CSIRO PUBLISHING

Australian Journal of Zoology, 2011, **59**, 145–155
http://dx.doi.org/10.1071/ZO11031

Distribution, abundance and demography of green pythons (*Morelia viridis*) in Cape York Peninsula, Australia

Daniel James Deans Natusch[A,C] *and David Francis Stewart Natusch*[B]

[A]School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia.
[B]Resource Development Ltd, Hunterville 4730, New Zealand.
[C]Corresponding author. Email: d_natusch_14@hotmail.com

Abstract. The green python (*Morelia viridis*) is an iconic snake species highly sought after in the pet trade and is the target of illegal collection. Despite their popularity, some important ecological attributes of green pythons remain unknown, making their effective conservation management difficult. Detection-only surveys were conducted throughout the potential range of the green python in Australia, and intensive mark–recapture surveys were conducted in the areas where there have been previous records. In total, 298 green pythons were located in the Iron, McIlwraith and Kawadji–Ngaachi Ranges of Cape York, distributed over an estimated area of 2289 km^2, where they frequented rainforest habitats and adjacent vine thickets. They were not found in the Lockerbie Scrub or Jardine River Catchment, despite anecdotal records. Green python density was estimated to be 540 km^{-2} in the Iron Range and 200 km^{-2} in the McIlwraith Range, where the percentages of adults captured were 56% and 83%, respectively. The differences between abundance and population demographics in the Iron and McIlwraith ranges may be due to differences in prey abundance and the impacts of collection. The results of this study provide baseline data to conservation managers and policy makers for the future conservation management of this species in Australia.

Received 2 May 2011, accepted 3 October 2011, published online 23 November 2011

Introduction

Understanding species distribution and abundance patterns is a fundamental goal of ecology (Krebs 1972; Ricklefs and Miller 2000). There is, however, little detailed information about the distribution and demographic status of most Australian reptile species (Cogger *et al*. 1993), which limits the effectiveness of strategies intended to assist in their conservation (Rodrigues *et al*. 2006).

The green python (*Morelia viridis*) is a small to medium-sized (≤2 m) python species restricted to closed forest habitats in New Guinea and the adjacent Cape York Peninsula in Australia (Barker and Barker 1994; O'Shea 1996). They exhibit a remarkably vivid ontogenetic colour change, such that juveniles are born either yellow or red but later change to green (Wilson *et al.* 2007). These characteristics make green pythons very popular in captive collections and have resulted in their illegal collection and trade (Auliya 2003; Lyons and Natusch, in press; TRAFFIC 2009).

Despite their popularity, little is known about the distribution and demography of green pythons in the wild. Of the five main rainforest blocks on Cape York (Fig. 1), green pythons have been reliably recorded only in the Iron and McIlwraith ranges. There are anecdotal reports of green pythons being found in the rainforests of the Lockerbie Scrub (Waldren 1996; Kend 1997; S. Templeton, pers. comm. 2007) and Jardine River catchment (anonymous, pers. comm. 2007), but these have not been confirmed.

Most green pythons have been recorded in the Iron Range region; however, it is not known whether this reflects high population density or is merely a representation of accessibility and search effort. Wilson and Heinsohn (2007) have predicted the distribution area of green pythons in Cape York to be 300 km^2 and 3127 km^2 based on climatic modelling and vegetation mapping, respectively, and a population density estimate of 400–500 km^{-2} has been published for the rainforest ecosystem in Iron Range National Park (Wilson and Heinsohn 2007), where only half of the population were found to be mature adults.

In the present study, extensive surveys of potentially suitable habitat were made to test the distribution prediction of Wilson and Heinsohn (2007). In addition, intensive surveys were made in several areas where there are previous records of green pythons to determine habitat use and relative abundance at each site. This information provides a benchmark for the future conservation management of green pythons in Australia.

Materials and methods

Study sites

The study area extended from the tip of Cape York to the southern extremity of the McIlwraith Range (Fig. 1). Temperatures are high year-round and most rain falls between December and April. The rest of the year it is predominantly dry (Frith and Frith 1995). Most of the peninsula is flat and the dominant

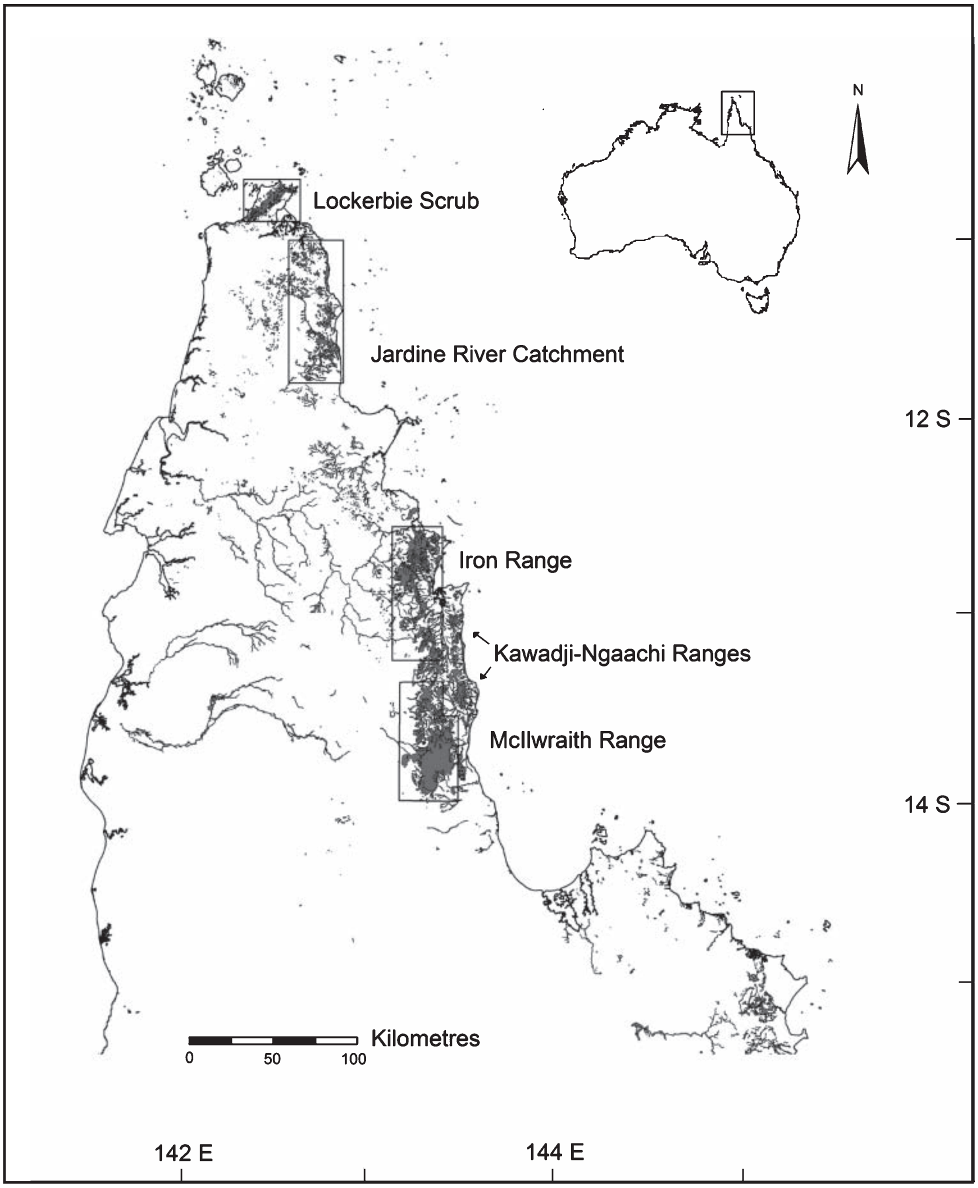

Fig. 1. Distribution of closed forests and the five sites surveyed for green pythons on Cape York Peninsula.

vegetation is tropical woodland. On the east coast, however, the northern outlier of the Great Dividing Range adds topographic, climatic and biological diversity to the region, receiving enough year-round rainfall to sustain tracts of complex vine forest.

