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Molecular phylogeny of the Australian venomous snake genus *Hoplocephalus* (Serpentes, Elapidae) and conservation genetics of the threatened *H. stephensii*

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Abstract

The Australian elapid snake *Hoplocephalus stephensii* (Stephens' Banded Snake) is patchily distributed in disjunct forest remnants in eastern Australia and is listed as threatened in both states in which it occurs (Qld and NSW). Here we focus on the phylogeography of *H. stephensii* to address (1) the genetic distinctiveness of this taxon within its genus and (2) the level of genetic diversity present within and between disjunct populations from throughout the species' range. We sequenced an approximately 900 base pair DNA fragment of the mitochondrial genome that includes half of the ND4 gene and three tRNA genes. We obtained sequence data from 15 *H. stephensii* individuals drawn from four populations, plus representatives of the other *Hoplocephalus* species. Phylogenetic analyses of the data produced a single fully resolved tree. The two coastal taxa (*H. bungaroides and H. stephensii*) are very closely related (2.6–3.1% sequence divergence) whereas the inland taxon *H. bitorquatus* is more distantly related to the other two (7.6% vs *H. bungaroides;* 7.8–8.3% vs *H. stephensii*). Genetic diversity is low within *H. stephensii* (nine mitochondrial haplotypes with 1–3 haplotypes with only single base pair differences within populations). The largest split (1.7% sequence divergence) occurs between the northern population and the three southern populations and corresponds to the species distribution north and south of the McPherson Range on the Queensland-New South Wales border. The three southern populations display much less molecular divergence (maximum of 0.6% sequence divergence), consistent with the presence of generally continuous forest throughout the species' range until European invasion of Australia 200 years ago, and with radiotelemetric studies that have found high vagility in these arboreal snakes. Thus, on the basis of genetic distinctiveness we argue that (1) *Hoplocephalus bitorquatus* should receive high conservation priority; and (2) managers should treat the Queensland and NSW populations of *H. stephensi* as separate conservation units.

Introduction

Information on the genetic relationships of organisms can help managers to focus their efforts on truly distinctive taxa. This approach has become increasingly popular over recent years, with the development of methods to take phylogenetic distinctiveness into account when setting conservation priorities (Moritz 1994, 1995; Moritz and Faith 1998). Inevitably, however, the data necessary to make such judgements are available for a small minority of taxa, even for highly threatened organisms. For example, phylogenetic relationships among snake species have been highly controversial, with numerous conflicts between conclusions based on alternative data sets (i.e. for Australian elapid snakes: Keogh 1998; Keogh et al. 1998). Much of this difficulty revolves around the high frequency of parallel and convergent evolution in morphological traits of these animals, so that molecular data sets offer special promise for resolving such ambiguities (Keogh et al. 2000).

Australia is home to more than 90 species of venomous elapid snakes, and it is the only snake fauna in the world that is not dominated by the primarily non-venomous colubrid snakes. Many of Australia's elapids are ecologically specialised (e.g. Shine 1991) and due largely to habitat destruction, several species are now listed as threatened or endangered (Cogger et al. 1993; Reed and Shine 2001). As is commonly the case, these threatened taxa do not constitute a random subset of the fauna; instead, some lineages (e.g. brownsnakes, *Pseudonaja*) have flourished in disturbed habitats whereas others have declined. The most dramatic example of the latter situation involves the broad-headed snakes (genus *Hoplocephalus*), a group of three arboreal species from eastern Australia. These are among the most morphologically distinctive Australian elapids (indeed, it is the only genus whose membership has remained stable through the numerous taxonomic rearrangements of the Australian elapids over the last 50 years: Mengden 1983). All three *Hoplocephalus* species have declined considerably over recent decades, and all are listed as threatened under relevant wildlife legislation (Lunney et al. 2000).

