for each sex using the maximum SVL of snakes captured during the study (0.51 m for males and 0.66 m for females). Growth rates were estimated by methods in Kaufmann (1981) using the following equation:

$$G = 100((S_2 - S_1)/t)$$

where S_1 is the SVL at the beginning of time interval t , S_2 is the SVL at the end of time interval t and growth rate (G) is expressed as the percentage increase in SVL per day. Recaptured snakes were generally measured only once per calendar year.

Statistical analysis

We used the Chi-square goodness-of-fit test to compare the observed counts of PHS categorised by sex. To compare our observed distributions of PHS size classes with a normal distribution, we used the Shapiro–Wilk test of normality. Where the data implied a skewed distribution, measured variables were transformed using natural logarithms to satisfy assumptions of normality. We used the Pearson correlation coefficient to compare the relationship between log-transformed SVL and log-transformed tail length of PHS. To investigate whether there was sexual dimorphism in PHS tail lengths relative to body size, we used a single-factor analysis of covariance (ANCOVA), with log-transformed SVL as the covariate and log-transformed tail length as the dependant variable. To examine any sex-divergence in growth rates of PHS we used the Student's t -test. All statistical analysis was performed in the computer package *R* Studio 3.1.2 (R Development Core Team 2014).

Population modelling

We used MARK 8.0 (White and Burnham 1999) to estimate PHS demographic parameters. Capture histories were constructed for each individual snake. Our data were arranged into 13 sampling periods, with intervals varying from 35 to 253 days. The Cormack–Jolly–Seber (CJS) method (Cormack 1989) was chosen to estimate apparent annual survival (ϕ) and capture probabilities (p). We investigated the degree to which the data conformed to CJS model assumptions by carrying out goodness-of-fit tests using the program RELEASE (Burnham *et al.* 1987). The goodness-of-fit test determined whether either of the first two of the following four CJS model assumptions were violated:

1. Every animal present in the population at the time of the i th sample ($i = 1, 2, \dots, k$) has the same probability of recapture (p_i)
2. Every marked animal present in the population immediately after the i th sample has the same probability of survival (ϕ_i) until the $(i + 1)$ th sampling time ($i = 1, 2, \dots, k - 1$)
3. Marks are not lost or overlooked.
4. All samples are instantaneous and each release is made immediately after the sample (Pollock *et al.* 1990).

We fitted nine different candidate models to the data in which apparent survival and capture probabilities were either constant, varied over time, and/or influenced by body size (two attribute groups). Individual snakes were grouped by body size at first capture (<350 mm SVL = subadults; ≥ 350 mm SVL = adults) and represented minimum reproductive SVL thresholds described by Shine (1983). Models were compared using the Akaike's Information Criterion (AIC_c) and ranked

from smallest to largest, as recommended by Buckland *et al.* (1997). Model comparisons were considered to have meaningful support where ΔAIC_c values were < 2 and essentially no support when ΔAIC_c was > 7 (Burnham and Anderson 1998). Consequently, only models $< 2 \Delta AIC_c$ were considered for further analysis. We then calculated model-averaged estimates for survival and capture probability to account for uncertainty in model selection (Burnham and Anderson 1998). Finally, we estimated the density of PHS in our study area using the methods of Hamer and Mahony (2007), as follows:

$$N = n/p$$

where n is the number of snakes marked and p is capture probability (model-averaged). The standard error of the estimate was approximated as:

$$s.e.(N) = n(s.e.(p))/p^2$$

Results

Demographic characteristics

In total, 194 captures of 113 individual PHS (20 males, 38 females and 55 individuals where the sex was not determined) were recorded between 2009 and 2015. The frequency of capturing female PHS was significantly greater than that of male PHS ($\chi^2 = 5.586$, d.f. = 1, $P = 0.018$). SVL ranged from 320 mm to 514 mm (mean = 434 ± 12 , s.e.) for male PHS and 260 mm to 660 mm (mean = 443 ± 14 , s.e.) for female PHS (Fig. 2). Morphometric data from our study population revealed an approximately normal distribution of size classes ($w = 0.969$, $P = 0.029$). However, the subset of size class data for each sex trended towards skewed distributions (i.e. male PHS: $w = 0.944$, $P = 0.401$; female PHS: $w = 0.956$, $P = 0.157$). Tail lengths in male PHS ranged from 50 mm to 102 mm (mean = 84 ± 3) and were strongly correlated with SVL ($r = 0.883$, $P \leq 0.001$, $n = 16$) (Fig. 3). Tail lengths in female PHS ranged from 40 mm to 110 mm (mean = 77 ± 3) and were also highly correlated with SVL ($r = 0.913$, $P \leq 0.001$, $n = 35$) (Fig. 3). Relative to body size (SVL), male PHS had significantly longer tails than female PHS ($F_{1,48} = 23.04$, $P \geq 0.001$). The individual growth rate of PHS was estimated at 0.22% of SVL increase per day (Fig. 4). Growth rates were also estimated for each sex (males, 0.15%; females, 0.20%) but did not differ significantly ($t = 2.110$, d.f. = 17, $P = 0.753$).

