CSIRO PUBLISHING
www.publish.csiro.au/journals/ajz Australian Journal of Zoology, 2009, 57, 119–124

Natural history of the slaty grey snake (*Stegonotus cucullatus*) (Serpentes : Colubridae) from tropical north Queensland, Australia

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Abstract. Slaty grey snakes (*Stegonotus cucullatus*) are medium to large members of the Colubridae that are common throughout the eastern and northern tropics of Australia. Although intensive field studies have been conducted on populations in the Northern Territory for over 10 years, no ecological data have been presented on free-ranging specimens of populations inhabiting tropical north Queensland. During a 10-year period we collected opportunistic data on 120 free-ranging specimens from the seasonally Wet Tropics in north Queensland. These snakes provided data on body sizes, activity times, food habits and reproduction. Male *S. cucullatus* were larger than females and had larger heads. More snakes were found during the warmer, humid parts of the year (wet season). *S. cucullatus* ate a wide range of vertebrate prey, including reptile eggs that were obtained seasonally. Females produced one clutch per year, and no relationship was found between maternal snout–vent length and clutch size.

Introduction

The slaty grey snake (*Stegonotus cucullatus*) Duméril, Bibron & Duméril (1854) is a relatively common colubrid snake that occurs in north Queensland, from the vicinity of Townsville (Trembath and Lloyd 2005; Bower and Trembath 2006) to Cape York and through the Top End of the Northern Territory (Wilson and Swan 2008). Throughout this distribution *S. cucullatus* is most often associated with waterways (Wilson and Swan 2008), including artificial wetlands and natural floodplains of the Top End (Brown *et al*. 2005). In north-east Queensland *S. cucullatus* is most often associated with rainforest habitats, but can be found in seasonally dry tropical savannah areas, where it appears to be restricted to riparian habitats and associated vine thickets (Trembath and Fearn, pers. obs.).

To date the only quantitative ecological information on Queensland *S. cucullatus* has been derived from preserved museum specimens (Shine 1991). Though this method allows the compilation of large datasets, it involves pooling geographically widespread samples obtained over long periods, which can mask possible instances of ecological variation throughout the taxon's range (Trembath and Fearn 2008). Additionally, problems may arise if species groups are poorly understood at the time of study and investigators unwittingly combine species in their analysis (Fearn and Trembath 2009). *S. cucullatus* in the Northern Territory is well studied, with works on seasonal activity (Brown and Shine 2002; Brown *et al*. 2002), movements (Brown *et al*. 2005), dispersal (Dubey *et al*. 2008) and sexual selection (Dubey *et al*. 2009) appearing in recent years.

In this paper we present data on body size, body condition, seasonal activity, dietary habits, and reproduction from a large sample of wild-caught individuals inhabiting rainforest in north Queensland.

Methods

Between 1997 and 2006 living and road-killed specimens of *S. cucullatus* were examined at two rainforest localities in tropical coastal Queensland. All specimens were obtained from the vicinity of Tully (17°45′30″S, 145°38′02″E) and the Lamb Range on the outskirts of Cairns (16°58′55″S, 145°41′11″E). Both sites have high year-round rainfall (Fig. 1) and vegetation consists of closed rainforest (simple notophyll vine forest) with adjoining modified habitats (formerly rainforest) of grazing land, as well as banana and sugarcane plantations.

We obtained specimens primarily by nocturnal road driving (60 km h^{-1}) at both localities throughout the year. Road-killed specimens collected while travelling roads between the study sites were included in the dataset if the adjacent roadside vegetation consisted of >50% rainforest. For each snake we recorded the date and location of capture. Immediately after capture, sex was determined by eversion (or not) of hemipenes, snout–vent length (SVL) and tail length (TL) were measured