The vegetation of Cape York has been classified by Neldner and Clarkson (1995) and correlated with a distinct combination of geology and landforms to form regional ecosystems (Sattler and Williams 1999). Because green pythons are most frequently recorded in rainforest, topographic and regional ecosystem maps for Cape York were used to identify five potentially suitable sites considered large enough to sustain a green python population (Fig. 1). The vegetation types of the three main sites studied are described in Table 1, which also identifies the regional ecosystems involved.

Survey method

Detection-only surveys

Surveys for green pythons were conducted in all five major areas of potentially suitable habitat in Cape York (Fig. 1) between November 2007 and March 2010. The removal sampling design proposed by MacKenzie *et al*. (2002) was employed, whereby sites were surveyed for no more than two occasions and, if snakes were found on the first survey, further searching at the site was discontinued. Two surveys were considered sufficient (see MacKenzie and Royle 2005) as preliminary searches indicated that, if present, green pythons have a high probability of detection. The distances walked during surveys at each separate location depended on the extent of suitable habitat. Survey areas were stratified to include habitats that were close to rainforest where green pythons have been recorded most often. Most surveys were

Table 1. Transect definitions, survey effort, abundance and density of green pythons at the three sites intensively surveyed in Cape York

Study area	Regional ecosystem	Vegetation description	Total transect length (km)	Transect width (m)	Survey area (km^2)	Search time (h)	Snakes caught	Snakes recaptured	Pop. est. (s.e.)	Snakes h^{-1}	Snakes km^{-2}
Lockerbie Scrub 2007/08	3.5.3	Semideciduous notophyll vine forest on lateritic Carnegie Tableland	21.4	20.4	0.44	89.4	0	0	–	0	–
	3.2.1	Evergreen notophyll vine forest on coastal dunes and beach ridges	1	15.1	0.02	8	0	0	–	0	–
	3.5.5	*Corymbia novoguinensis* or *C. nesophila* ± *C. tessellaris* woodland on sandplains	2.1	30	0.06	13.7	0	0	–	0	–
McIlwraith Range 2008/09	3.12.3	Evergreen to semideciduous notophyll vine forest of the slopes of the McIlwraith Uplands	9.1	13.8	0.13	171.6	47	8	25 (±23)	0.32	200
	3.12.21	Deciduous vine thicket dominated by *Cochlospermum gillivraei*, *Canarium australianum* and *Acacia aulacocarpa* on granite slopes	2.1	30	0.06	14	3	1	–	0.29	–
	3.12.10	*Eucalyptus cullenii* and *Corymbia clarksoniana* woodland on acid volcanic ranges	0.6	30	0.02	8.1	0	0	–	0	–
Iron Range 2009/10	3.12.3	Evergreen to semideciduous notophyll vine forest on the slopes of the McIlwraith Uplands	12.8	15.1	0.19	166.6	131	35	104 (±90)	1.00	540
	3.2.11	Low microphyll vine forest dominated by *Acacia crassicarpa* and *Syzygium banksii* on coastal dunes	1.6	14	0.02	23.3	12	6	–	0.77	–
	3.3.31	*Eucalyptus tetrodonta* ± *Corymbia clarksoniana* woodland on coastal plains	1	30	0.03	11.6	0	0	–	0	–

made on foot and snakes were located at night (after 2000 hours) with the aid of a hand-held spotlight. The location of each snake found was recorded using a hand-held GPS unit and the surrounding habitat noted.

Intensive surveys

Intensive surveys were carried out in areas where green pythons had previously been reported (Wilson and Heinsohn 2007), including the rainforests of the Lockerbie Scrub, Iron Range and McIlwraith Range. Each site was surveyed during the wet season between December and March and transects were set up in the most common and accessible habitats at each site. Emphasis was placed on selection of vine forest habitats having associated open forest areas to establish habitat preference.

Transect numbers and lengths differed between each habitat type (Table 1) due to logistic constraints. The habitats surveyed in Cape York are heterogeneous in structure so that the probability of detecting green pythons differs at different locations. To account for this, and to enable calculation of the survey area, the width of each transect was determined by averaging the distance at which a green python could reliably be sighted from the centreline at 150 randomly distributed points within each habitat type (Table 1).

Each transect was surveyed at one-week intervals and all transects were surveyed within a one-week period, or cycle. The times taken to traverse a transect were recorded to determine encounter rates. All green pythons were captured by hand and marked using a combination of scale clipping (Brown and Parker 1976) and insertion of a passive integrated transponder (Gibbons and Andrews 2004) so that individuals could be identified if relocated. Individual green pythons were measured to the nearest 0.5 cm using a steel ruler to determine snout to vent length (SVL) and the sex of mature individuals was established by cloacal probing. Following their examination and measurement, all snakes were released immediately at the point of capture.

Analysis

The maximum-likelihood approach of MacKenzie *et al*. (2002) employed by the computer program PRESENCE was used to estimate the proportion of sites occupied (Ψ) and the probability of detection (p) for green pythons in the Lockerbie Scrub, and McIlwraith and Iron Ranges. Data from both intensive and detection-only surveys were combined to provide input parameters and it was assumed that all sites were closed to changes in occupancy at the species level since each was surveyed within a single season (MacKenzie *et al*. 2002). Both Ψ and p can be expressed as log-it function of site-specific covariates and habitat was chosen, *a priori*, as the covariate in our analysis.

Habitats were divided into three classes: rainforests, vine/riparian forests and open habitats (which consisted mostly of woodlands but also included swamp, grasslands and heath). Two models were run for each area to estimate site occupancy: (1) a null model where both Ψ and p were held constant, and (2) a model where p was held constant while Ψ was allowed to vary with each habitat type. Results were used only from the second model as it was preferred when ranked using Akaike information criterion values (see Burnham and Anderson 2001).

A single constant model was used to estimate p with detection data from rainforest sites only as there were some habitats where no green pythons were found (see Results). Combining all habitats and using habitat as a covariate resulted in the model not reaching numerical convergence – probably due to the low number of detections in non-rainforest habitats (Gu and Swihart 2004).

At one survey site no green pythons were detected so PRESENCE could not be employed since it relies on detections to estimate parameters (MacKenzie *et al*. 2002). Probability of detection in this area was, therefore, estimated with 95% certainty using the equation presented by McArdle (1990):

$$D = 1 - (1 - \alpha)^{1/N}$$

where D is the probability of detection, α the specified level of confidence and N the number of surveys for green pythons in all habitats in the area.