We have used molecular techniques to examine genetic structure and distinctiveness at two levels within *Hoplocephalus*. First, we examine phylogenetic relationships among the three species because previous suggestions on this topic, based on morphology (Wallach 1985) and karyotypes (Mengden 1985), have produced contradictory topologies. Also, information on these relationships, and on the degree of genetic distinctiveness of each taxon, may reveal which taxa contribute most to biodiversity at the genetic level. Second, we examine the phylogeographic structure among populations of *H. stephensii* from across its range. The levels of genetic divergence between now-isolated populations of this species can tell us which remnant forest patches we need to conserve in order to maximise molecular genetic diversity within the species.

Materials and methods

Study species

The three species within the genus *Hoplocephalus* (*bitorquatus*, *bungaroides*, and *stephensii*) are highly morphologically derived relative to other Australian elapids, reflecting the fact that they are more highly adapted to arboreal habits than are any other members of this extensive radiation (Shine 1983). All three species display highly keeled ventral scales and wide, angular heads (Hutchinson 1990) and are distributed in eastern Australia (Cogger 2000). However, they differ considerably in habitat use. *Hoplocephalus bungaroides* is largely restricted to southeastern coastal habitats that include exposed sandstone outcrops. The snakes spend the cooler months of the year under exfoliated boulders on these outcrops, moving to trees within the adjacent eucalypt forests in summer (Webb and Shine 1997a, b). *Hoplocephalus bitorquatus* has a wider distribution than *H. bungaroides*, including semi-arid areas west of the Great Dividing Range. Anecdotal reports suggest that the species lives on large trees close to rivers (Shine 1991). Lastly, *Hoplocephalus stephensii* is found along a near-coastal strip from the Newcastle area in central eastern New South Wales to the Gympie area in southern Queensland. However, *H. stephensii* is distributed very patchily throughout this range, being restricted to remnant areas of dense forest. The species is listed as threatened in both Queensland and New South Wales (Lunney et al. 2000).

Data on morphology (Wallach 1985; Keogh 1999), immunological distances (Schwaner et al. 1985), karyology (Mengden 1985) and mitochondrial DNA (Keogh et al. 1998, 2000) strongly support the monophyly of a lineage comprising the genera *Austrelaps*, *Hoplocephalus*, *Notechis* and *Tropidechis* (Keogh 1999; Keogh et al. 2000). Extensive data on mitochondrial DNA show that '*Echiopsis*' *atriceps* (now *Paroplocephalus atriceps*) is also part of this lineage (Keogh et al. 2000). However, relationships within *Hoplocephalus* remain unclear (see above).

Samples

We obtained samples of *H. stephensii* to encompass sites close to the northern and southern extremes of the species' range (Newcastle and Brisbane) as well as areas in between (Coffs Harbour and Lismore). We included samples from 3 to 4 individuals from each of these four regions (Table 1; Figure 1) to evaluate intra-population level variation. Because of the threatened status of this species, we used sloughed skins or scale clips to obtain DNA sequences. The samples were obtained during an ongoing study into the ecology of this species; no animals were killed for these samples. We also included two samples each of *Hoplocephalus bitorquatus* and *Hoplocephalus*

Table 1. Summary of specimens sampled and their locality information. Due to their conservation status, all genetic samples of *Hoplocephalus* used in this study were obtained in the form of shed skins or scale clips, thus these animals were not killed. SAM = South Australian Museum. The haplotype identification number corresponds to those in Table 2 and Figure 1