CMR modelling

Between November 2010 and October 2015 we conducted 87 surveys with individual transects surveyed on 2–31 occasions. We used data from 61 captures of 30 known PHS captured between 2011 and 2015 for CMR analysis. A goodness-of-fit test on the full CJS model showed no significant deviation ($\chi^2 = 8.806$, d.f. = 16, $P = 0.921$), suggesting that the assumptions of the model were met and thus constituted an appropriate framework to estimate demographic parameters (Lebreton *et al.* 1992). The most parsimonious models were generally those with the least number of parameters (Table 1). The difference in ΔAIC_c of the top three models was < 2 , suggesting that each was equally plausible. Model-averaging was used to estimate

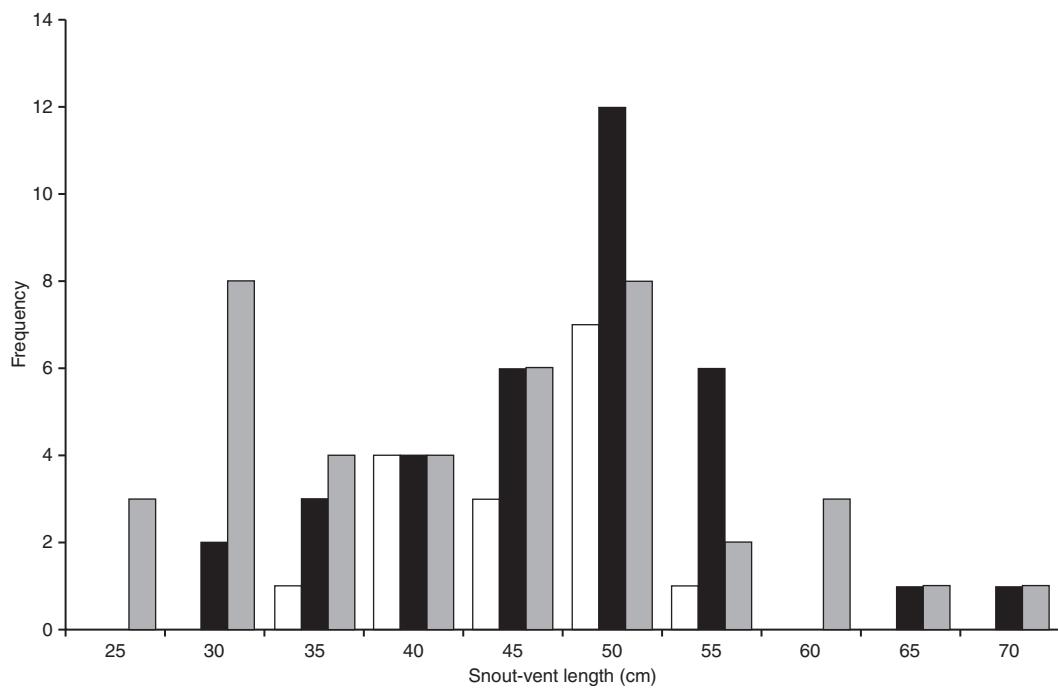


Fig. 2. Frequency of snout–vent length for *Hoplocephalus bitorquatus* captured between 2009 and 2015 ($n=91$) in southern Queensland. Numbers on the x -axis represent the upper limit of each snout–vent length grouping. White bars, males ($n=16$); black bars, females ($n=35$); grey bars, unknown sex ($n=40$).