The open-population Jolly–Seber method was used to analyse the recapture histories of each green python population surveyed. This method was chosen because it allowed comparison with the estimates of Wilson and Heinsohn (2007) at their Iron Range study site. Due to the relatively short survey period and focus of the present work on population estimation, it was assumed that probability of survival was the same for all animals and that both marked and unmarked snakes had the same probability of capture.

Following the classification of Wilson *et al*. (2006*a*), green pythons were divided into three groups based on colour and sexual maturity. Yellow individuals were classed as juveniles, green individuals smaller than the size at sexual maturity (males 84 cm, females 99 cm: Shine and Slip 1990) were classed as immature, and green individuals larger than the minimum size at sexual maturity were classed as adults.

Results

In total, 301 green pythons were located in three broad areas of Cape York. Most were captured during intensive wet season surveys; however, ~25% were found either opportunistically or during detection-only surveys. Two of the records were obtained from the Queensland Museum and one from an anonymous naturalist.

Distribution

Green pythons were found in suitable habitat from the Pascoe River in the north to the southern extremity of the McIlwraith Range (Fig. 2). They were not found either in the Lockerbie Scrub or the Jardine River catchment. Elevations where green pythons were found varied from 1 m above sea level in the Iron Range to 681 m above sea level in the McIlwraith Range. They inhabit 14% of the regional ecosystems surveyed in Cape York (Table 2) and 50% of those in the Iron–McIlwraith Ranges region and every closed forest ecosystem (Fig. 3), but were never found in woodlands, swamp, heath or grassland.

Assuming their occurrence in all suitable habitats within the Iron–McIlwraith Range region, green pythons have a potential distribution area of 2289 km^2 (Fig. 3). The evergreen to semideciduous notophyll vine forest (regional ecosystem 3.12.3) was the habitat in which most snakes were found and this appears to be the preferred habitat for green python. In detection-only surveys green pythons were found in all but one case in this habitat. The National Parks in the Iron and McIlwraith ranges include 73% of regional ecosystem 3.12.3

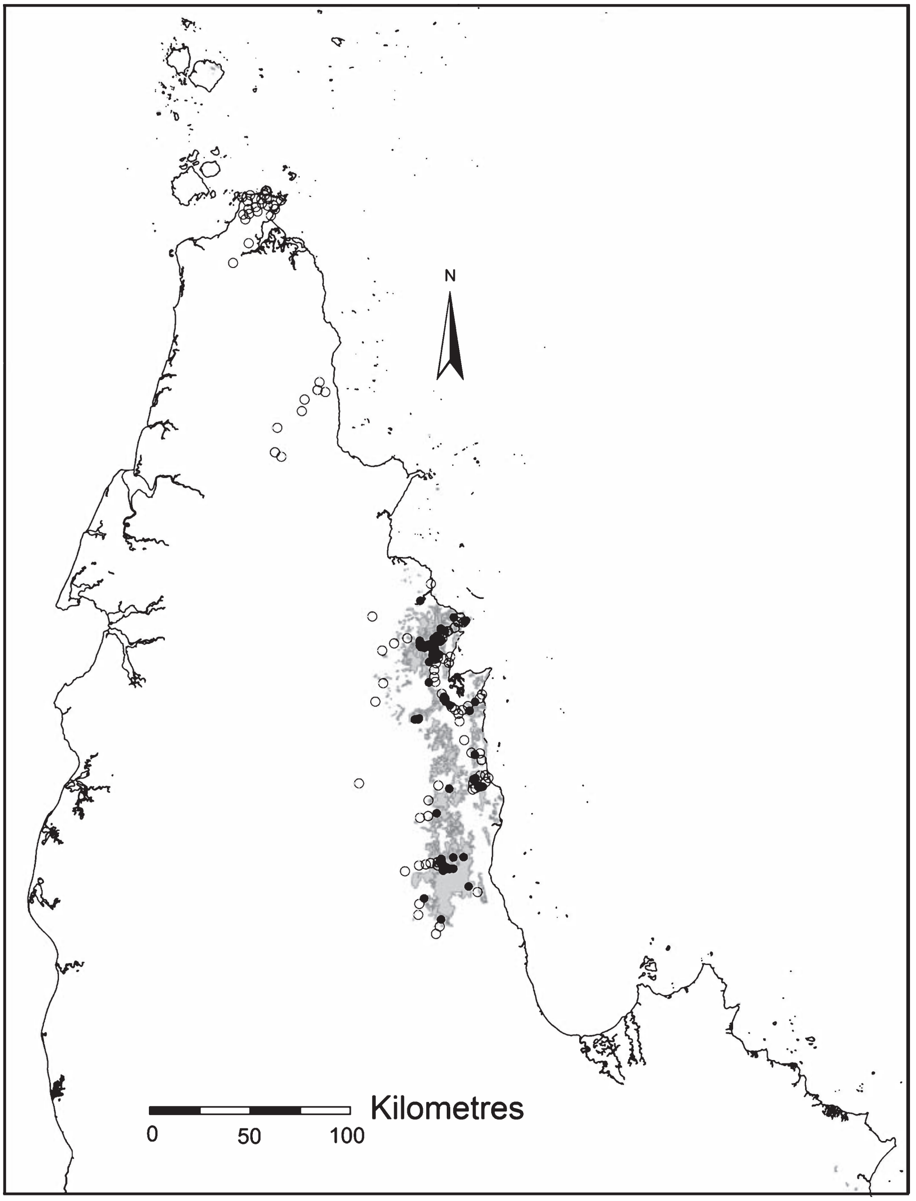

Fig. 2. Distribution of habitats suitable to green pythons (light grey) and survey sites where green pythons were found to be present (●) or absent (○).

habitat, and 66% of all the regional ecosystems where green pythons were located are protected within these two parks (Table 2).

Absent or undetected?

In all, 111 person-hours were spent searching in three habitat types in the Lockerbie Scrub, but no green pythons were found. The survey method was changed after eight cycles and rainforest, swamp, woodland and vine thicket habitats were searched randomly for a further 78 person-hours. Despite this extra effort, no green pythons were discovered.

The probability of occupancy in all habitats in the Lockerbie Scrub is estimated to be 0. Given the number of individual surveys at Lockerbie (139) green pythons should have been detectable with 95% certainty for a detection probability as low as 0.02 (Table 3). For rainforest habitats in the McIlwraith and Iron ranges the probabilities of detecting a green python on a given survey were 0.3 and 0.62, respectively, which are significantly greater than the probability in the Lockerbie Scrub (Table 3). Similarly, green pythons were never detected in open habitats during surveys and the probability of their occupying these habitats was estimated to be 0 for both the Iron and McIlwraith ranges (Table 3).