Species (our lab number)	Museum Number	Haplotype ID	Locality
Austrelaps superbus	SAM R19835		Penola State Forest, South Australia
Notechis scutatus	SAM R31329		Coffin Bay, South Australia
Tropidechis carinatus	SAM R30596		No data available
Hoplocephalus bitorquatus			Dalby area, Queensland
Hoplocephalus bitorquatus			Dalby area, Queensland
Hoplocephalus bungaroides			Morton National Park, New South Wales
Hoplocephalus bungaroides			Morton National Park, New South Wales
Hoplocephalus stephensii (Seq1)		1	D'Aguilar Range, 20 km North-west of Brisbane, Queensland
Hoplocephalus stephensii (DOC153)		2	Mt. Glorious, Boombana, 20 km North-west of Brisbane, Queensland
Hoplocephalus stephensii (Sk08)		2	Mt. Nebo, 9 km West of Brisbane, Queensland
Hoplocephalus stephensii (Sk23)		3	Whian Whian State Forest, 30 km North-east of Lismore, New South Wales
Hoplocephalus stephensii (Sk20)		3	Whian Whian State Forest, 30 km North-east of Lismore, New South Wales
Hoplocephalus stephensii (Sk16)		3	Whian Whian State Forest, 30 km North-east of Lismore, New South Wales
Hoplocephalus stephensii (Sk01)		3	Tyalgum, 20km West of Murwillumbah, New South Wales
Hoplocephalus stephensii (Sk24)		4	35 km North-east of Grafton, New South Wales
Hoplocephalus stephensii (01)		5	10 km West of Coffs Harbour, New South Wales
Hoplocephalus stephensii (03)		5	Bruxner Park, Coffs Harbour, New South Wales
Hoplocephalus stephensii (02)		6	Bruxner Park, Coffs Harbour, New South Wales
Hoplocephalus stephensii (Sk02)		7	75 km North of Newcastle, New South Wales
Hoplocephalus stephensii (Sk25)		7	35 km South-west of Newcastle, New South Wales
Hoplocephalus stephensii (Sk09)		8	40 km South-west of Newcastle, New South Wales
Hoplocephalus stephensii (Sk26)		9	30 km South-west of Newcastle, New South Wales

bungaroides to provide information on phylogenetic relationships among the three *Hoplocephalus* species. The Australian copperhead (*Austrelaps superbus*), rough scaled snake (*Tropidechis carinatus*) and tiger snake (*Notechis scutatus*) were used as outgroups as they are closely related to *Hoplocephalus* (Keogh 1998, 1999; Keogh et al. 2000).

DNA sequencing

For each sample we targeted an approximately 900 base pair (bp) DNA fragment of the mitochondrial genome which included the 3' half of the ND4 gene and most of the tRNA cluster containing the Histidine, Serine and Leucine tRNA genes. The target fragment was amplified using modified primers ND4 and Leu (Arévalo et al. 1994). This region was targeted because work at comparable taxonomic levels in other squamate reptile groups has revealed useful levels of variability (Kraus et al. 1996; Benabib et al. 1997; Forstner et al. 1998; Scott and Keogh 2000). All laboratory procedures are as in Scott and Keogh (2000) and so we do not repeat them here. Because ND4 is protein coding, alignment was straightforward. Aligned sequences were translated into amino acid sequences using the vertebrate mitochondrial genetic code. No premature stop codons were observed, so we conclude that all sequences obtained are true mitochondrial copies.

Phylogenetic analyses

Parsimony, neighbour-joining and maximum likelihood analyses were performed using PAUP* Ver-