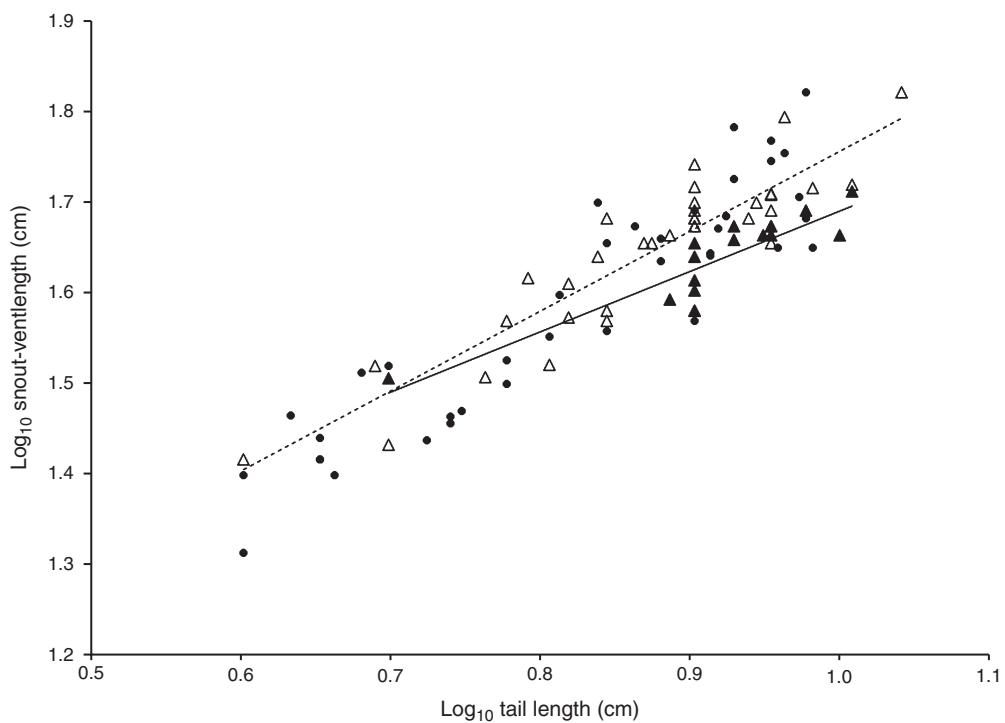


Fig. 3. Correlation between snout–vent length and tail length of *Hoplocephalus bitorquatus* captured between 2009 and 2015 ($n=91$) in southern Queensland. Solid triangles and solid line, males ($n=16$); open triangles and dashed line, females ($n=35$); dots, unknown sex ($n=40$).

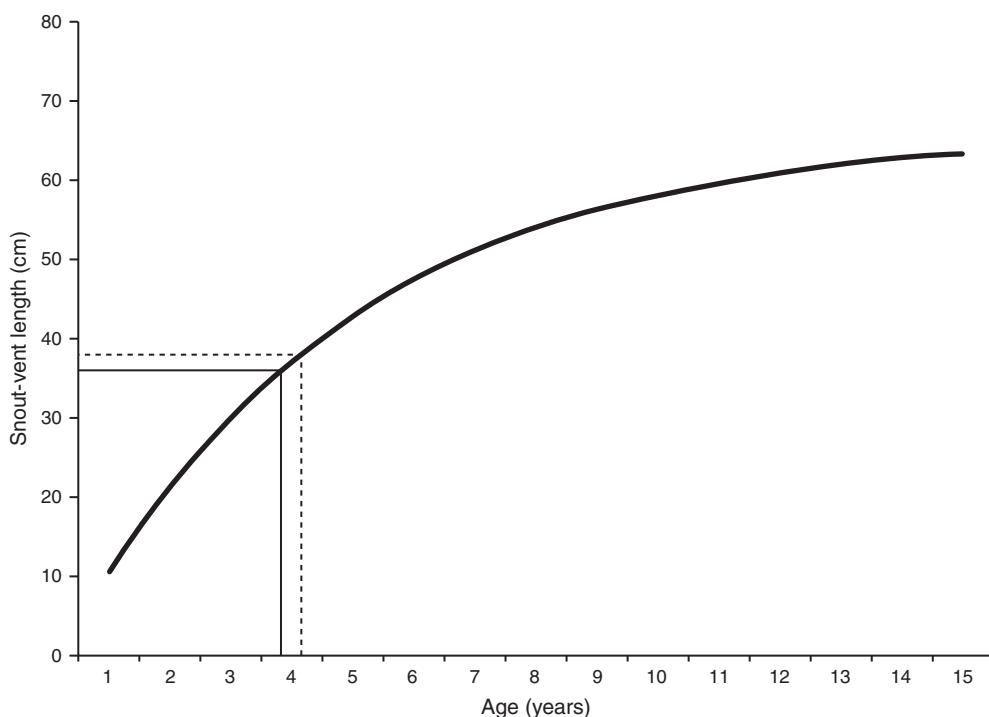


Fig. 4. Predicted relationship between age and snout–vent length of *Hoplocephalus bitorquatus* captured between 2009 and 2015 in southern Queensland. Combined data from all snake growth measurements are represented by the solid black line ($n = 23$ individuals, $N = 58$ captures). Dashed axis lines represent snout–vent length attained at sexual maturity for female *Hoplocephalus bitorquatus*, as described by Shine (1983). Grey-axis lines represent snout–vent length attained at sexual maturity for male *Hoplocephalus bitorquatus*, as described by Shine (1983).