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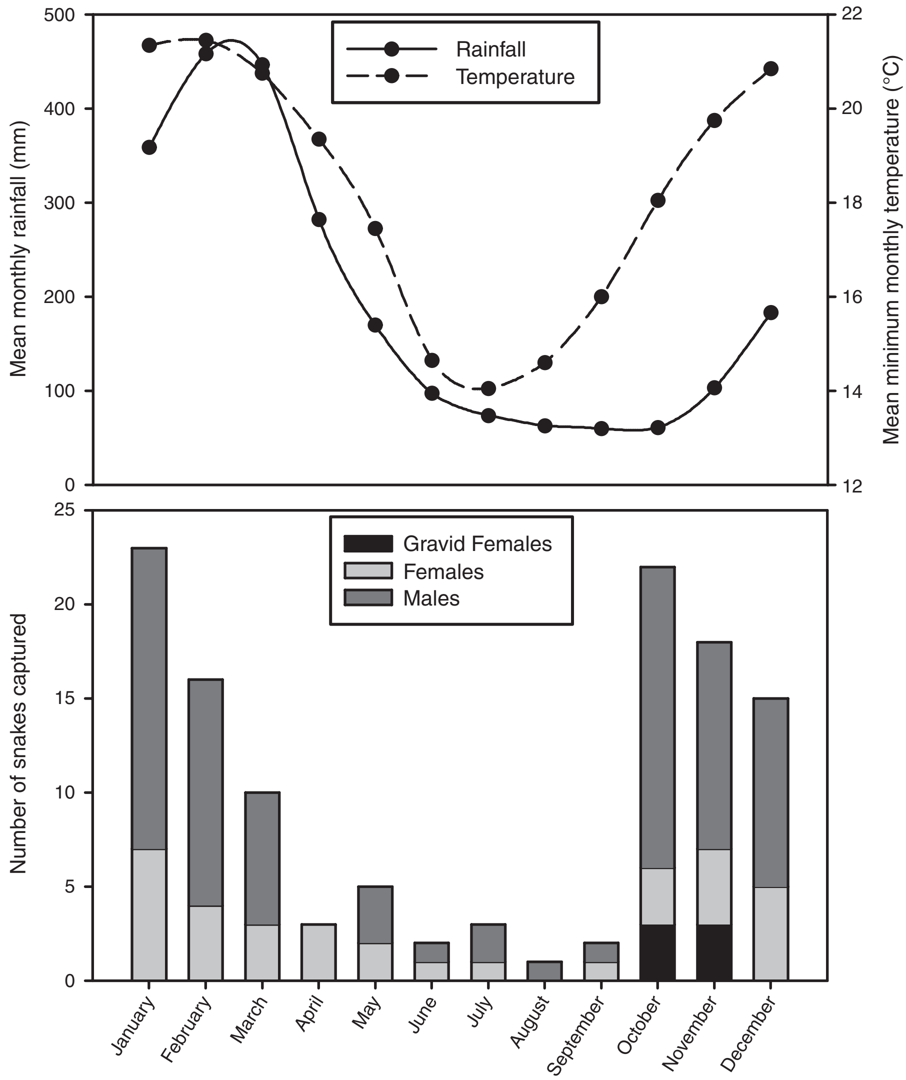

Fig. 1. Climate data and activity patterns of *Stegonotus cucullatus* from the Wet Tropics area, Queensland. Climate data downloaded from Anon. (2006).

by stretching the animal along a tape measure, and mass was recorded using spring-balance scales. Head length (HL) was measured from the tip of the snout to the joining of the upper and lower jaws, the latter also being the point at which head width (HW) was measured. Living snakes were induced to regurgitate any ingested prey items, and palpated for faecal samples and presence of eggs in females. Road-killed specimens were dissected for trophic and reproductive data. Reproductive status of females was determined by checking for the presence of shelled eggs, enlarged oviducts, or ovarian follicles >5 mm in diameter (Shine 1991). Males were not assessed for maturity.

Prior to statistical analysis, all variables were log-transformed to improve normality and homogeneity of variance. All snakes that exhibited partial tail loss were excluded from tail length analysis. We used SigmaStat and SPSS for all analyses.

Results

During nocturnal driving, we obtained 120 live *S. cucullatus* and six dead specimens (Table 1).