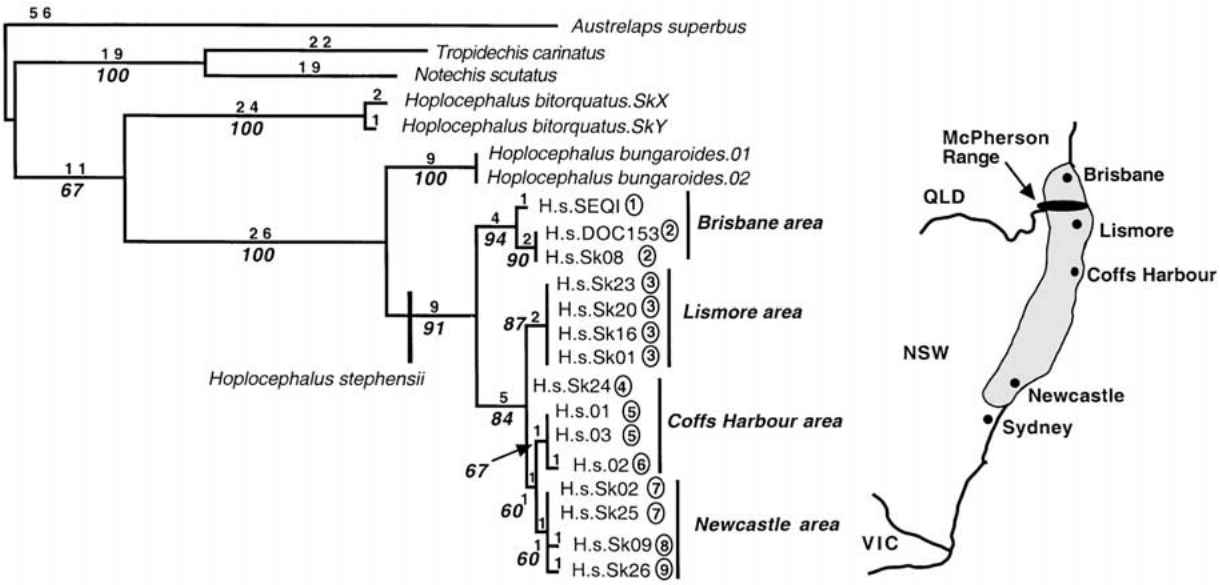

Figure 1. Single most parsimonious tree recovered from an unweighted parsimony analysis. This tree is identical to those obtained by distance and maximum-likelihood analyses. Numbers above the nodes are branch lengths and numbers below the nodes are bootstrap values. Numbers in circles correspond to our haplotype numbers used in Tables 1 and 2. The map shows the distribution of *Hoplocephalus stephensii* (modified from Cogger 2000), with the localities of our major sample sites and the McPherson Range. The range covers a distance of approximately 700km north to south.

sion 4.0 (Swofford 2000). For our parsimony analyses we used unweighted data and also used the ti/tv ratio estimated from the data via maximum likelihood. Neighbour-joining distance analyses used Jukes-Cantor (1969) genetic distances. We also did a transversions-only analyses. We used the objective criteria provided by the computer program ModelTest 3.06 (Posada and Crandall 1998) to select the most appropriate model of molecular evolution for our maximum likelihood analyses using the Akaike Information Criterion. A total of 1000 bootstrap pseudoreplicates were performed in the parsimony analysis to examine the relative support for each branch.

Results

The edited alignment is 859 nbp in length, comprising 694nbp of the 3' end of ND4 and 165nbp of the HSL tRNA cluster, including complete sequences of tRNAs Histidine and Serine and partial sequence of tRNA-Leucine. For the entire data set, a total of 170 sites were variable and 104 parsimony informative. The actual ti/tv ratio estimate via maximum likelihood for the entire data set was 5.83. Modeltest 3.06 analyses suggested that the general time reversible plus proportion of invariant sites (0.7024) substitution model was the most appropriate for our data, and so it was used in our maximum likelihood analyses. Regardless of the type of phylogenetic analyses performed, only a single tree topology was recovered so in Figure 1 we show the results for an unweighted parsimony analysis (length = 218 steps, CI = 0.81, RI = 0.85, RC = 0.69, HI = 0.19).

Phylogenetic relationships among species of Hoplocephalus

The monophyly of each of the three species was supported by high bootstrap values. *Hoplocephalus stephensii* is most closely related to *bungaroides* and these species are separated by a Jukes-Cantor genetic distance of only 2.7–3.0%, whereas *bitorquatus* is more distantly related with a genetic distance of 7.6–8.3% from the other two *Hoplocephalus* taxa. The close relationship between *stephensii* and *bungaroides* is even more obvious when transitions are removed from the data set. Based on a transversion-only analysis, the tree shown in Figure 1 reduces to just two major clades, *bitorquatus* on the one hand and *bungaroides*/*stephensii* on the other.

