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# RAPID AND REPEATED ORIGIN OF INSULAR GIGANTISM AND DWARFISM IN AUSTRALIAN TIGER SNAKES

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*Abstract.*—It is a well-known phenomenon that islands can support populations of gigantic or dwarf forms of mainland conspecifics, but the variety of explanatory hypotheses for this phenomenon have been difficult to disentangle. The highly venomous Australian tiger snakes (genus *Notechis*) represent a well-known and extreme example of insular body size variation. They are of special interest because there are multiple populations of dwarfs and giants and the age of the islands and thus the age of the tiger snake populations are known from detailed sea level studies. Most are 5000–7000 years old and all are less than 10,000 years old. Here we discriminate between two competing hypotheses with a molecular phylogeography dataset comprising approximately 4800 bp of mtDNA and demonstrate that populations of island dwarfs and giants have evolved five times independently. In each case the closest relatives of the giant or dwarf populations are mainland tiger snakes, and in four of the five cases, the closest relatives are also the most geographically proximate mainland tiger snakes. Moreover, these body size shifts have evolved extremely rapidly and this is reflected in the genetic divergence between island body size variants and mainland snakes. Within south eastern Australia, where populations of island giants, populations of island dwarfs, and mainland tiger snakes all occur, the maximum genetic divergence is only 0.38%. Dwarf tiger snakes are restricted to prey items that are much smaller than the prey items of mainland tiger snakes and giant tiger snakes are restricted to seasonally available prey items that are up three times larger than the prey items of mainland tiger snakes. We support the hypotheses that these body size shifts are due to strong selection imposed by the size of available prey items, rather than shared evolutionary history, and our results are consistent with the notion that adaptive plasticity also has played an important role in body size shifts. We suggest that plasticity displayed early on in the occupation of these new islands provided the flexibility necessary as the island's available prey items became more depauperate, but once the size range of available prey items was reduced, strong natural selection followed by genetic assimilation worked to optimize snake body size. The rate of body size divergence in haldanes is similar for dwarfs ($h_g$ = 0.0010) and giants ($h_g$ = 0.0020–0.0025) and is in line with other studies of rapid evolution. Our data provide strong evidence for rapid and repeated morphological divergence in the wild due to similar selective pressures acting in different directions.

*Key words.*—Genetic assimilation, haldanes, mitochondrial DNA, *Notechis*, phenotypic plasticity, phylogeography, rapid evolution.

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Island biota have received intense research attention from evolutionary biologists because they are thought to represent less complex systems due to fewer, simpler, or stronger selective pressures (Whittaker 1998; Schluter 2001). Body size is the characteristic that tends to change most readily on islands, and it is a well-known phenomenon that islands can support populations of gigantic or dwarf forms that are similar to their mainland conspecifics in most aspects except adult body size (Case 1978). However, the variety of explanatory hypotheses have been difficult to disentangle.

The most common explanations for shifts in island body size are the relaxation of predation or competition pressures and random genetic drift, but the evolution of body size in general and body size shifts specifically is a complex and controversial issue because there are a number of other nonmutually exclusive explanations for the patterns we see in nature (Case 1978; Barton 1996; Whittaker 1998; Schluter 2001). For example, careful field experiments with the well-known *Anolis* lizard radiation have demonstrated that morphological shifts can occur extremely rapidly (Losos et al. 1997) and repeatedly (Losos et al. 1998) as the lizards adapt to new environments with the help of phenotypically plastic traits (Losos et al. 2000). In marine iguanas the differing food energy levels available on different islands are important in determining adult body size (Wikelski and Trillmich 1997), but sexual selection in the form of sexual size dimorphism also is involved in complex ways in this (Wikelski et al. 1997) and other (Madsen and Shine 1992) species. Head size of island populations of European adders appears to be determined by the size of available prey items (Forsman 1991), whereas relaxation of predation pressure as opposed to simple retention of an ancestral condition (phylogenetic constraint) seems to have selected for large size in chuckwallas lizards (Petren and Case 1997). A recent thorough review of body size shifts in island populations of snakes concluded that the different sizes of prey items available on islands was the most important determining factor in adult snake body size (Boback 2003)