Body sizes and sexual size dimorphism

Male *S. cucullatus* attained larger sizes than females (Table 1). Males and females differed significantly in mean SVL and mass (SVL: *t*-test, $F_{2,118} = 4.731$, $P < 0.001$; mass: *t*-test, $F_{2,116} = 4.478$, $P < 0.001$). Relative tail length also differed significantly between the sexes (Fig. 2) (ANCOVA with sex as factor, ln(SVL) as covariate, ln(tail) as dependent variable: interaction, $F_{2,98} = 300.43$, $P < 0.001$; intercepts, $F_{1,99} = 0.360$, $P = 0.550$). Male head length and width relative to SVL was larger than that of females (Fig. 3) (ANCOVA with sex as factor, ln(SVL) as covariate, ln(HL) as dependent variable:

Table 1. Sample sizes, body sizes, and mass of *Stegonotus cucullatus* from the Wet Tropics area, Queensland
SVL, snout–vent length; TL, tail length; HL, head length; HW, head width

Sex		SVL (mm)	TL (mm)	HL (mm)	HW (mm)	Mass (g)
Males	Mean ± s.e.	971.80 ± 24.97	236.07 ± 5.01	22.88 ± 0.90	17.40 ± 0.81	248.27 ± 18.98
	Range	415–1441	112–302	12–32	10–25	17–800
	n	80	64	27	27	79
Females	Mean ± s.e.	772.80 ± 25.07	203.27 ± 6.50	18.66 ± 1.08	13.77 ± 0.86	122.38 ± 11.30
	Range	413–1080	113–260	13–23	10–17	21–340
	n	40	36	9	9	39

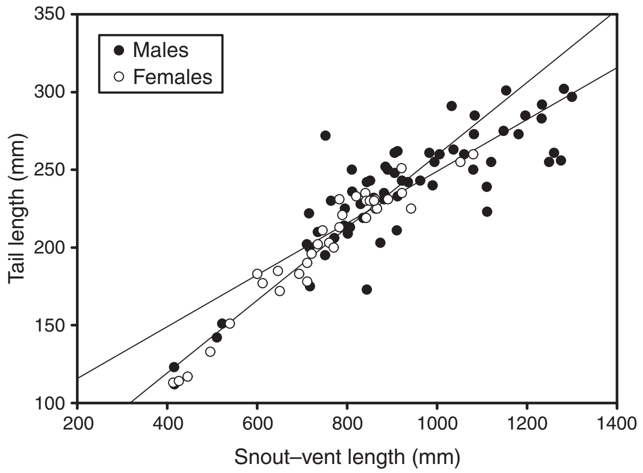

Fig. 2. Tail length relative to snout–vent length of male and female *Stegonotus cucullatus* from the Wet Tropics area, Queensland.

interaction, $F_{2,35} = 288.51$, $P < 0.001$; intercepts, $F_{1,36} = 83.33$, $P < 0.001$), (ANCOVA with sex as factor, ln(SVL) as covariate, ln(HW) as dependent variable: interaction, $F_{2,35} = 70.93$, $P < 0.001$; intercepts, $F_{1,36} = 72.90$, $P < 0.001$).

Body condition

Male and female *S. cucullatus* differed significantly in mass relative to SVL; at the same body length, males were heavier than females (Fig. 4) (ANCOVA with sex as factor, ln(SVL) as covariate, ln(mass) as dependent variable: interaction, $F_{2,116} = 1066.69$, $P < 0.001$; intercepts, $F_{1,119} = 1018.61$, $P < 0.001$).

Seasonal activity

Although *S. cucullatus* was encountered in all months of the year, no females were found during August (Fig. 1). Both sexes were most frequently encountered during the wet season and warmer weather (Fig. 1). Multiple linear regression analysis showed that minimum monthly temperature, interacting with rainfall, predicted the numbers of *S. cucullatus* encountered for both males (one-way ANOVA, $F_{2,9} = 5.825$, $P = 0.024$) and females (one-way ANOVA, $F_{2,9} = 17.963$, $P < 0.001$) (Table 2). The combination of these factors accounted for 56–80% of the variation in this study (Table 2).