Table 2. Pair-wise Jukes-Cantor (1969) genetic distances between mitochondrial haplotypes. Haplotype ID numbers for *Hoplocephalus stephensii* (1–9) correspond to those used in Table 1 and Figure 1, and abbreviations are used for outgroup species names

	A.s.	*T.c.*	*N.s.*	*H.bit*	*H.bung*	1	2	3	4	5	6	7	8	9
A.s.	–													
T.c.	0.12193	–												
N.s.	0.11650	0.05122	–											
H.bit.	0.11079	0.08977	0.09242	–										
H.bung.	0.10803	0.10625	0.09379	0.07621	–									
1	0.10807	0.10208	0.09106	0.08157	0.02705	–								
2	0.10807	0.10623	0.09516	0.08292	0.02580	0.00363	–							
3	0.09970	0.10766	0.09653	0.07889	0.03082	0.01463	0.01587	–						
4	0.09969	0.10765	0.09653	0.07889	0.02831	0.01218	0.01340	0.00242	–					
5	0.10247	0.10765	0.09653	0.08157	0.02831	0.01463	0.01587	0.00485	0.00242	–				
6	0.10385	0.10904	0.09791	0.08292	0.02956	0.01587	0.01710	0.00606	0.00363	0.00121	–			
7	0.09968	0.10766	0.09653	0.08157	0.02831	0.01463	0.01587	0.00485	0.00242	0.00242	0.00363	–		
8	0.09829	0.10627	0.09516	0.08023	0.02705	0.01587	0.01710	0.00606	0.00363	0.00363	0.00485	0.00121	–	
9	0.10107	0.10905	0.09791	0.08292	0.02956	0.01587	0.01710	0.00606	0.00363	0.00363	0.00485	0.00121	0.00242	–

Phylogenetic relationships among populations of Hoplocephalus stephensii

Genetic variation within *H. stephensii* was low, with only 22 sites variable out of the entire data set. Of these, only 17 were parsimony informative (1st codon positions: 7 substitutions, all PI; 2nd codon positions: 2 substitutions, 1 PI; 3rd codon positions, 13 substitutions, 9 PI). The data show phylogeographic structure, with samples within a region being more closely related to each other and to nearby populations than to more distant ones. Animals from the Newcastle area in southern New South Wales are most closely related to the Coffs Harbour animals from central New South Wales, and these in turn form a sister clade to animals from the Lismore area in northern New South Wales, and together all these animals form a sister group to those found in the Brisbane area (Figure 1). Despite this significant phylogeographic patterning, the amount of genetic divergence among populations was low. The maximum observed genetic divergence between *H. stephensii* samples was only 1.7% between the Brisbane and Coffs Harbour-Newcastle populations. Despite this, nine mitochondrial haplotypes were detected across the entire range of *H. stephensii* with 1–3 haplotypes in each geographic region (Tables 1 and 2, Figure 1). Within a single geographic region, the maximum genetic divergence was only 0.36% (in the Brisbane area).

Discussion

Our data set on mitochondrial DNA successfully resolved phylogenetic relationships among the three species of Australian broadheaded snakes, and clarified phylogeographic structure among *Hoplocephalus stephensii* populations within the extensive but highly fragmented geographic range of this threatened species.

Phylogenetic relationships among Hoplocephalus species

Hoplocephalus is the most morphologically derived and thus best defined genus of Australian elapid snake – the presence of strongly keeled ventral scales and an angular head in all three species represent unique synapomorphies among Australian elapid snakes (Wallach 1985; Hutchinson 1990). Our molecular data also strongly support the monophyly of *Hoplocephalus*. Our data also fully resolve the phylogenetic relationships among the three *Hoplocephalus* species, but historically, these relationships have been less clear with disagreements between topologies based on karyotypes (Mengden 1985) and those based on a diverse data set largely from internal anatomy (Wallach 1985). Wallach (1985) suggested that *bungaroides* was the sister taxon to a clade containing *bitorquatus* and *stephensii*, whereas Mengden (1985) proposed that *stephensii* was the sister taxon to a

bungaroides – bitorquatus clade. A reanalysis of Wallach's (1985) data set concluded that there was insufficient phylogenetic signal for any conclusions to be drawn (Lee 1997). Our molecular data reject both of these suggestions, and instead suggest that *bungaroides* and *stephensii* are more closely related to each other than either is to *bitorquatus*. We tested these alternative topologies with a nonparametric Templeton Test (Templeton 1983) using our own data in PAUP* and were able to strongly reject both Mengden's and Wallach's alternative hypotheses (for Mengden, z = 3.38, P = 0.0008; for Wallach, z = –3.74, P = 0.0002).