Tiger snakes range across southern Australia from southern Western Australia east to Esperance, to southern South Australia, Victoria, Tasmania, and up the eastern coastal areas north of Brisbane. Tiger snakes also are found on many offshore islands that are 1–30 km off the mainland in Western Australia, South Australia, and in the Bass Strait off Tasmania (Fig. 1). Others have quantified body size variation in island and mainland tiger snakes in detail. Based on the measurement of 860 tiger snakes by Shine (1987) and 2668 tiger snakes by Schwaner and Sarre (1990), we know that mainland adult body size shows some regional variation but is nonetheless comparatively homogeneous relative to the island populations that display body size shifts. Adult mainland tiger snakes typically reach sizes of approximately 78–92 cm snout-vent length (SVL) (Shine 1987; Schwaner and Sarre 1990). Some offshore islands also are populated by tiger



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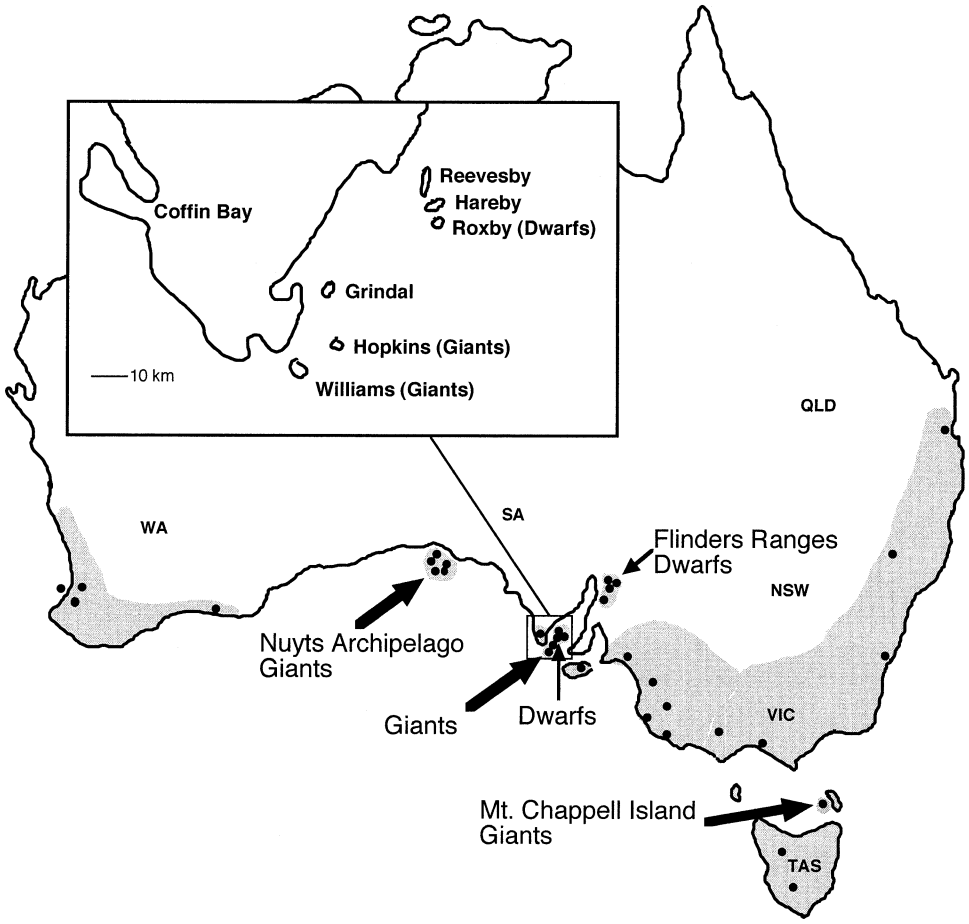


FIG. 1. Distribution map of Australian tiger snakes with sample localities and body size variants noted. The insert is a blow up of the Sir Joseph Banks Group and the Port Lincoln Island Group in South Australia where islands with dwarfs (Roxby), giants (Hopkins and Williams), or typical mainland sized tiger snakes (other islands) are found within 30 kilometres of each other.

snakes that reach a similar average adult size to those on the mainland, but other islands are home to populations that exhibit extreme shifts in adult body size relative to their mainland counterparts. Roxby Island is populated only by dwarfs that reach an average of approximately 70 cm SVL and weigh less than 200 g whereas Mount Chappell Island is populated by giants that reach an average of approximately 120 cm but can range up to 160 cm SVL and well over 1 kg (Schwaner 1985; Shine 1987; Schwaner and Sarre 1988, 1990). Giant tiger snakes of a similar size also are found on the islands of the Nuyts Archipelago in the Great Australian Bite and on Hopkins and Williams Island in the Port Lincoln and Neptune Island groups in South Australia (Schwaner 1985; Robinson et al. 1996). With the exception of one highly isolated population of dwarfs in the Flinders Ranges of South Australia, all mainland tiger snake populations that have been examined are intermediate in adult body size to the island populations that display extreme body size shifts.