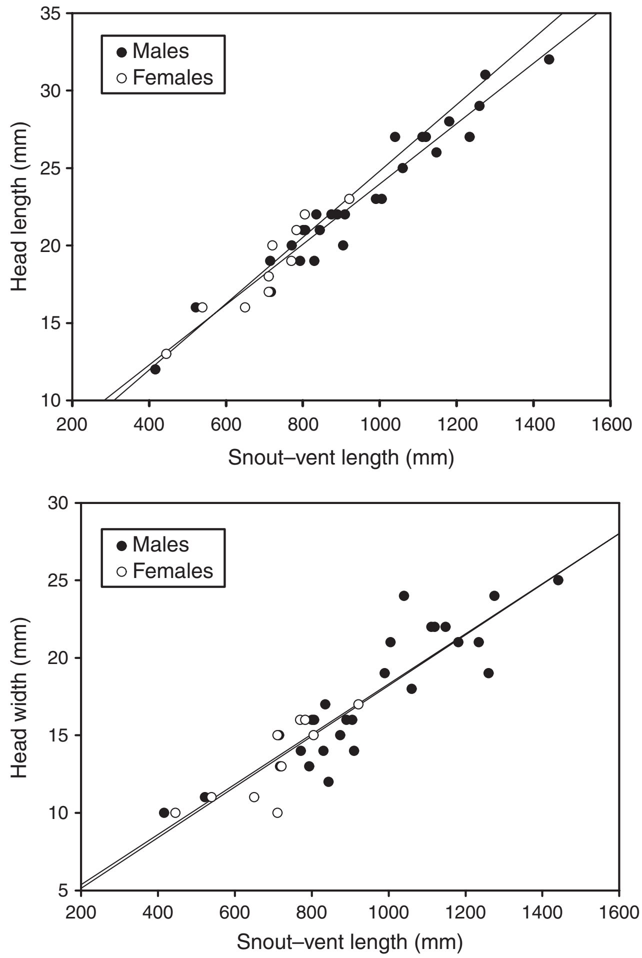

Fig. 3. Head length and width relative to snout–vent length of male and female *Stegonotus cucullatus* from the Wet Tropics area, Queensland.

Food habits

In total, 64 prey items were obtained from 24 specimens. The diversity of these items indicates that *S. cucullatus* preys on a wide range of vertebrates (Table 3). Reptile eggs ($n = 50$) appeared to be a seasonally available prey that was taken only during the wetter months of the year (Fig. 5*A*). Small *S. cucullatus* (<650 mm SVL) ingested, on average, the same number of items as medium-sized to large snakes (730–950 mm

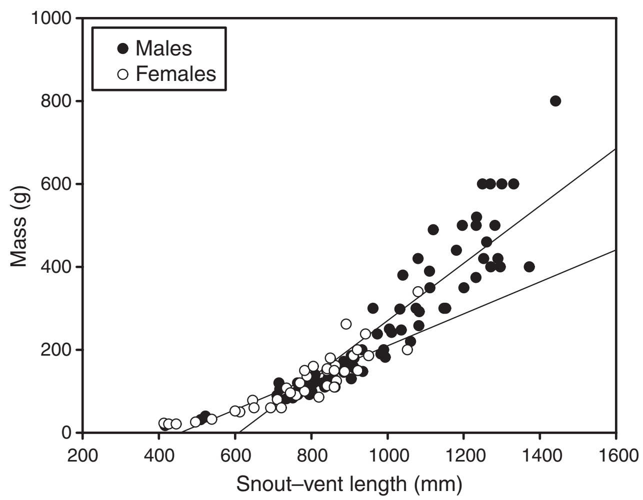

Fig. 4. Body mass relative to snout–vent length of male and female *Stegonotus cucullatus* from the Wet Tropics area, Queensland.

Table 2. Multiple regression analysis of the effect of average monthly temperature and rainfall on detection of *Stegonotus cucullatus* of both sexes in the Wet Tropics area, Queensland
*, $P < 0.05$

Sex	Variable	F	P	d.f.	Model R^2
Male	Temperature and rainfall	5.825	0.024*	2,9	0.56
	Temperature (°C)	9.048	0.013*	1	
	Rainfall (mm)	1.314	0.278	1	
Female	Temperature and rainfall	17.963	<0.001*	2,9	0.80
	Temperature (°C)	14.563	0.003*	1	
	Rainfall (mm)	1.015	0.338	1	

Table 3. Prey items identified from the stomachs of *Stegonotus cucullatus* from north Queensland ($n = 24$)

Prey type	Records	Prey size
Amphibia		
Hylidae		
Litoria junguy	1	
Mammalia		
Muridae		
Rattus sp.	3	
Reptilia		
Sauria (eggs)	24	7–13 mm
Sauria (unidentified)	1	
Agamidae		
Hypsilurus boydii (eggs)	10	30 mm
Scincidae		
Carlia sp. (eggs)	4	
Egernia freerei (tails)	4	32–100 mm
Gnypetoscincus queenslandiae	2	50 mm
Varanidae		
Varanus scolaris	1	121 mm
Serpentes (eggs)	12	
Typhlopidae		
Rhamphotyphlops polygrammicus	2	280 mm
Total	64	