Density and abundance

There were marked differences in the relative abundance of green pythons amongst the intensively surveyed sites (Table 1). After accounting for the difference in survey area (Table 1), green

Table 2. Area of each habitat type in which green pythons were found on Cape York and the extent of these habitats in protected areas
IR, Iron Range; MR, McIlwraith Range; KN, Kawadji–Ngaachi Ranges. All values are in square kilometres, taken from Neldner and Clarkson (1995). Figures in parentheses are percentages of the total of each vegetation type found in the respective protected area

Regional ecosystem	Habitat type	Description	Sites present	Extent within the Iron Range NP	Extent within the McIlwraith Range NP	Total extent in area of occupancy
3.11.3	Rainforest	Simple evergreen notophyll vine forest with *Acacia* spp. or *Eucalyptus* spp. emergents on exposed metamorphic and granitic slopes	IR, MR	48 (14)	142 (41)	347
3.12.21	Vine thicket	Deciduous vine thicket dominated by *Cochlospermum gillivraei*, *Canarium australianum* and *Acacia aulacocarpa* on granite slopes	IR, MR	20 (11)	109 (57)	190
3.12.3	Rainforest	Evergreen to semideciduous notophyll vine forest on the slopes of the McIlwraith Uplands	All	314 (24)	633 (49)	1304
3.2.11	Vine thicket	Low microphyll vine forest dominated by *Acacia crassicarpa* and *Syzygium banksii* on coastal dunes	IR, KN	18 (20)	23 (25)	92
3.3.1	Rainforest	Semideciduous mesophyll vine forest on alluvia, and metamorphic and granitic foothills and lower hill slopes	All	28 (8)	164 (46)	356
Total of all vegetation types				428 (15)	1071 (44)	2289

pythons were encountered more frequently in the Iron Range than in the McIlwraith Range ($\chi^2 = 32.1$, d.f. = 1, $P < 0.001$) (Table 1). At both sites the density of green pythons was determined for evergreen to semideciduous notophyll vine forest only, as captures in deciduous and beach vine thickets were too few (Table 1). Green python encounter rates in the Iron Range were higher in rainforest than in vine thicket, whereas snakes were encountered equally often in rainforest and vine thicket in the McIlwraith Range. Between sites, snakes were encountered more frequently in the Iron Range than in the McIlwraith Range in both habitats (Table 1). Density, encounter rates and detection probability of green pythons in the McIlwraith Range was roughly half that of the Iron Range, suggesting that detection probability may be directly related to abundance.

Of the snakes captured in the Iron Range during this study, 11 had been previously tagged during the study of Wilson *et al.* (2006*a*). Each of these snakes was larger than 100 cm SVL; nine were female (mean SVL = 127 cm; range = 101–137 cm) and two male (mean SVL = 113 cm; range 110.5–115.5 cm).

Population demographics

The green python sex ratio between sites was broadly similar. The numbers of identified adult male and female snakes captured in the McIlwraith Range were marginally not significant (14 males, 26 females, versus a null of 50% male: $\chi^2 = 3.6$, d.f. = 1, $P = 0.058$). By comparison, captures of each sex in the Iron Range were broadly similar (50 males, 67 females: $\chi^2 = 2.47$, d.f. = 1, $P = 0.116$) (Fig. 4).

The age profile of green pythons differed between study areas (Fig. 4). In the Iron Range, 56% of the snakes captured were adults, similar to the number of immature individuals captured, regardless of sex ($\chi^2 = 2.47$, d.f. = 1, $P = 0.116$). In the McIlwraith Range, however, 83% of snakes were adults, outnumbering immature individuals of both sexes ($\chi^2 = 16.9$, d.f. = 1, $P < 0.001$) (Fig. 4). Furthermore, the proportion of snakes captured over 120 cm SVL was different between sites (Iron Range = 15%, McIlwraith Range = 32%: $\chi^2 = 6.1$, d.f. = 1, $P = 0.01$).

Discussion

Distribution

Green pythons are distributed in closed forest habitats in the Iron–McIlwraith Ranges region and have been recorded for the first time in the coastal Kawadji–Ngaachi Ranges. Within the Iron–McIlwraith Ranges region there are 2289 km^2 of suitable habitat (Table 2). This is a significantly larger area than the bioclimatic prediction of Wilson and Heinsohn (2007), but is less than their predicted distribution based on regional ecosystems. The difference in the area of regional ecosystems used between the two studies arises because Wilson and Heinsohn (2007) overlaid green python capture records on GIS habitat maps and small mapping inaccuracies led to green pythons being recorded in four woodland regional ecosystems. In the present study, regional ecosystem preference was established directly from green python capture locations, which were never within woodlands (Table 2).

Green pythons have a strong association with evergreen to semideciduous notophyll vine forest in the Iron–McIlwraith Ranges region. During detection-only surveys, there was only one occasion when a green python was not located in this habitat. Detection probability was low in vine/riparian habitats with large standard errors (Table 3). This was because green pythons were detected at only a few of the sites surveyed but were reasonably abundant at intensively surveyed vine forest sites in the McIlwraith and Iron ranges (Table 1). By contrast, green pythons were not found in surveys of 35 regional ecosystems at

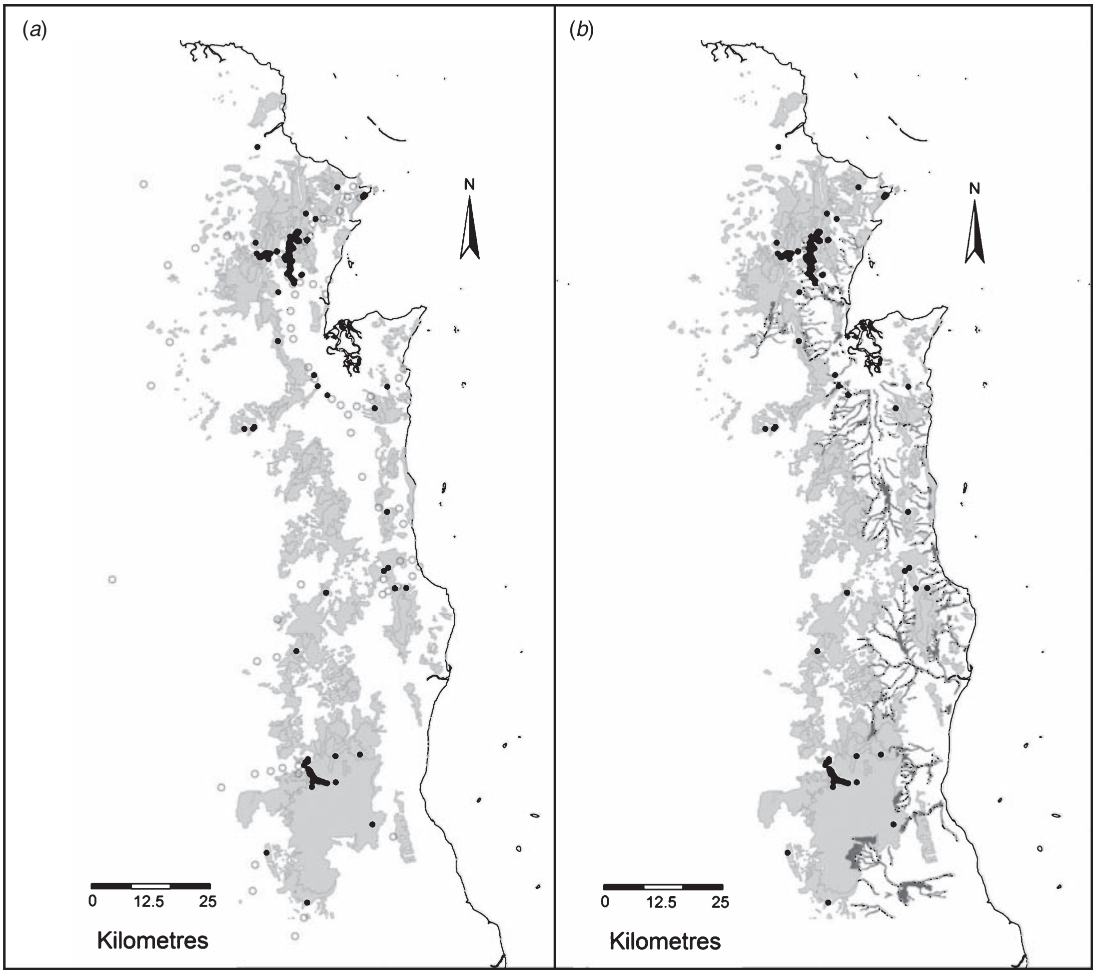

Fig. 3. Distribution of suitable habitats in the Iron-McIlwraith Range region (light grey). Presence (●) and absence (○) sites are mapped without rainforest creek lines (regional ecosystem 3.3.1) (*a*) and presence sites are mapped showing connecting creek corridors (dark grey) (*b*).