There are several key attributes of this system that make it ideal for testing alternative hypotheses: (1) In most examples of insular body size variation, the body size differences are comparatively small, but in tiger snakes the body size shifts are substantial and in particular the difference in size between dwarfs and giants is extreme (Schwaner 1985; Shine 1987; Schwaner and Sarre 1988, 1990). (2) Most studies of insular body size variation have focused on a single shift in adult body size and on single islands, but in tiger snakes there are separate island populations of giants and dwarfs and replicate examples of each (Schwaner 1985; Schwaner and Sarre 1988, 1990). (3) There are many islands populated by tiger snakes that reach the same adult size as those on the mainland, including islands in the same geographic area as islands populated with giants or dwarfs, implying that there have been different selection pressures acting on the island populations that display body size shifts (Schwaner 1985; Shine 1987; Schwaner and Sarre 1988, 1990). (4) Importantly, we also know the age of the islands and thus the age of the tiger snake populations from detailed sea level studies; most are 5000–7000 years old and all are less than 10,000 years old (Robinson et al. 1996).

A number of hypotheses have been suggested to explain body size shifts in island tiger snakes. Natural selection acting to optimize snake body size to available prey size is supported strongly by the compelling correlation between snake size and available prey size (Schwaner 1985; Shine 1987; Schwaner and Sarre 1988, 1990), but other possibilities exist. Island tiger snakes display no obvious male-male competition and they are the top predator on all the islands on which they

occur, and so competition, predation, and sexual selection already have been rejected as possible explanations (Schwaner 1985; Schwaner and Sarre 1988, 1990). Phenotypic plasticity was discounted early as a possible explanation of this phenomenon in tiger snakes as growth rate differences between dwarfs and giants seemed to be genetically based (Barnett and Schwaner 1984; Schwaner 1985) but a recent common garden experiment has demonstrated that both plasticity and genetic history act to influence body size in island tiger snakes (Aubret et al. 2004). If this is true, then we would predict that island populations should be most closely related to nearby mainland populations even though snake body size and available prey items may differ. We were interested in testing this hypothesis against the alternative explanation that the current distribution of adult body sizes may simply represent relictual distributions of what were once wide-spread ancestral phenotypes prior to island isolation. We also were interested in examining the implied rapid rate of morphological change in these island populations. We have specifically tested these hypotheses in a phylogenetic framework.

## Methods

### *Samples*

Tiger snakes are morphologically highly variable in color and pattern as well as body size and this variability has contributed to taxonomic disagreement. Some authorities have recognized a number of subspecies, but the most recent revision recognized just two species (*Notechis ater* and *Notechis scutatus*) and admitted that the difference between the species was somewhat arbitrary (Rawlinson 1991). We strategically chose 33 individuals to cover the full distribution of both species and the full range of morphological diversity including all relevant island and mainland populations that display body size variation (Figs. 1, 2).