SVL) (*t*-test, $F_{2,12} = -1.688$, $P = 0.120$) (Fig. 5*B*). On average, large adults (>950 mm SVL) ingested a smaller number of items than medium-sized (730–950 mm SVL) specimens (*t*-test, $F_{2,16} = 2.745$, $P < 0.014$) (Fig. 5*B*). Larger snakes ingested prey of greater mass than did smaller individuals (Fig. 5*C*) ($r^2 = 0.48$, $n = 6$). Snakes containing prey had consumed 1–3 different prey items (Fig. 5*D*). Although snakes in all size classes would ingest at least one prey type, snakes >735 mm SVL could ingest 2–3 different prey types (Fig. 5*D*).

Reproduction

Six of the females examined for reproduction ($n = 40$) were gravid. Gravid females were collected in October and November (Fig. 1), and ranged from 782 to 922 mm SVL (mean = 851 mm). The number of oviducal egg clutches ranged from 4 to 8 and no correlation was observed between oviducal clutch size and SVL of gravid females ($r^2 = 4.45$, $n = 6$).

Discussion

Stegonotus cucullatus can be readily sampled by driving available roads in rainforest habitats. Both roads in our study sites were non-through roads, with little nocturnal vehicular traffic and consequently few road-killed snakes.

Sexual size dimorphism was evident in the north Queensland population, with males being larger in SVL, HL, HW, TL and mass, supporting findings from the Northern Territory (Brown *et al*. 2005) as well as the museum-based sample presented by Shine (1991). Body condition was also greater in males than females. Sexual size dimorphism may be linked to male combat in snakes (Shine 1978, 1994) and male combat has been noted between *S. cucullatus* males in the Northern Territory (Brown et al. 2002). However, no detailed observations or photographs have been published on such combat from anywhere in the taxon's range, possibly indicating that it may rarely (if ever) occur or is unseen, owing to the snake's cryptic habitats within the closed rainforest of north Queensland. Male *S. cucullatus* in our sample are longer, heavier and have larger heads than females, a situation that is a common and widespread morphological difference between males and females throughout the animal kingdom (Bonnet *et al.* 1998). Other than male–male combat, the superior size of males can be explained by the larger mass of skeletal muscles for mate searching or enlargement of organs related to sperm competition (e.g. larger kidneys: Bonnet *et al.* 1998). A recent study on the Northern Territory populations (Dubey *et al*. 2009) has found that larger male *S. cucullatus* are able to sire more offspring in multiple paternity matings than smaller conspecifics; however, the specific mechanism as to how this enhances male body size in *S. cucullatus* remains unknown. Given their largely nocturnal habits and a preference for structurally complex habitats (rainforest), determining factors that enhance male reproductive fitness (e.g. male–male combat) and hence larger body size will be extremely difficult to quantify (Shine *et al*. 2000).

Seasonal activity of *S. cucullatus* was highly related to temperature and rainfall, with more specimens captured during the wetter, warmer months. A recent radio-tracking study of Northern Territory *S. cucullatus* found that snakes moved more during the wet season (Brown *et al*. 2005). These findings would