Table 1. CJS model selection results for annual survival and capture probabilities of *Hoplocephalus bitorquatus* in red gum forests of southern Queensland ($n = 30$ individuals, $N = 61$ captures)

AIC_c, Akaike's Information Criterion; ΔAIC_c, difference between any model and the top model; k, number of parameters in each model; ., constant survival or capture; t, time varying survival or capture. Only models within 7 ΔAIC_c of the top model are included

Survival (ϕ)	Capture (p)	AIC _c	ΔAIC _c	AIC _c weights	Model likelihood	k	Deviance
2 size groups (./.)	2 size groups (t./.)	145.08	0.00	0.39	1.00	5	100.10
1 size group (.)	2 size groups (t./.)	145.11	0.04	0.38	0.98	4	102.55
2 size groups (t./.)	2 size groups (t./.)	146.43	1.35	0.20	0.51	7	96.32
1 size group (.)	2 size groups (t/t)	151.61	6.53	0.01	0.04	12	86.58

apparent annual survival and capture probability. Annual survival was lower for subadult snakes (0.23 ± 0.01) than for adults (0.81 ± 0.08). Capture probability was also lower for subadult snakes (0.16 ± 0.14 per session) than for adults (0.33 ± 0.06).

On the basis of our CMR data we estimated PHS density at our study site to be $12.6 \pm 6.8 \text{ ha}^{-1}$ ($6.8 \pm 5.8 \text{ ha}^{-1}$ for subadults, $5.8 \pm 1.1 \text{ ha}^{-1}$ for adults). Extrapolating this across 121 ha^2 of red-gum forest that comprised our study area, we calculate that $\sim 1527 \pm 832$ (95% CI: 695–2359) PHS occurred within this particular regional ecosystem.

Discussion

This study provides the first analysis of demographics in a PHS population. Snake detection in general was low, reflective of

the species' cryptic nature and habit of sequestering in tree hollows for extended periods (Fitzgerald *et al.* 2010). Therefore, the precision of our parameter estimates may be influenced by the relatively small number of recaptures. Our data, however, expand substantially on available information regarding life-history characteristics for the species.

Demographic characteristics

Unlike most endothermic vertebrates (which cease growing beyond sexual maturity) reptiles sustain continued growth throughout their lives (Shine and Charnov 1992). Despite this, the von Bertalanffy growth model has been proven to accurately describe growth rate in snake populations (Madsen and Shine 2000; Brito and Rebelo 2003; Stanford and King 2004; Wilson *et al.* 2006). The SVL attained at sexual maturity for PHS has

been estimated at ~360 mm for males and ~380 mm for females (Shine 1983). Based on this (and our calculated asymptote), our data suggest that PHS grow slowly and attain maturity after about four years. Slow maturation appears to be combined with low fecundity in PHS, with females generally giving birth to no more than five young (Shine 1983). Furthermore, reproduction in sexually mature adult PHS may be infrequent. On the basis of adult-sized female PHS museum specimens, Shine (1983) estimated that 42% ($n=26$) had inactive ovaries, suggesting that reproduction occurs every two years. Propensity for low reproductive output appears to be common within the genus, with female broad-headed snakes giving birth to ~6.8 young (every second year) from the age of about six (Webb *et al.* 2002), and Stephen's banded snakes giving birth to ~3.8 young from about four years (Fitzgerald *et al.* 2004). These biological traits conform to the model of a 'k-strategist', particularly in comparison with other small elapids. In terms of our study, this paradigm may be further supported by the implication of a PHS population that appears to be at demographic equilibrium. For example, most of our study population appears to consist of sexually mature adults, balanced with relatively equal proportions of subadults and older animals on either side respectively.