### *DNA extraction, amplification, and sequencing*

We assembled a large mitochondrial DNA dataset including complete sequences of cytochrome *b*, ND2 and control region, and partial sequences of ND4 and 16SrRNA, as well as flanking tRNA sequences. All laboratory procedures for obtaining the cytochrome *b*, ND4, and 16s data can be found elsewhere (Keogh 1998; Keogh et al. 1998, 2000; Slowinski and Keogh 2000; Scott and Keogh 2000). For the following description of our ND2 and control region primers, the primer positions relate to 3′ positions of *Dinodon semicarinatus* (Genbank accession number NC_001945). ND2 was initially amplified with the primers L4437 (Macey et al. 1998; position 4801) and either tRNA-Trp (Position 5886; 5′—CTCCTG CTTAGGGCTTTGAAGGC) or tRNA-Asn (Position 6002; 5′—CTAAAATRTTRCGGGATCGAGGCC). We used the amplification primers as well as the following internal primers for ND2 sequencing: H4980 (Position 5339; Macey et al. 1998), H5245 and H5340 (Positions 5235 and 5330, respectively; Slowinski and Lawson, unpubl. data). Initial attempts were made to amplify the entire control region with primers designed to match cytochrome *b* and 12S sequences obtained in our laboratory from a range of elapids (El_CytbIII, position 15929, 5′-CTATTACATGAACAGCCACTAAACC; El_12SI, position 71, 5′-AATAGGAGGTTTAAGACCAAGACC; El_12SII, position 287, 5′-GGTCGCTGGCACGAGATTGACCG GCCC). These large control region fragments were sequenced and a number of internal primers designed and a variety of primer combinations assessed. We were able to amplify a fragment of approximately 680 bp from the 5′ end of the control region using El_CytbIII and ElCRII (Position 16613; 5′-C AAAGGCCTTGGAAAAAGCTAGTAG). Based on this fragment we designed two *Notechis*-specific light strand internal primers (TS_CRI, position 16471, 5′-GGTGTCCCTT GGTTTAGCTCAGC; TS_CRII, position 16440, 5′-GTTG GTAATCATGACTATCCCG). These two primers, as well as the elapid-specific El_CRI (Position 16511; 5′-CCCTCT ATCCTTCCACTTCAGGCATACAGTCC) were used in combination with El_12SI to amplify and sequence the 3′ end of the control region. Amplification and sequencing procedures for generating ND2 and control region data were identical to those described elsewhere (Keogh et al. 2000, Scott and Keogh 2000).

### *Phylogenetic analysis*

Sequences were aligned by ClustalX (Thompson et al. 1997) and refined by eye. A partition homogeneity test in PAUP* version 4.0b10 (Swofford 2002) could not reject the null hypothesis that the data were homogeneous with regard to phylogenetic signal ($P > 0.01$), thus all analyses were based on the combined data set. The sister species *Tropidechis carinatus*, similar in size to mainland tiger snakes, was chosen as the outgroup based on a detailed phylogeny of the Australian viviparous elapid snake radiation (Keogh et al. 2000).

We used maximum-likelihood (ML) and Bayesian approaches to analyze the data. We used the the computer program ModelTest version 3.06 (Posada and Crandall 1998) to select the most appropriate model of molecular evolution for our data and to estimate empirical nucleotide frequencies, substitution rates, gamma distribution, and proportion of invariant sites which we used in our ML analyses implemented in PAUP* (Swofford 2002). Our Bayesian analyses were done with the computer program Mr Bayes (ver 3.0b4; Huelsenbeck and Ronquist 2001) and all parameters were estimated from the data during the run. We used the default value of four Markov chains per run and also ran the full analysis five times to make sure overall tree space was well sampled. We ran each analysis for a total of 1,000,000 generations and sampled the chain every 100 generations, resulting in 10,000 sampled trees. Log-likelihood values reached a plateau after approximately 100,000 generations (1000 sampled trees), and we discarded the first 3000 trees as the burn-in phase and used the last 7000 trees to estimate Bayesian posterior probabilities. We performed 1000 bootstrap pseudoreplicates under maximum likelihood and also used Bayesian posterior probabilities to assess branch support. We also tested the significance of log-likelihood differences between our optimal ML tree and topologies representing various alternative morphological and taxonomic hypotheses with the Shimodaira-Hasegawa test in PAUP* (Shimodaira and Hasegawa 1999, see also Goldman et al. 2000) using full optimization and 1000 replicates.