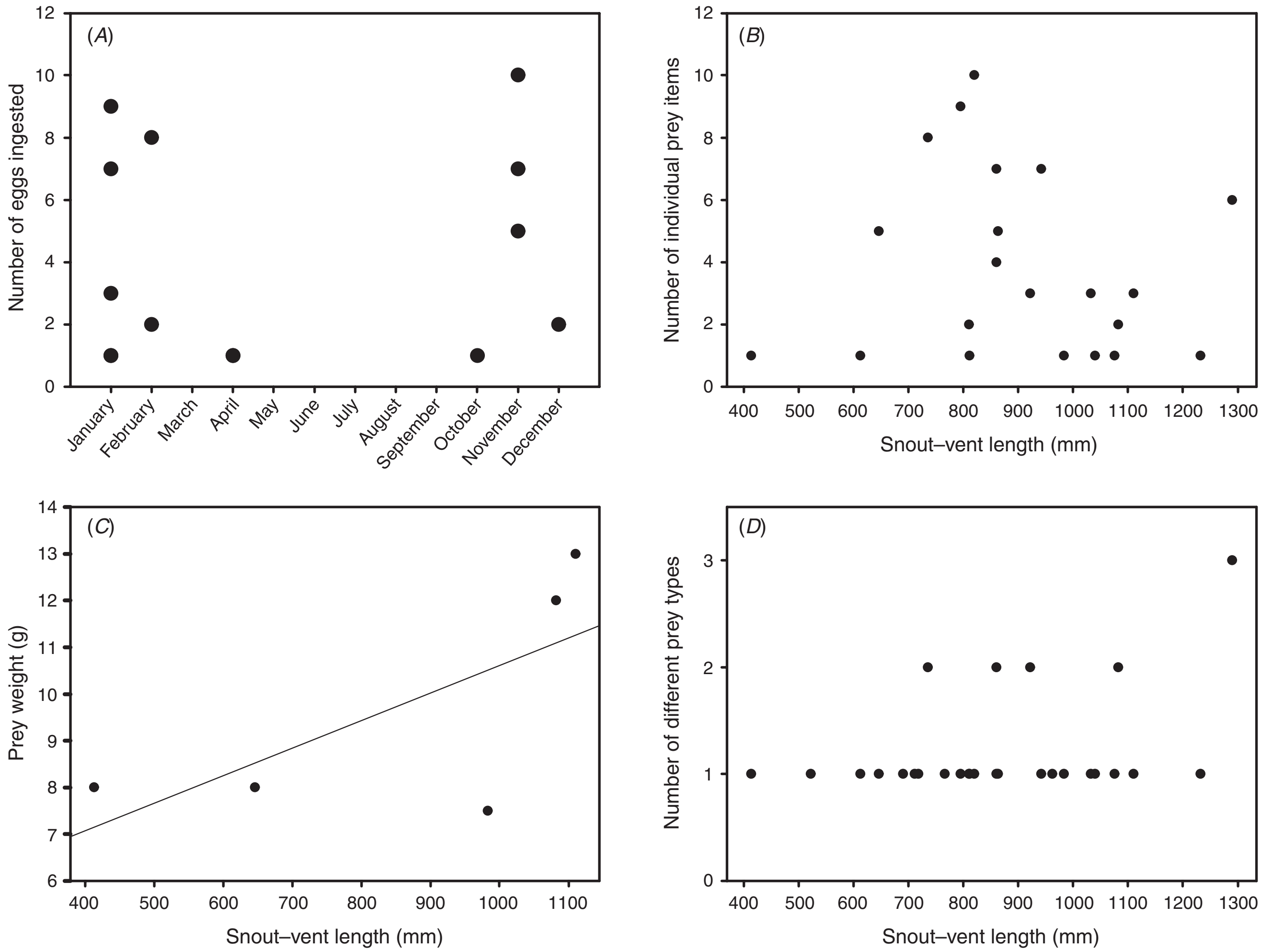

Fig. 5. Dietary analysis of *Stegonotus cucullatus* from tropical north Queensland, Australia. (*A*) Number of reptile eggs in the stomachs of *S. cucullatus* for each month of the year; (*B*) snout–vent length versus number of individual prey items; (*C*) prey weight; and (*D*) number of different groups of prey types.

suggest that, because of these greater movements during the wet, more snakes would be encountered during that season. However, studies from these areas show that more snakes are actually encountered during the dry season (Brown *et al*. 2002). This increase in detection rates is believed to occur because of mate-searching activities by male *S. cucullatus* (Brown *et al*. 2002). Although the exact timing of male mate-searching is unknown for North Queensland, our studies show the opposite pattern of rate of encountering *S. cucullatus*, with more specimens encountered during the wet season. This may be related to the availability of prey (see below), and the fact that the Northern Territory sample was collected by foot as well by car at Fogg Dam, an artificial reservoir that contains water, and presumably high prey densities, all year round. Habitat and sampling differences may account, in part, for this apparent discrepancy in reported activity times between two regions that have broadly similar climatic regimes.