The sex ratio of our study population was observed to be female-biased (i.e. 66% of PHS where sex was determined). Although this is possibly a function of variation in capture probabilities between the sexes, we were unable to unequivocally demonstrate this (with CMR analysis) using the data we collected. Assuming that the primary sex ratio (at birth) in our study population is 1 : 1, the female-biased sex ratio we observed would suggest that survival rates are lower for males. However, given our small sample size, we did not attempt to estimate survival rates by sex during this study. Biased sex ratios can have conservation implications for populations recognised as small and/or vulnerable (Grayson *et al.* 2014). Although female-biased populations are considered less concerning (i.e. the ability to increase population birth rates), mate limitation can occur when ratios are extreme and increases the potential for inbreeding (Wedekind 2002).

CMR modelling

In general, adult survival rates estimated during this study were slightly higher than those reported for other snake populations (e.g. Bonnet *et al.* 2002; King *et al.* 2006; Hyslop *et al.* 2012; Sewell *et al.* 2015). However, our survival estimates for PHS were similar to those of other *Hoplocephalus* species. Using age-specific model classes, Webb *et al.* (2002) estimated annual survival in broad-headed snakes (beyond three years of age) to be 0.82 ± 0.06 (s.e.). We also estimated apparent annual survival to be age-dependent (0.81 for adults and 0.23 for subadults). Age-dependent survival rates among snakes are not uncommon, with juveniles presumably being more vulnerable to sources of mortality (e.g. Webb and Whiting 2005). However, Pike *et al.* (2008) suggested that interpretations of low juvenile survival rates in many reptile populations may simply be a function of sampling issues. For example, estimating apparent survival rates using CMR relies on the assumption that every animal present has the same probability of being detected;

however, this may not be the case for our study population. We encountered most (79%) subadult PHS (i.e. <350 mm SVL) perched in trees; in comparison, only 40% of adults were encountered in trees. If this is a function of age-dependant habitat partitioning (i.e. juvenile snakes are principally arboreal) our survival estimate for subadult PHS may have been influenced by low detection probability (e.g. adult snakes presumably being more conspicuous at ground level). Our analysis supported a discrepancy in capture probabilities, with only 16% of subadult snakes recaptured per session. Our capture probability estimate of 33% for adult snakes was similar to the 30% by Webb *et al.* (2002) for the closely related broad-headed snakes.

Population density for this species has not previously been estimated. Our density estimate of ~ 13 PHS $\text{ha}^{-1} \pm 7$ (s.e.) within red gum forests may be considered high amongst snake taxa, although density estimates of >20 adults ha^{-1} have been reported for other elapids (e.g. Carnac Island tiger snakes, *Notechis scutatus*: Bonnet *et al.* 2002). Despite ancillary survey effort outside of red gum forests (41 transect surveys), detection remained extremely low ($n=1$, unpubl. data). Therefore, snake density could not be estimated for the more extensively distributed regional ecosystems not considered by our study. On the basis of other data associated with this study we suspect that PHS density is significantly lower in adjoining habitats and largely limited by the number of live hollow-bearing trees available to individuals (M. B. Shelton, S. S. Phillips and R. L. Goldingay, unpubl. data).

Conservation implications

Conformity to *k*-selection by *Hoplocephalus* spp. implies that population recovery is likely to be slow following decline (Purvis *et al.* 2000). This has particular relevance to the conservation biology of the PHS, which may be incapable of compensating for the short-term loss of individuals in a population. Being a habitat specialist, fragmentation of lacustrine and riparian red gum forests across eastern Australia is likely to threaten remaining PHS populations. Furthermore, frog-eating snake populations in Australia may also be subjected to decline where cane toads become established (Phillips *et al.* 2003). Without empirical evidence, predictions about PHS vulnerability to cane toads can only be based on hypotheses about causal mechanisms (Brown *et al.* 2011). For example, the dietary habitat, geographic distribution and relatively large gape width of PHS would suggest that they are at potential risk from toad invasions. Yet populations of PHS do persist in some areas where cane toads have been established for several decades (e.g. Einasleigh Uplands bioregion). The density of PHS in these ecosystems does appear to be much lower than that of our study site (pers. obs.); however, quantifying the effect toads have on these PHS populations may be difficult without comparative assessment of other density-dependent factors (i.e. available tree cavities). Given the impending arrival of cane toads to our study site, baseline data from this study can provide future opportunities to measure the response of a PHS population after toad invasion. Given that detailed aspects of PHS ecology have received limited attention to date (Fitzgerald *et al.* 2010), future studies would help clarify the species' true conservation

status and become potentially important for the conservation management of the species.

Conflicts of interest

The authors declare no conflicts of interest.

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