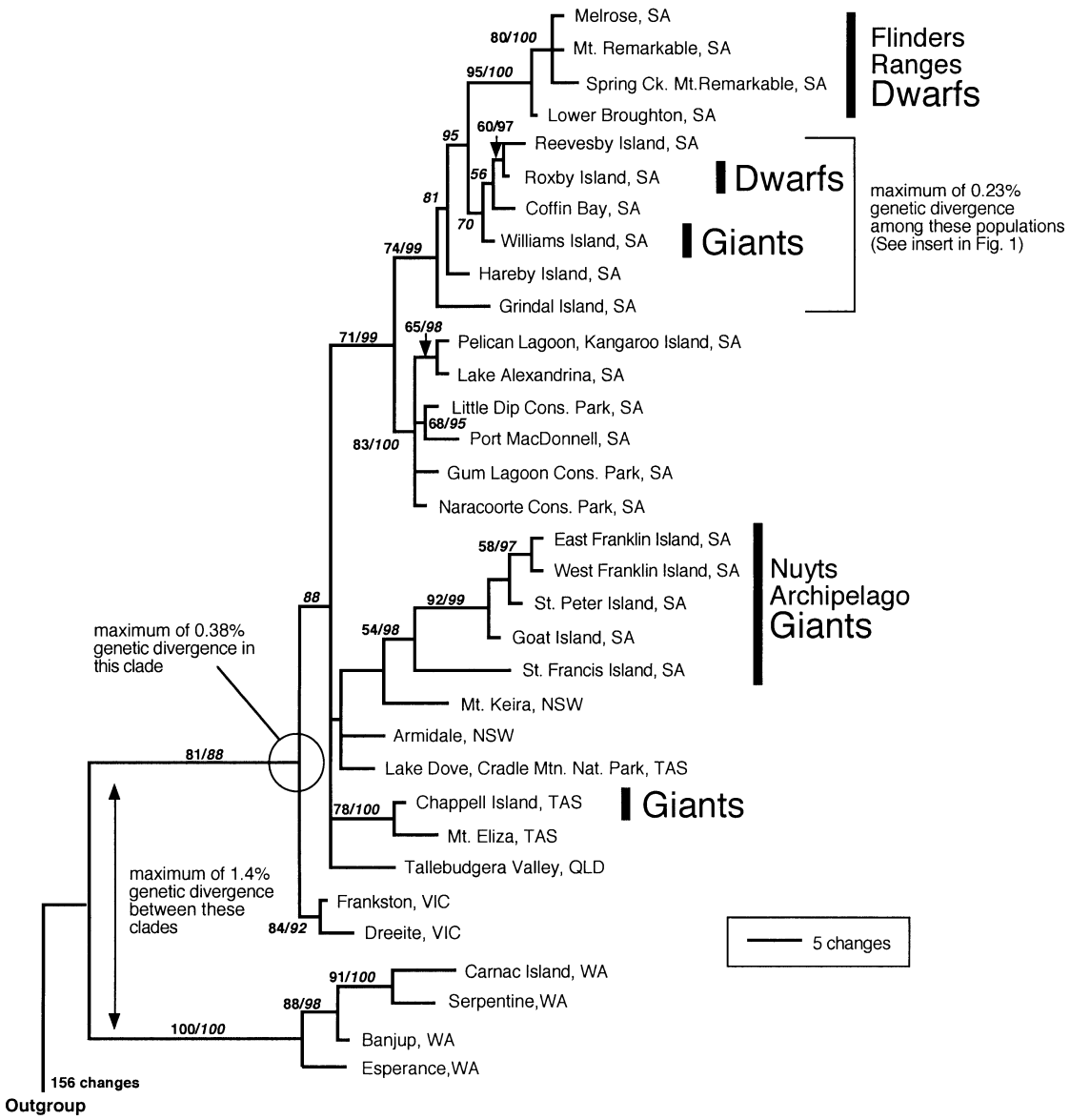


FIG. 2. Maximum-likelihood phylogram based on the GTR+G+I model. Bootstrap values based on 1000 ML pseudoreplicates are in normal text and Bayesian posterior probabilities are in italics. Gigantic tiger snakes are known from three distantly separated regions and have evolved three times independently. Dwarf tiger snakes are known from two regions (one island) and have evolved two times independently.

*Rates of divergence*

To facilitate comparison with other studies of rapid evolutionary change we also calculated haldanes as a standard measure of evolution based on the formula of Gingerich (2001) and the recommendations of Hendry and Kinnison (1999). Schwaner and Sarre (1990) measured 2668 tiger snakes from various mainland localities and most of the relevant islands. Using males only, we used the means and back calculated the standard deviations from the 99% confidence intervals presented in figure 1 of Schwaner and Sarre (1990). We used a generation time of four years and a single island isolation time of 7800 to approximate the actual isolation time based on Robinson et al. (1996). We picked three island populations for comparison because the age of island formation (and thus divergence) was known and compared them to the nearest mainland population as indicated on our phylogeny (East Franklin Island giants vs. New South Wales mainland snakes, Roxby Island dwarfs vs. South Australian mainland snakes, and Chappell Island giants vs. Tasmanian snakes).

## RESULTS

The dataset comprised 4805 nucleotide base pairs of mitochondrial DNA of which 277 were variable and 89 phylogenetically informative under parsimony with the outgroup included. Within tiger snakes only, 140 sites were variable and 85 informative under parsimony. With the exception of 16s which evolves at a slower rate, the other four genes

contributed roughly similar amounts of parsimony informative variable sites (gene, length, number of parsimony informative sites: ND2, 1075, 23; ND4, 865, 19; Cytochrome *b*, 1127, 18; Control region, 999, 18; 16s, 485, 5; various tRNAs, 254, 2).