Table 3. Proportion of sites occupied (Ψ) and probability of detection (*p*) of green pythons in Cape York

At the Lockerbie Scrub *p* was derived from the equation given by McArdle (1990) and is based on search effort

Study area	Habitat	Ψ (s.e.)	*p* (s.e.)
McIlwraith Range	Rainforests	0.93 (0.06)	0.30 (0.04)
McIlwraith Range	Vine/riparian	0.24 (0.20)	–
McIlwraith Range	Open habitats	0.00 (0.01)	–
Lockerbie Scrub	All habitats	0.00 (0.00)	0.02
Iron Range	Rainforests	1.00 (0.00)	0.62 (0.05)
Iron Range	Vine/riparian	0.67 (0.27)	–
Iron Range	Open habitats	0.00 (0.00)	–

more than 100 sites, including woodland, swamp, grassland and heath.

The rainforests of the Iron and McIlwraith ranges are functionally separated by a 7 km stretch of woodlands on the Ngalapichi Plateau. Similarly, the rainforested Kawadji–Ngaachi Ranges are separated from one another and from the larger McIlwraith and Iron ranges by the grasslands and woodlands of the Lockhart and Nesbit River valleys. In principle, green pythons could use riparian creek corridors to move between rainforest blocks (Fig. 3), as is the case with other rainforest-dependant fauna (Jansen 2005). However, while they were observed in riparian forest in the present study they were never found during surveys of this habitat type near the Lockhart River, Nesbit River and Falloch Creek tributaries, suggesting that dispersal between these three, potentially linked, rainforest areas may be infrequent.

Despite anecdotal records of green pythons in the rainforests of the Jardine River catchment and the Lockerbie Scrub, they have never been found during surveys at these sites (Grant and Leung 1993; Cohen 1994; Grant and Leung 1994). Although the results of our analysis indicate absence, it should be noted that the model used relies on detections to estimate parameters, and, as such, a single detection would greatly alter our results. We suggest that given the high detectability of green pythons at other sites (Table 3), and our 95% confidence in finding green

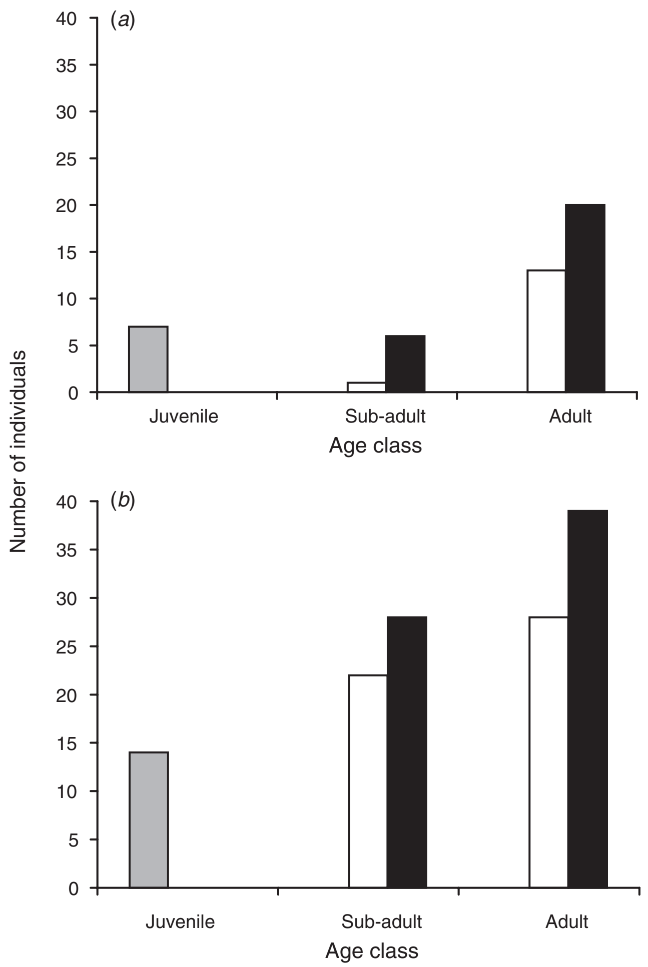

Fig. 4. Age class distributions of female (black columns), male (white columns) and sex-unknown (grey column) green pythons captured in the (*a*) McIlwraith and (*b*) Iron ranges.

pythons given a detection probability of 0.02, it is unlikely that green pythons were present yet undetected in the Lockerbie Scrub.

The current distributions of many Australo-Papuan flora and fauna are attributable to the historical biogeography of this region (Flannery 1988). A land connection between Australia and New Guinea was in place as recently as the late Pleistocene (Voris 2000), enabling an interchange of flora and fauna between the two landmasses. However, the expansion of rainforest vegetation beyond its current extent has occurred only briefly during periods of climatic suitability (Nix and Kalma 1972; Kershaw *et al.* 2007*a*) and an exchange of rainforest-dependant species is permitted only at these times. The difference between rainforest flora (Webb and Tracy 1981; Crisp *et al.* 2001) and fauna (Kikkawa *et al.* 1981) between the Wet Tropics, Cape York and New Guinea suggest at least two recent rainforest connections across what is now Torres Strait.

Palynological evidence from the Wet Tropics and Gulf of Carpentaria suggests that there have been only two periods within the last 250 000 years when rainforests in northern Australia have developed beyond their current extent (Hopkins *et al.* 1996; Kershaw *et al.* 2007*b*). The first occurred ~125 000 years ago and the second ~6000 years ago (Kershaw 1978, 1994; Hopkins *et al.* 1996; Kershaw *et al.* 2007*b*). It is unlikely, however, that green pythons were able to migrate between Australia and New Guinea at these times because the Torres Strait land-bridge was submerged (Geyh *et al.* 1979; Chappell and Shackleton 1986; Collins *et al.* 2006; Woodroffe 2009; Yu and Zhao 2010). Furthermore, recent palynological studies suggest that, during the Holocene at least, the extent of rainforests in Cape York and Torres Strait were similar to the present (Luly *et al.* 2006; Rowe 2007*a*, 2007*b*).

It appears likely, therefore, that rainforest species residing in Australia and New Guinea have been separated for considerably longer than previously thought (Westerman *et al.* 2001; Hocknull *et al.* 2007; Norman *et al.* 2007; Macqueen *et al.* 2010). If green pythons have been present in Australia for 250 000 years, their absence from the rainforests of the Lockerbie Scrub and Jardine River is because these rainforests disappeared during the glacial periods of the Pleistocene. Unlike the Iron–McIlwraith Range region, the Lockerbie Scrub and Jardine River catchment areas have relatively low topography and probably did not act as moist refugia during times of rainforest contraction (Webb and Tracy 1981). This fits with the findings of other studies, which show that Pleistocene rainforest contraction into moist refugia has resulted in the vicariance and extinction of other rainforest taxa in north Queensland (Dodson 1989; Schneider and Moritz 1999; Hocknull *et al.* 2007). The absence of green pythons in the Lockerbie Scrub and Jardine River Catchment is consistent with that of other rainforest-dependant fauna in Cape York (Legge *et al.* 2004).

