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Natural history of the common tree snake, *Dendrelaphis punctulatus* (Serpentes : Colubridae), in the wet–dry tropics of north Queensland

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Abstract. Common tree snakes, *Dendrelaphis punctulatus*, are medium to large colubrid snakes that are relatively common in the eastern and northern parts of tropical Australia. The only previous study on this species involved museum specimens from across the taxon's range. During a seven-year period we collected data on 131 field-caught specimens from a melanotic population in the Townsville district of north Queensland. *Dendrelaphis punctulatus* was found to be primarily diurnal, with a peak in activity centred around the reproductive period during the transition from dry to wet seasons. Females were larger than males with respect to all measured parameters, including mass and head size. Reproduction in females was strongly seasonal and clutch size was related to maternal body size. Prey items consisted of frogs, lizards and locusts.

Introduction

The genus *Dendrelaphis* comprises some 20 species occurring in primarily tropical habitats from India throughout south-east Asia and eastwards through New Guinea, northern Australia and the Solomon Islands (Daniel 1983; O'Shea 1996; De Lang and Vogel 2005). Perhaps reflecting a recent colonisation from the north (Shine 1991), the two Australian species, *D. punctulatus* and *D. calligastra*, also occur in New Guinea (O'Shea 1996).

The common tree snake, *Dendrelaphis punctulatus* (Gray 1826), is a medium to large (>1.8 m total length) relatively common colubrid snake ranging from Illawong, south of Sydney (Swan 1990), north throughout coastal tropical Queensland (Covacevich and Couper 1991) to Cape York and west through the Top End of the Northern Territory and into the far north of Western Australia (Storr *et al.* 1986). Throughout this distribution, *D. punctulatus* is primarily associated with mesic coastal forest and woodland habitats and is a common snake throughout urban habitats within its range (Fearn and Trembath, pers. obs.). Throughout this extensive range, several broad and apparently discreet dorsal colour variations occur, from predominantly olive green in southern portions of the range as well as closed wet tropical forests in north Queensland, predominantly melanotic specimens in strongly seasonal wet–dry tropical woodlands in the Townsville region of north Queensland, and shades of yellow in the tropical north-west of Australia (Shine 1991; Greer 1997). In the Wet Tropics of north Queensland as well as the rainforest blocks on Cape York, *D. punctulatus* is broadly sympatric with the morphologically similar but smaller *D. calligastra* (Covacevich and Couper 1991).

Remarkably, very little quantified information is available concerning the ecology of *D. punctulatus*: most of the literature consists of anecdotal observations of both wild and captive specimens (summarised in Greer 1997). The only quantitative ecological information on *D. punctulatus* in Queensland 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; Trembath *et al.* 2009). Additionally, problems may arise if species are poorly understood taxonomically at the time of study and investigators unwittingly combine species in their analysis (Fearn and Trembath 2009). In this paper we present data on body size, body condition, sexual dimorphism, seasonal activity, dietary habits and reproduction from a single population of wild-caught, melanotic individuals inhabiting strongly seasonal wet–dry tropical woodland in the Townsville district of tropical north Queensland.

Methods

Between 1997 and 2006, living and road-killed specimens of *D. punctulatus* were examined from Townsville (19°19′53″S, 146°45′6″E) within a 30-km radius of James Cook University in the strongly seasonal wet–dry tropics. Vegetation in the Townsville area is dominated by eucalypt savannah woodland with a grassy understorey. Diurnal temperatures are always high (25.0–31.4°C mean daily maximum: Ridpath 1985) and day length varies little. Rainfall is markedly seasonal and its monthly distribution pattern within the wet season (October to March) varies between years (Ridpath 1985).

Most of the specimens were collected opportunistically and diurnally while crossing roads and tracks in and around the

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grounds of James Cook University or as a result of 'nuisance' snake callouts to the authors in and around student residential colleges. 'Nuisance' specimens were also collected from urban and periurban residences by staff of the Queensland Parks and Wildlife Service and later examined by the authors. Road-killed specimens were collected opportunistically from throughout the study area but only recently killed specimens (i.e. that were dead for no more than a few hours) were collected.