The protein coding regions of our data translated without any premature stop codons and our 16s sequence data is congruent with other elapid 16S data (Keogh 1998; Keogh et al. 1998, Slowinski and Keogh 2000), thus we assume that the target genes were amplified rather than paralogues. The complete alignment can be obtained from the senior author. ModelTest 3.06 analyses indicated that the general time reversible (GTR) plus gamma (G) distribution plus proportion of invariant sites (I) was the best model of molecular evolution for our data and we used our gamma distribution of 0.9435 and our proportion of invariant sites of 0.6448. Our ML and Bayesian analyses produced very similar parameter estimates and both analyses recovered about the same topology (Fig. 1).

Our phylogeny demonstrates two important features of tiger snake evolutionary history (Fig. 1). First, tiger snake populations are extremely closely related with a maximum overall genetic divergence of only 1.4% between Western Australia and the other populations in southeastern Australia. Within southeastern Australia (where all of the populations of giants and dwarfs are found) the maximum genetic divergence is only 0.38%. Nonetheless, the phylogeny is sufficiently resolved to demonstrate that there are three clades of island giants and two clades of dwarfs. In each case the closest relatives of the giant or dwarf populations are mainland tiger snakes, and in four of the five cases, the closest relatives are also the most geographically proximate mainland tiger snakes.

We tested the alternative hypotheses that giants and dwarfs each evolved once and hence formed monophyletic clades. We were able to soundly reject the hypothesis that giants are monophyletic (-ln greater by 99.72, $P = 0.001$). We were not able to statistically reject the hypotheses that the two populations of dwarfs are monophyletic (-ln greater by 11.09, $P = 0.568$) because of the very small amount of genetic divergence between them. However, the strong bootstrap support for monophyly of the Flinders Ranges dwarfs and the close relationship between the Roxby Island dwarfs and the Reevesby Island population strongly suggests that these two populations do not represent a single origin of dwarfism.

The rate of body size divergence in haldanes is similar for dwarfs and giants and demonstrates that these body size shifts have occurred very rapidly (East Franklin Island giants vs. New South Wales mainland snakes, $h_g = 0.0025$); Roxby Island dwarfs vs. South Australian mainland snakes, $h_g = 0.0010$; Chappell Island giants vs. Tasmanian snakes, $h_g = 0.0020$).

## Discussion

### *Evolution of body size*

Our phylogenetic analyses suggest that each of the three populations of giants and both of the populations of dwarfs have evolved independently. The detailed data available on tiger snake diets strongly support the prey-size hypothesis with a perfect matching between predator and prey size (Schwaner 1985; Shine 1987; Schwaner and Sarre 1988, 1990). Our interpretation is that these body size shifts have evolved independently and very rapidly due to similar and strong selective pressures on the different islands and our results are consistent with the view that there is both a genetic and an adaptive plasticity component to tiger snake body size shifts (Aubret et al. 2004). Our results also are consistent with those of a very thorough review and analysis of island body size shifts in snakes that strongly supports the notion that most body size shifts are due to changes in the size of prey items (Boback 2003). A shift to a novel food source is one of the most common reasons for rapid phenotypic divergence (Reznick and Ghalambor 2001).