Relative abundance and habitat preference

The population estimates, encounter rates and total number of snakes caught (Table 1) show that green pythons are more detectable and probably more abundant in the Iron Range than in the McIlwraith Range. This phenomenon occurs in other snake species over similarly small areas (Parker and Plummer 1987). The density estimates in notophyll vine forest (Regional Ecosystem 3.12.3) given in this study for the Iron Range area are very close to the estimates of Wilson and Heinsohn (2007) for the same region, despite the different methods used to determine survey area. The low recapture rate is probably due to green pythons not spending large amounts of time on the ground. The disparity between the abundance of green pythons in notophyll vine forest in the Iron and McIlwraith ranges is noteworthy. The only obvious difference between the two sites is altitude, which ranges from 0–50 m over the Iron Range study site and 350–681 m over the McIlwraith site, and may have a role in limiting green python abundance. In support of this idea, Henderson and Henderson (1995) found that encounter rates of the tropical and arboreal *Corallus hortulanus* were significantly lower above than below 400 m; however, green pythons in this study were equally abundant between 350 m and 681 m in the McIlwraith Range, and are known to occur up to 2000 m elevation in New Guinea (McDowell 1975; O'Shea 1996). It seems improbable, therefore, that an increased elevation of only 300 m can explain the different encounter rates at the Iron and McIlwraith Range study sites.

The relative abundance of snakes in an area is often correlated with the abundance of suitable prey species (Arnold 1972). This has been shown to be true in Australian ecosystems (Bonnet *et al*. 2002*b*; Madsen *et al*. 2006) and it may be that the Iron Range has a higher density of suitable prey species than the McIlwraith Range. There are abundance estimates for three known prey species (*Antechinus leo*, *Melomys capensis* and *Rattus leucopus*: Leung 1999*a*, 1999*b*, 1999*c*) in the Iron Range; however, there are none for the McIlwraith Range so this hypothesis cannot be tested.

As found by Wilson and Heinsohn (2007) in the Iron Range National Park, green pythons were most abundant in notophyll vine forest (Table 1), but were also present in vine thickets adjacent to rainforest. Similarly, in the McIlwraith Range green pythons were found only on sections of vine thicket transects that were in close proximity to rainforest and never at more than 1 km from this habitat type (Natusch unpubl. data). The vine thickets in Cape York are relatively open and species-poor compared with nearby rainforests (Stanton and Fell 2005) and it may be that green python ambush sites and prey species are proportionately scarce. By contrast, the 12 snakes found in vine thicket in the Iron Range were all of varying sizes, including juveniles, suggesting a permanent breeding population and not merely emigrants from nearby areas.

Population demographics

In both the McIlwraith and Iron ranges, females outnumbered males (where sex could be determined); however, this difference is not significant (Fig. 4) and much less pronounced than documented by Wilson *et al*. (2006*a*, 2006*b*), who reported significantly more immature females (59) than males (4). The sex divergence found in the present study relates to the sexes maturing at different sizes, and cannot explain the difference found by Wilson *et al*. (2006*a*) for immature snakes.

The difference between age profiles in the McIlwraith and Iron Range samples is noteworthy. The results from the Iron Range fit with those of Wilson and Heinsohn (2007), with only ~50% of the sample population being sexually mature. In the McIlwraith Range, however, the higher proportion of adult snakes is significant and the number of snakes over 120 cm SVL in the sample indicates a greater number of large individuals at this site. It is possible that, due to its accessibility, collection for the pet trade in Iron Range has skewed the population demographic towards immature snakes, although the number of green pythons taken from the area is not known. Given a probable non-annual reproduction and potentially slow emigration rate (Wilson *et al*. 2006*a*, 2006*b*), however, the high proportion of immature snakes may be indicative of the recovery of this localised population. This is in accord with observations in other snake populations recovering from human predation (Webb *et al*. 2002; Sasaki *et al*. 2008) and specifically green pythons (Lyons and Natusch, in press).

Conclusions

This study has shown that the green python, a species long thought to be rare, is relatively common and widespread within suitable habitat in Cape York Peninsula.

Extrapolation of the green python densities in the study areas suggests that the total population in Cape York Peninsula is considerably larger than hitherto thought. While such extrapolation should be viewed with caution, the population within the Iron Range and McIlwraith Range National Parks is estimated to be >30 000 individuals, based conservatively on the lowest confidence limits for density estimates in a single regional ecosystem (3.12.3). It should be noted, however, that our extrapolation applies only to a single regional ecosystem in which green pythons were found, and does not include suitable habitat outside the National Parks. The total number of snakes is, therefore, likely to be much greater.

For conservation purposes the Australian green python population can effectively be treated as a single unit. Although green pythons occur in three areas that are isolated from one another, each area is characterised by the same core habitat and all three are in close proximity. Furthermore, most habitats suitable to green pythons fall within only three land tenures, two of which are National Parks.

This work supports the conclusion of Wilson and Heinsohn (2007) that green pythons do not satisfy any of the criteria to qualify them as vulnerable in Australia (IUCN 2001). Neither do they meet the criteria to be classified as near-threatened in Queensland (*Nature Conservation Act 1992*). Further surveys in the Iron Range area would provide valuable information on the dynamics of green python populations, clarifying how the demographic composition of these snakes fluctuates in time. In addition, long-term monitoring would provide a more reliable foundation for determining what, if any, changes in policy may be required for effective management of green pythons in the face of future threats such as anthropogenic climate change. Given that this may occur at a rate far faster than natural cycles of climate change, green pythons and other rainforest species may be less able to adjust to the consequent habitat changes than they have been in the past.

Acknowledgements

Thank you to Mike Archer and Sue Hand for supervising this project. We thank Bill Koutsamanis, Jess Lyons, Frank Maltzahn, Matt McCloskey, Lachlan McIntyre, Rowan McIntyre and Sara Spence for help in the field. Naomi Hobson, Tim Jaffer, John and Jackie Mulholland, and Scott Templeton provided generous logistic support. Robert Heinsohn, Jonothan Webb and David Wilson suggested improvements to this work. Thank you to the Traditional Owners of Cape York for providing access to their lands for this research. This study was completed with the help of funding from the Australian Geographic Society, Linnean Society of New South Wales and SeaSwift Far North Queensland. Research was carried out under Department of Environment and Resource Management permits WISP04847807 and WITK04847707 and completed under the University of New South Wales Animal Ethics permit 07/60A.

References

Arnold, S. (1972). Species densities of predators and their prey. *American Naturalist* **106**, 220–236. doi:10.1086/282763

Auliya, M. (2003). 'Hot Trade in Cool Creatures: a Review of the Live Reptile Trade in the European Union in the 1990s with a Focus on Germany.' (TRAFFIC: Belgium)

Barker, D. G., and Barker, T. M. (1994). 'Pythons of the World: Volume 1. Australia.' (Advanced Vivarium Systems Inc.: Escondido, CA.)