In congruence with earlier studies of diet (Shine 1991; Brown *et al*. 2002), *S. cucullatus* preyed upon a wide range of vertebrate prey. Prey was recorded in the stomachs of 20% of specimens in our study, compared with 1.1% found by Brown *et al*. (2005). This low feeding rate in the Northern Territory population is thought to occur because *S. cucullatus* relies on foraging within narrow cracks on the floodplain, and these may constrain foraging because of the inaccessibility of prey. Also, high temperatures may facilitate rapid digestion of small, soft-skinned prey such as amphibians, resulting in low detection rates (Brown *et al*. 2005). However, high temperatures regularly occur at the north Queensland sites, suggesting that differential digestion rates due to temperature is not an important factor in terms of prey prevalence in sampled *S. cucullatus*. Our population inhabits a closed rainforest system with greater structural complexity and vertebrate diversity (Ingram and Raven 1991) than the habitat studied in the Northern Territory, perhaps enabling these partially arboreal snakes (Greer 1997) to forage more effectively for a wider variety of potential prey from ground level to arboreal microhabitats. Year-round high temperatures would also facilitate rapid digestion and hence low rates of detection of amphibians in stomachs of snakes at our study sites.

Reptile eggs comprised a significant proportion of the diet of *S. cucullatus* in our study, which supports the findings of Shine (1991). While saurian eggs are an important component of the diet, they appear to be consumed seasonally. The most commonly recorded eggs were those of large agamids (Boyd's forest dragons (*Hypsilurus boydii*) and eastern water dragons (*Physignathus leuseurii*)), which are common at our study sites (D. Trembath and S. Fearn, pers. obs.), and typically lay eggs in road verge embankments at the onset of the wet season (Doody *et al.* 2006). Snake eggs (most likely of *Dendrelaphis* spp.) were also recorded on 12 occasions during the same period, which appears to coincide with timing of egg deposition for a range of Wet Tropics snakes (Trembath and Fearn, unpubl. data). In the Northern Territory populations of *S. cucullatus* the eggs of keelback snakes (*Tropidonophus mairii*) are common dietary items in the dry season (Brown *et al*. 2005). Although *T. mairii* is known to mate throughout the year (Shine 1991), females produce multiple clutches in the dry season (Brown and Shine 2006), thus exposing *S. cucullatus* to a seasonally saturating food source. *S. cucullatus* appears to be a flexible, opportunistic, generalist carnivore taking advantage of abundant local resources. Intensive regional studies would inform detailed dietary preferences, including the relative importance of oophagy.

We obtained reproductive data only from females, as the lack of road-killed male snakes prevented us from determining their size at sexual maturity. Females were sexually mature at 782–922 mm SVL (mean SVL = 851 mm), which is in accordance with the study by Shine (1991), who recorded a mean SVL of 842 mm at sexual maturity. No correlation was found between maternal SVL and clutch size, which also agrees with the results obtained by Shine (1991). While evidence of double-clutching has been presented for the Northern Territory population (Brown *et al*. 2002), all gravid females in our study were obtained in October and November, indicating that reproduction in our sample was highly seasonal and that only one clutch of eggs may be produced annually.

Our study demonstrates that *S. cucullatus* is an abundant and flexible predator in rainforest habitats in north Queensland. An apparent seasonal reliance on squamate eggs in both our study sites and the Northern Territory, but at opposite times of the year (wet season versus dry season), may indicate a dietary specialisation unusual among colubrids and medium-sized Australian snakes in general. Further studies (particularly at higher altitudes with different climatic regimes and reptile assemblages) may yield more information on the trophic ecology of *S. cucullatus*, and whether climate or access to reptile eggs, or both, are the best predictors of activity, range and abundance.

Acknowledgements

Sincere thanks to the following people for their assistance or help in the field: John Blackburn, Chris Camacho, Alex Castle, David Freier, Ryan Hodgson, Gavin Huddleston, Kathy Huddleston, Ray Lloyd, Steve Patane, David Poppi, Damien King, York Morgan, Jodi Rowley, Joe Sambono, Jason Schaffer, Lin Schwarzkopf and Ed Smith. Thanks also to the Bureau of Meteorology for permitting the download of climatic data. Thanks to Paul Horner for suggestions on an earlier version of the manuscript. Additional thanks to the anonymous reviewers, whose comments helped improve this manuscript. This work was conducted under the following permits from the Queensland Parks and Wildlife Service (NO/001446/98/SAB and F1/000330/00/SAA) and Environmental Protection Agency (#WITK02196804, #WISP02196704, and #WISP01039503).

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Handling Editor: Jane Melville
Manuscript received 2 December 2008, accepted 2 June 2009