Mainland Australian tiger snakes tend to be active opportunistic foragers that feed on a wide variety of frogs but they also take lizards, mammals, and occasionally birds that can range in size up to approximately 70 g (Schwaner 1985; Shine 1987; Schwaner and Sarre 1988, 1990). A thorough study of tiger snake diets demonstrated that mainland tiger snakes are ecologically homogeneous with respect to diet (Shine 1987). Importantly, islands that are populated by adult tiger snakes that are of similar size to mainland tiger snakes also are inhabited by prey items of similar size to those taken by mainland tiger snakes (Schwaner 1985; Shine 1987; Schwaner and Sarre 1988, 1990; Robinson et al. 1996). However, the diets of giant and dwarf tiger snakes populations are quite different due to prey availability. The only prey items available to Roxby Island dwarf tiger snakes are three small species of lizard with a maximum weight of approximately 10 g (Schwaner 1985). Much less is known about the Flinders Ranges dwarf tiger snakes, but anecdotal evidence suggests that they may feed only on seasonally available tadpoles. The giant tiger snakes on the islands of the Nuyts Archipelago and the giant tiger snakes on Hopkins and Williams Island in the Port Lincoln and Neptune Island groups are limited to three lizard species with a maximum weight of approximately 16 grams and two large mammals and a large bird species (300–350 g) (Schwaner 1985; Robinson et al. 1996). The largest tiger snakes occur on Mount Chappell Island where these snakes are limited to five lizard species with a maximum weight of 16 g and mutton bird chicks that weigh up to 350 g. These chicks are available for less than one month of the year and during this time the snakes gorge themselves because these are their only source of food for the year (Schwaner 1985; Schwaner and Sarre 1988). Thus, populations of dwarf tiger snakes are restricted to prey items that are much smaller than the prey items of mainland tiger snakes and the populations of giant tiger snakes are restricted to seasonally available prey items that are three times larger than the prey items of mainland tiger snakes. The close match between adult body size and the size of available prey items is demonstrated very clearly by Schwaner (1985, fig. 6).

A close matching of large adult body size to large available prey items is intuitive to understand because small snakes simply cannot eat large prey items, but this same logic does not necessarily follow for large snakes that could eat multiple small prey items if they are available. The food availability hypothesis suggests that the observed close match between adult body size and prey size could be due to the relative

availability of prey items rather than just prey size (Case 1978). Populations of giant island tiger snakes have access to high quality and very easy to catch large prey items, but these are only available seasonally. In contrast, the Roxby Island dwarfs have access only to small lizards that are available year round and also are in high densities (Schwaner 1985). It is conceivable that these snakes should be able to obtain large numbers of lizard prey items but there are some important difficulties with this argument. There is a simple prey handling issue, large snakes with large mouths find it more difficult to both catch and manipulate small prey items (King 2002). Further, even though the lizards are in high densities, they are difficult to catch, and this would be exacerbated by large snake body size. It has been demonstrated in other species that large snakes prefer larger prey items (Mushinski et al. 1982; Miller and Mushinski 1990) and that large snakes simply drop small prey items from their diet (King 2002).

*The speed of morphological change*

These body size shifts are remarkable because of the speed with which they have repeatedly evolved. We evaluated this in terms of the levels of genetic divergence among populations and in haldanes to facilitate comparison with other studies of rapid evolution. The islands on which these body size variants occur were all less than 10,000 years old when they were isolated due to increasing sea levels. Our phylogeny demonstrates that tiger snake populations are extremely closely related with a maximum overall genetic divergence of only 1.4% between Western Australia and the other populations in southeastern Australia. Within southeastern Australia, where populations of island giants, populations of island dwarfs, and mainland tiger snakes all occur, the maximum genetic divergence is only 0.38%. This extraordinary example of fast morphological divergence is best exemplified by the distribution of body sizes and genetic divergence among island populations in the Sir Joseph Banks and the Port Lincoln Island groups in South Australia (see insert, Fig. 1). In this region are islands of giant tiger snakes that are less than 30 km from other island populations with dwarfs and still other islands populated by tiger snakes of similar adult size to the mainland. The dwarf population on Roxby Island is less than 3 km from tiger snakes of typical mainland size on Hareby Island. The mainland and island populations in this region are extremely closely related (maximum of 0.23% divergence) and this is consistent with the notion that tiger snakes comprised a single large population in this region prior to island isolation. Indeed, the data suggests that the distribution of tiger snakes in southern and eastern Australia was largely continuous prior to the isolation of these island populations less than 10,000 years ago.

A recent review and critique of rates of microevolutionary change provided a framework for comparison with numerous other studies of rapid evolution. Hendry and Kinnison (1999) calculated haldanes (and darwins) for 20 studies of rapid morphological evolution or divergence. Most of the studies reviewed in Hendry and Kinnison (1999) were based on a time scale of less than 100 years and report much more subtle morphological shifts than in tiger snake body size. Our values are in line with these studies, demonstrating that strong directional selection has been imposed on multiple tiger snake populations, probably since soon after island isolation. Importantly, the values are nearly identical not only between the two independently evolved giant populations (East Franklin Island and Chappell Island) but also between these giant populations and the dwarf snakes on Roxby Island, suggesting that the strength of selection has been similar on the different islands but acting in opposite directions.