The well-corroborated molecular phylogeny (Figure 1) also makes ecological sense. The basal species within the *Hoplocephalus* clade (*bitorquatus*) resembles the closest outgroup taxa we have included (tigersnakes *Notechis* and rough-scaled snakes *Tropidechis*) in living in riparian habitats and feeding on frogs (Shine and Charles 1982; Shine 1987). Unfortunately, there is virtually nothing known about the closest sister species, *Paroplocephalus atriceps*. The two species within the coastal clade of *Hoplocephalus* have departed from this niche, evolving to exploit more densely forested habitats, with diets shifting to lizards and small mammals (Shine 1983; Webb and Shine 1998c; Fitzgerald et al. in press). Tigersnakes and rough-scaled snakes occasionally forage in arboreal habitats under such circumstances (Shine 1977; Shine and Charles 1982), but *Hoplocephalus* has developed this arboreality to a much greater degree. The dietary divergence evident in the two coastal *Hoplocephalus* is similar to that displayed in isolated island populations of *Notechis* (Worrell 1958; Shine 1987; Schwaner 1988; Bonnet et al. 1999).

The genetic difference between *H. bungaroides* and *H. stephensii* is much smaller than interspecific differences reported by previous studies using the same section of mtDNA in reptiles. For example, Kraus et al. (1996) reported 5.5% to 24.4% ND4 sequence divergence in pairwise comparisons between 30 species of pit vipers. Forstner et al. (1998) used this gene segment to study relationships among seven species of North American *Cnemidophorus* lizards. They found 9.2% to 30% sequence divergence between species, and up to 2.6% divergence within a single species. We have used this gene to examine intraspecific relationships in an endangered lizard and found 5.76% divergence between two populations (Scott and Keogh 2000). Benabib et al. (1997) used the ND4 gene to study five species of North American lizards of the *Sceloporus scalaris* species group. In the species for which they had the largest number of samples (*Sceloporus bicanthalis*) they found a maximum difference of 30bp among these samples and the values between species ranged from 40 to 159. In contrast, we found a total of only 22 differences between *H. stephensii* and *H. bungaroides*. These comparisons suggest that the phylogenetic divergence between *H. bungaroides* and *H. stephensii* may have been a very recent event.

Phylogeography of Hoplocephalus stephensii

The largest split within *H. stephensii* is between the Brisbane populations and the southern populations with a genetic divergence of 1.7%. This split corresponds to the distribution of the species on either side of the McPherson Range. The McPherson Range is continuous with the Great Dividing Range which runs north to south, but the McPherson Range runs east from the Great Dividing Range, virtually to the east coast. While the McPherson Range may not constitute a barrier for the species at present, the genetic distance evident between the populations north and south of the range suggests that it has historically been an important barrier to gene flow. Using a rough mitochondrial calibration of 2% sequence divergence/million years (Brown et al. 1979; Wilson et al. 1985), this disparity suggests that the ancestors of the Brisbane populations of *H. stephensii* were separated from the ancestors of the more southern populations approximately 850,000 years ago.

This biogeographic region has received relatively little research attention, but it has been identified as an important barrier in both plants and other animals. For example, it has been identified as an important hybrid zone in birds (Ford 1987) and a major barrier between lowland and dry forest plant species (Crisp et al. 1995). There has been only one other substantial molecular phylogeographic study on a vertebrate that is distributed on both sides of the McPherson Range. A phylogeographic study of the widespread sedge frog, *Litoria fallax*, showed that the species is divided into two highly genetically divergent clades north and south of the McPherson Range (James and Moritz 2000). Detailed analyses showed that this result is not due to lineage sorting and instead is due to restricted gene flow over the McPherson Range. While *Litoria fallax* occupies a different type of forest than *H. stephensi*, our results taken together with those of Crisp et al. (1995) and James and Moritz (2000) suggest that

the McPherson Range could represent a major historical barrier to dispersal in a variety of animals and plants.