Bonnet, X., Pearson, D., Ladyman, M., Lourdais, O., and Bradshaw, D. (2002*b*). 'Heaven' for serpents? A mark–recapture study of tiger snakes (*Notechis scutatus*) on Carnac Island, Western Australia. *Austral Ecology* **27**, 442–450. doi:10.1046/j.1442-9993.2002.01198.x

Brown, W. S., and Parker, W. S. (1976). A ventral scale clipping system for permanently marking snakes (Reptilia, Serpentes). *Journal of Herpetology* **10**, 247–249. doi:10.2307/1562986

Burnham, K. P., and Anderson, D. R. (2001). Kullback–Leibler information as a basis for strong inference in ecological studies. *Wildlife Research* **28**, 111–119. doi:10.1071/WR99107

Chappell, J., and Shackleton, N. J. (1986). Oxygen isotopes and sea level. *Nature* **324**, 137–140. doi:10.1038/324137a0

Cogger, H., Cameron, E., Sadlier, R., and Eggler, P. (1993). 'The Action Plan for Australian Reptiles.' (Australian Nature Conservation Agency: Canberra.)

Cohen, M. P. (1994). Survey of the terrestrial vertebrate fauna at Heathlands, Cape York Peninsula during March/April, 1993. Report to Queensland Department of Environment and Heritage, Cairns.

Collins, L. B., Zhao, J., and Freeman, H. (2006). A high precision record of mid–late Holocene sea-level events from emergent coral pavements in the Houtman Abrolhos Islands, southwest Australia. *Quaternary International* **145–146**, 78–85. doi:10.1016/j.quaint.2005.07.006

Crisp, M. D., Laffan, S., Linder, H. P., and Monro, A. (2001). Endemism in the Australian flora. *Journal of Biogeography* **28**, 183–198. doi:10.1046/j.1365-2699.2001.00524.x

Dodson, J. R. (1989). Late pleistocene vegetation and environmental shifts in Australia and their bearing on faunal extinctions. *Journal of Archaeological Science* **16**, 207–217. doi:10.1016/0305-4403(89)90066-6

Flannery, T. F. (1988). Origins of the Australo-Pacific mammal fauna. *Australian Zoological Reviews* **1**, 15–24.

Frith, D. W., and Frith, C. B. (1995). 'Cape York Peninsula: A Natural History.' (Reed Books Australia: Sydney.)

Geyh, M. A., Streif, H., and Kudrass, H. R. (1979). Sea-level changes during the late Pleistocene and Holocene in the Strait of Malacca. *Nature* **278**, 441–443. doi:10.1038/278441a0

Gibbons, J. W., and Andrews, K. M. (2004). PIT tagging: simple technology at its best. *Bioscience* **54**, 447–454. doi:10.1641/0006-3568(2004)054[0447:PTSTAI]2.0.CO;2

Grant, J. D., and Leung, L. (1993). Wet Season terrestrial fauna survey of the Lockerbie Scrub, Cape York Peninsula, April–May 1993. Report to the Queensland Department of Environment and Heritage, Cairns.

Grant, J. D., and Leung, L. (1994). Storm Season terrestrial fauna survey of the Lockerbie Scrub, Cape York Peninsula, February 1994. Report to the Queensland Department of Environment and Heritage, Cairns.

Gu, W., and Swihart, R. K. (2004). Absent or undetected? Effects of non-detection of species occurrence on wildlife–habitat models. *Biological Conservation* **116**, 195–203. doi:10.1016/S0006-3207(03)00190-3

Henderson, R. W., and Henderson, K. F. (1995). Altitudinal variation in body temperatures in foraging tree boas (*Corallus enhydris*) on Grenada. *Caribbean Journal of Science* **31**, 73–76.

Hocknull, S. A., Zhao, J., Feng, Y., and Webb, G. E. (2007). Responses of Quaternary rainforest vertebrates to climate change in Australia. *Earth and Planetary Science Letters* **264**, 317–331. doi:10.1016/j.epsl.2007.10.004

Hopkins, M. S., Head, J., Ash, J. E., Hewett, R. K., and Graham, A. W. (1996). Evidence of a Holocene and continuing recent expansion of lowland rain forest in humid, tropical North Queensland. *Journal of Biogeography* **23**, 737–745. doi:10.1111/j.1365-2699.1996.tb00035.x

IUCN (2001). IUCN Red List Categories and Criteria: Version 3.1. (IUCN Species Survival Commission, Cambridge, UK).

Jansen, A. (2005). Avian use of restoration plantings along a creek linking rainforest patches on the Atherton Tablelands, North Queensland. *Restoration Ecology* **13**, 275–283. doi:10.1111/j.1526-100X.2005.00035.x

Kend, B. (1997). 'Pythons of Australia.' (Canyonland Publishing Group: Provo, USA).

Kershaw, A. P. (1978). Record of last interglacial–glacial cycle from northeastern Queensland. *Nature* **272**, 159–161. doi:10.1038/272159a0

Kershaw, A. P. (1994). Pleistocene vegetation of the humid tropics of northeastern Queensland, Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology* **109**, 399–412. doi:10.1016/0031-0182(94)90188-0

Kershaw, A. P., van der Kaars, S., and Flenley, J. R. (2007*a*). The Quaternary history of far eastern rainforests. In 'Tropical Rainforest Responses to Climatic Change'. (Eds M. B. Bush and J. R. Flenley.) (Springer: New York.)

Kershaw, A. P., Bretherton, S. C., and van der Kaars, S. (2007*b*). A complete pollen record of the last 230 ka from Lynch's Crater, north-eastern Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology* **251**, 23–45. doi:10.1016/j.palaeo.2007.02.015

Kikkawa, J., Monteith, G., and Ingram, G. J. (1981). Cape York Peninsula: major region of faunal interchange. In 'Ecological Biogeography of Australia'. (Ed. A. Keast.) pp. 1695–1742. (Dr. W. Junk: The Hague.)

Krebs, C. J. (1972). 'Ecology: the Experimental Analysis of Distribution and Abundance.' (Harper & Row Publishers: New York.)

Legge, S., Heinsohn, R., and Garnett, S. (2004). Availability of nest hollows and breeding population size of eclectus parrots, *Eclectus roratus*, on Cape York Peninsula. *Wildlife Research* **31**, 149–161. doi:10.1071/WR03020

Leung, L. (1999*a*). Ecology of Australian tropical rainforest mammals. I. The Cape York antechinus, *Antechinus leo* (Dasyuridae: Marsupialia). *Wildlife Research* **26**, 287–306. doi:10.1071/WR96042

Leung, L. (1999*b*). Ecology of Australian tropical rainforest mammals. II. The Cape York melomys, *Melomys capensis* (Muridae: Rodentia). *Wildlife Research* **26**, 307–316. doi:10.1071/WR96043

Leung, L. K.-P. (1999*c*). Ecology of Australian tropical rainforest mammals. III. The Cape York rat, *Rattus leucopus* (Muridae: Rodentia). *Wildlife Research* **26**, 317–328. doi:10.1071/WR96044

Luly, J. G., Grindrod, J. F., and Penny, D. (2006). Holocene palaeoenvironments and change at Three-Quarter Mile Lake, Silver Plains Station, Cape York Peninsula, Australia. *The Holocene* **16**, 1085–1094. doi:10.1177/0959683606069398

Lyons, J. A., and Natusch, D. J. O. (in press). Wildlife laundering through breeding farms illegal harvest, population declines and a means of regulating the trade of green pythons (*Morelia viridis*) from Indonesia. *Biological Conservation*.