*Has phenotypic plasticity played a role?*

Our results strongly support the prey-size hypothesis (Schwaner 1985; Schwaner and Sarre 1988, 1990; Boback 2003), but phenotypic plasticity is a compelling alternative, especially given that tiger snakes display both dwarf and giant populations and that these body size shifts have happened repeatedly. Madsen and Shine (1993) showed with a common garden experiment that the dwarfism displayed in an island population of European grass snake was due to phenotypic plasticity alone. However, this is certainly not a universal result. For example, Bronikowski (2000) has shown with a detailed common garden experiment on garter snakes that large differences in growth rates can indeed have a strong genetic basis and moreover that these differences can be maintained over a very small geographic scale. Detailed studies on growth rates and asymptotic size in dwarf and gigantic tiger snakes are difficult due to conservation concerns, but Barnett and Schwaner (1984) reported very fast growth rates for captive neonates raised from one population of gigantic tiger snakes and Schwaner (1985) reported that under common garden conditions, dwarf tiger snakes from Roxby Island and giant tiger snakes from West Franklin Island grew at 10 mm/month and 30 mm/month, respectively.

More recently Aubret et al. (2004) used a common garden experiment to evaluate this idea more thoroughly by raising neonates from an island with large tiger snakes and large prey items and neonates from the nearby mainland with typically sized tiger snakes. In a split-clutch design offspring from both localities were fed the same mass of food but the prey items (mice) differed greatly in size. The island tiger snakes fed large prey items showed increased jaw length growth rates relative to their siblings fed smaller prey items and to the mainland tiger snakes which showed no such effect. Importantly, the island neonates still display bigger jaw lengths at birth even though they display the same body size at birth as their mainland counterparts. This experiment demonstrates convincingly that growth trajectories in the tested populations comprise both an adaptive plasticity component as well as a genetic component (Aubret et al. 2004) and their results are entirely consistent with our phylogenetic results showing multiple independent shifts in body size. We suggest that plasticity displayed early on in the occupation of these new islands provided the flexibility necessary as the island's available prey items became more depauperate, but once the size range of available prey items was reduced, strong natural selection followed by genetic assimilation worked to optimize snake body size (Losos et al. 2000; Pigliucci and Murren 2003; Doughty and Reznick 2004; Frankino and Raff 2004; Schlichting 2004).

*Taxonomic implications*

In the only revision of tiger snake taxonomy two species are recognized, *Notechis ater* and *Notechis scutatus* (Rawlinson 1991). Rawlinson's scheme includes all of the mainland New South Wales tiger snakes as *N. scutatus* and all of the Western Australian, Flinders Ranges, Tasmanian, and island populations as *N. ater*. This scheme is also used by Cogger (2000). In contrast, Wilson and Knowles (1988) recognize *N. ater* as all ''black'' tiger snakes in South Australia and Tasmania, including the island populations and *N. scutatus* as all the mainland tiger snakes (including Western Australia). A number of *Notechis ater* subspecies also have been recognized (reviewed in Rawlinson 1991): *Notechis ater ater* for the Flinders Ranges (SA) tiger snakes, *N. ater humphreysi* from New Year Island and *N. ater serventyi* from Chappell Island, both in the Bass Strait, *N. ater occidentalis* for the Western Australian tiger snakes, and *N. ater. niger* for the remaining South Australian offshore island tiger snakes. Each of these subspecific descriptions were based on few data and one of them was based on a comparison with erroneous data on eastern tiger snakes (Rawlinson 1991). Although more popular accounts have continued to recognize these subspecies, Rawlinson (1991) pointed out that only *Notechis ater* and *Notechis scutatus* were diagnosable and that even the division between the two species is somewhat arbitrary (Cogger 2000). We tested alternative topologies that reflect the classification schemes of Rawlinson (1991) and Wilson and Knowles (1988) and both schemes can be soundly rejected by our data (-ln greater by 46.77, $P = 0.036$ for Rawlinson, 1991; -ln greater by 81.52, $P = 0.001$ for Wilson and Knowles 1988). Both classification schemes use body size and color variation as two of the most important characteristics, but our molecular data clearly show that neither is phylogenetically useful in tiger snake taxonomy. Given the extremely small amount of genetic divergence between tiger snake populations across their range and the extremely short amount of time required for major body size shifts (and presumably color changes) to evolve, we conclude that tiger snakes comprise a single polymorphic species, *N. scutatus*, under a phylogenetic species concept.

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