We detected comparatively little genetic diversity between the three southern populations of *H. stephensii* that cover a geographic range of approximately 700 km north to south. This is despite the current isolation of these three populations in remnant patches of forest. While it is possible that this could simply represent a recent southern range expansion, the number of haplotypes detected is more consistent with the idea that this region was continuous forest habitat until European settlement of Australia 200 years ago (Flannery 1994). Our result also is consistent with the phylogeographic structure of *Litoria fallax*. *Litoria fallax* has a wide distribution north of the McPherson Range where it displays significant phylogeographic structure, but the species displays little phylogeographic structure south of the McPherson Range where it is associated with coastal open forest (James and Moritz 2000). *Hoplocephalus stephensi* principally occurs in open patches of rainforest and wet sclerophyll forests. At present the migration of *H. stephensii* between the isolated pockets of forest is impossible given the major barriers of cleared habitats. What we know of the ecology of the species supports the idea that historically there would have been very few barriers to gene flow. Radiotelemetric monitoring has shown that these snakes are highly vagile with home ranges up to > 40 ha (mean = 11 ha: Fitzgerald et al. submitted ms). Radio-tracked snakes sometimes moved > 400 m within a single night (Fitzgerald et al. submitted ms).

Implications for conservation

Our primary results are that *bitorquatus* is the most divergent species within the genus *Hoplocephalus*, and that genetic divergence within the range of *H. stephensii* is limited. Both of these results have implications for conservation planning. At the generic level, most conservation-related attention has been paid to the two coastal taxa. Major radiotelemetric studies of free-ranging snakes have been conducted on both species, making *H. bungaroides* and *H. stephensii* perhaps the two most intensively-studied Australian elapid snakes (Webb and Shine 1997a, b, 1998a, b, c, 2000; Shine et al. 1998; Fitzgerald 2002; Fitzgerald et al. 2001). In contrast, the pale-headed snake *H. bitorquatus* has attracted virtually no scientific study, despite reports of strong declines over much of its previous range (Cogger et al. 1993; Reed and Shine in press). This emphasis reflects a common phenomenon in conservation-oriented issues within Australia, with coastal (especially, rainforest) habitats attracting much more attention than habitats in the semi-arid zone – even when the latter are under vastly greater threat than the coastal areas (Lunney et al. 1994; Covacevich et al. 1998). There has been massive land degradation in semi-arid Australia, and many large trees around inland watercourses have been removed or killed due to harvesting, fire, agricultural practices, changing hydric regimes and increasing soil salinity (Lunney et al. 1994). Such trees are the primary habitat for *H. bitorquatus* and have disappeared from a large proportion of the species' historical range (B. Lazell, pers. comm.). Especially given its genetic distinctiveness, we suggest that *H. bitorquatus* should be an urgent focus of conservation-related research to identify the status of existing populations and to clarify habitat features important for the species' persistence.

While our sample sizes are small, the low genetic divergence among extant populations of *H. stephensii* is, in a sense, more encouraging for conservation initiatives. This genetic homogeneity suggests that the historical loss of isolated populations in remnant patches of forest may not have seriously reduced the total genetic diversity present over the species' range. The sole exception to this homogeneity is the division between northern and southern populations. Thus, we suggest that managers should treat Queensland and NSW populations as separate entities (as occurs at present because conservation largely remains a responsibility of the state rather than federal governments in Australia).

Apparently reflecting the high vagility of individuals of this taxon, the species has disappeared from all but the largest forest fragments within its former range (Fitzgerald 2002). This does not mean that the loss of such populations is unimportant: for example, their extirpation may have significant ecological effects on prey populations. The introduction of another arboreal snake species outside its natural range has had dramatic consequences for the local prey assemblage (Rodda et al. 1999), suggesting that such species may be important key predators. Moreover, the presence of *H. stephensi* in a forest should be seen by managers as an indication of the quality of remnant patches of forest, as the species is associated with the presence of ecologically significant forest components; abundant hollow-bearing trees and diverse vertebrate prey species (Fitzgerald 2002).

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