MacKenzie, D. I., and Royle, J. A. (2005). Designing efficient occupancy studies: general advice and tips on allocation of survey effort. *Journal of Applied Ecology* **42**, 1105–1114. doi:10.1111/j.1365-2664.2005.01098.x

MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, J. A., and Langtimm, C. L. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology* **83**, 2248–2255. doi:10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2

Macqueen, P., Seddon, J. M., Austin, J. J., Hamilton, S., and Goldizen, A. W. (2010). Phylogenetics of the pademelons (Macropodidae: *Thylogale*) and historical biogeography of the Australo-Papuan region. *Molecular Phylogenetics and Evolution* **57**, 1134–1148. doi:10.1016/j.ympev.2010.08.010

Madsen, T., Ujvari, B., Shine, R., and Olsson, M. (2006). Rain, rats and pythons: climate-driven population dynamics of predators and prey in tropical Australia. *Austral Ecology* **31**, 30–37. doi:10.1111/j.1442-9993.2006.01540.x

McArdle, B. H. (1990). When are rare species not there? *Oikos* **57**, 276–277. doi:10.2307/3565950

McDowell, S. B. (1975). A catalogue of the snakes of New Guinea and the Solomons, with special reference to those in the Bernice P. Bishop Museum. Part II. Aniliodea and Pythoninae. *Journal of Herpetology* **9**, 1–79. doi:10.2307/1562691

Neldner, V. J., and Clarkson, J. R. (1995). Vegetation of Cape York Peninsula. Department of Environment and Heritage, Brisbane.

Nix, H. A., and Kalma, J. D. (1972). Climate as a dominant control in the biogeography of northern Australia and New Guinea. In 'Bridge and Barrier: the Natural and Cultural History of Torres Strait'. (Ed. D. Walker.) pp. 61–91. (Research School of Pacific Studies, ANU: Canberra.)

Norman, J. A., Rheindt, F. E., Rowe, D. L., and Christidis, L. (2007). Speciation dynamics in the Australo-Papuan *Meliphaga* honeyeaters. *Molecular Phylogenetics and Evolution* **42**, 80–91. doi:10.1016/j.ympev.2006.05.032

O'Shea, M. (1996). 'A Guide to the Snakes of Papua New Guinea.' (Independant Publishing: Port Moresby.)

Parker, W., and Plummer, M. (1987). Population ecology. In 'Snakes: Ecology and Evolutionary Biology'. (Eds R. Siegel, J. Collins and S. Novak.) pp. 253–301. (Macmillan Publishing Company: New York.)

Ricklefs, R. E., and Miller, G. L. (2000). 'Ecology.' (W.H Freeman and Co.: New York.)

Rodrigues, A. S. L., Pilgrim, J. D., Lamoreux, J. F., Hoffmann, M., and Brooks, T. M. (2006). The value of the IUCN Red List for conservation. *Trends in Ecology & Evolution* **21**, 71–76. doi:10.1016/j.tree.2005.10.010

Rowe, C. (2007*a*). A palynological investigation of Holocene vegetation change in Torres Strait, seasonal tropics of northern Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology* **251**, 83–103. doi:10.1016/j.palaeo.2007.02.019

Rowe, C. (2007*b*). Vegetation change following mid-Holocene marine transgression of the Torres Strait shelf: a record from the island of Mua, northern Australia. *The Holocene* **17**, 927–937. doi:10.1177/0959683607082409

Sasaki, K., Fox, S., and Duvall, D. (2008). Rapid evolution in the wild: changes in body size, life-history traits, and behavior in hunted populations of the Japanese Mamushi snake. *Conservation Biology* **23**, 93–102. doi:10.1111/j.1523-1739.2008.01067.x

Sattler, P., and Williams, R. (1999). The conservation of Queensland's bioregional ecosystems. Environmental Protection Agency, Brisbane.

Schneider, C., and Moritz, C. (1999). Rainforest refugia and evolution in Australia's Wet Tropics. *Proceedings of the Royal Society of London. Series B. Biological Sciences* **266**, 191–196. doi:10.1098/rspb.1999.0621

Shine, R., and Slip, D. J. (1990). Biological aspects of the adaptive radiation of Australian pythons (Serpentes: Boidae). *Herpetologica* **46**, 283–290.

Stanton, P., and Fell, D. (2005). The rainforests of Cape York Peninsula. Cooperative Research Centre for Tropical Rainforest Ecology and Management. Rainforest CRC, Cairns.

TRAFFIC (2009). Seizures and prosecutions. TRAFFIC North America, Washington. *Palaeogeography, Palaeoclimatology, Palaeoecology* **155**, 135–153.

Voris, H. K. (2000). Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. *Journal of Biogeography* **27**, 1153–1167. doi:10.1046/j.1365-2699.2000.00489.x

Waldren, I. (1996). Rainforests of Cape York Peninsula and their exploitation by herptiles. *Monitor* **8**, 5–14.

Webb, L., and Tracy, J. (1981). Australian rainforests: patterns and change. In 'Ecological Biogeography of Australia'. (Ed. A. Keast.) pp. 607–694. (Dr W. Junk: The Hague.)

Webb, J. K., Brook, B. W., and Shine, R. (2002). Collectors endanger Australia's most threatened snake the broad-headed snake *Hoplicephalus bungaroides. Oryx* **36**, 170–181. doi:10.1017/S0030605302000248

Westerman, M., Springer, M. S., and Krajewski, C. (2001). Molecular relationships of the New Guinean bandicoot genera *Microperoryctes* and *Echymipera* (Marsupialia: Peramelina). *Journal of Mammalian Evolution* **8**, 93–105. doi:10.1023/A:1011302314000

Wilson, D., Heinsohn, R., and Endler, J. (2007). The adaptive significance of ontogenetic colour change in a tropical python. *Biology Letters* **3**, 40–43.

Wilson, D., and Heinsohn, R. (2007). Geographic range, population structure and conservation status of the green python (*Morelia viridis*), a popular snake in the captive pet trade. *Australian Journal of Zoology* **55**, 147–154. doi:10.1071/ZO06078

Wilson, D., Heinsohn, R., and Wood, J. (2006*a*). Life-history traits and ontogenetic colour change in an arboreal tropical python, *Morelia viridis. Journal of Zoology* **270**, 399–407. doi:10.1111/j.1469-7998.2006.00190.x

Wilson, D., Heinsohn, R., and Legge, S. (2006*b*). Age- and sex-related differences in the spatial ecology of a dichromatic tropical python (*Morelia viridis*). *Austral Ecology* **31**, 577–587. doi:10.1111/j.1442-9993.2006.01519.x

Woodroffe, S. A. (2009). Testing models of mid to late Holocene sea-level change, North Queensland, Australia. *Quaternary Science Reviews* **28**, 2474–2488. doi:10.1016/j.quascirev.2009.05.004

Yu, K. F., and Zhao, J. X. (2010). U-series dates of Great Barrier Reef corals suggest at least +0.7 m sea level similar to 7000 years ago. *The Holocene* **20**, 161–168. doi:10.1177/0959683609350387

Handling editor: Raoul Mulder