For each snake we recorded the date and location of collection. For living snakes, sex was determined by eversion (or not) of hemipenes. For both living and dead snakes, snout–vent length (SVL) and tail length (TL) were measured by stretching the animal along a tape measure, and its mass was determined with 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 also palpated along the stomach to induce regurgitation of ingested prey items and palpated for faecal samples and the presence of eggs in females. Road-killed specimens were dissected for trophic and reproductive data. Males were not assessed for maturity but females were assessed for shelled eggs, enlarged oviducts, or ovarian follicles >5 mm in diameter. For analysis of SVL and mass, variables were compared using parametritc *t*-tests. Single-factor analysis of covariance (ANCOVA) using sex as the factor and log-transformed SVL as the covariate was used to tests for relative differences in TL, HL, and HW between the sexes. All snakes showing partial tail loss were excluded from tail length analysis. We used SigmaStat and SPSS for all analyses.

Results

Seasonal activity

In total, 131 *D. punctulatus* were examined in this study (Table 1). Most of these snakes ($n = 96$) were found opportunistically, with an additional sample ($n = 35$) obtained as road-killed specimens from throughout the Townsville area. Most specimens were encountered during the day (126 of 131 records), with only five specimens collected at night (Fig. 1). *D. punctulatus* were mostly found on the ground ($n = 98$), with few records in raised situations ($n = 30$). Female *D. punctulatus* were encountered in all months of the year, with no males being found in January and March (Fig. 2).

Table 1. Metric data collected for *Dendrelaphis punctulatus* from the Townsville area, Queensland

	Males			Females		
	Mean ± s.e.	Range	*n*	Mean ± s.e.	Range	*n*
SVL (mm)	928.95 ± 19.81	534–1202	47	1011.08 ± 25.15	382–1473	81
TL (mm)	355.34 ± 9.87	165–461	41	380.02 ± 9.58	138–552	72
HL (mm)	22.14 ± 0.96	13–35	21	24.31 ± 0.76	18–32	22
HW (mm)	12.85 ± 0.55	9–20	21	16.00 ± 0.95	18–28	21
Mass (g)	126.53 ± 8.65	20–350	47	168.74 ± 12.47	9–500	79

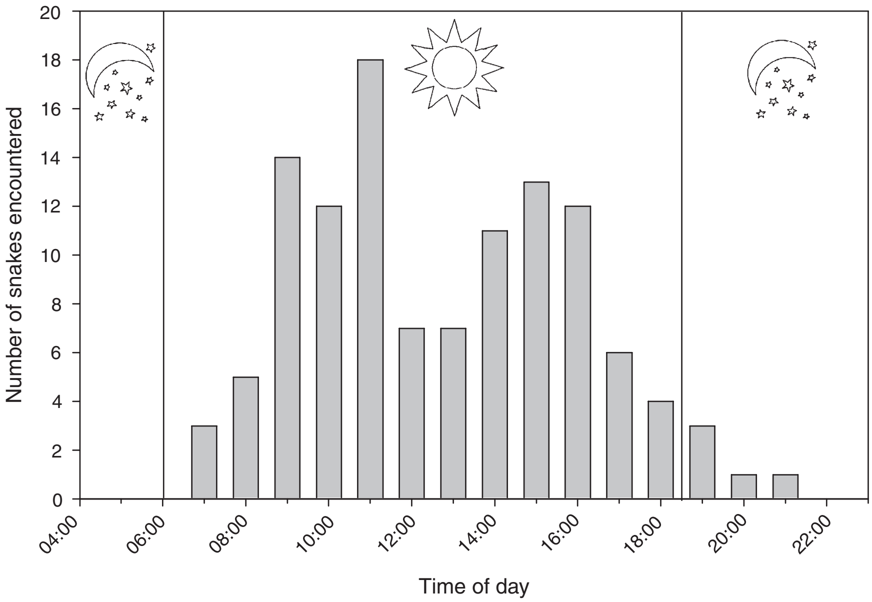

Fig. 1. Activity pattern for *Dendrelaphis punctulatus* from the Townsville area observed during hours of the day from 1997 to 2006.

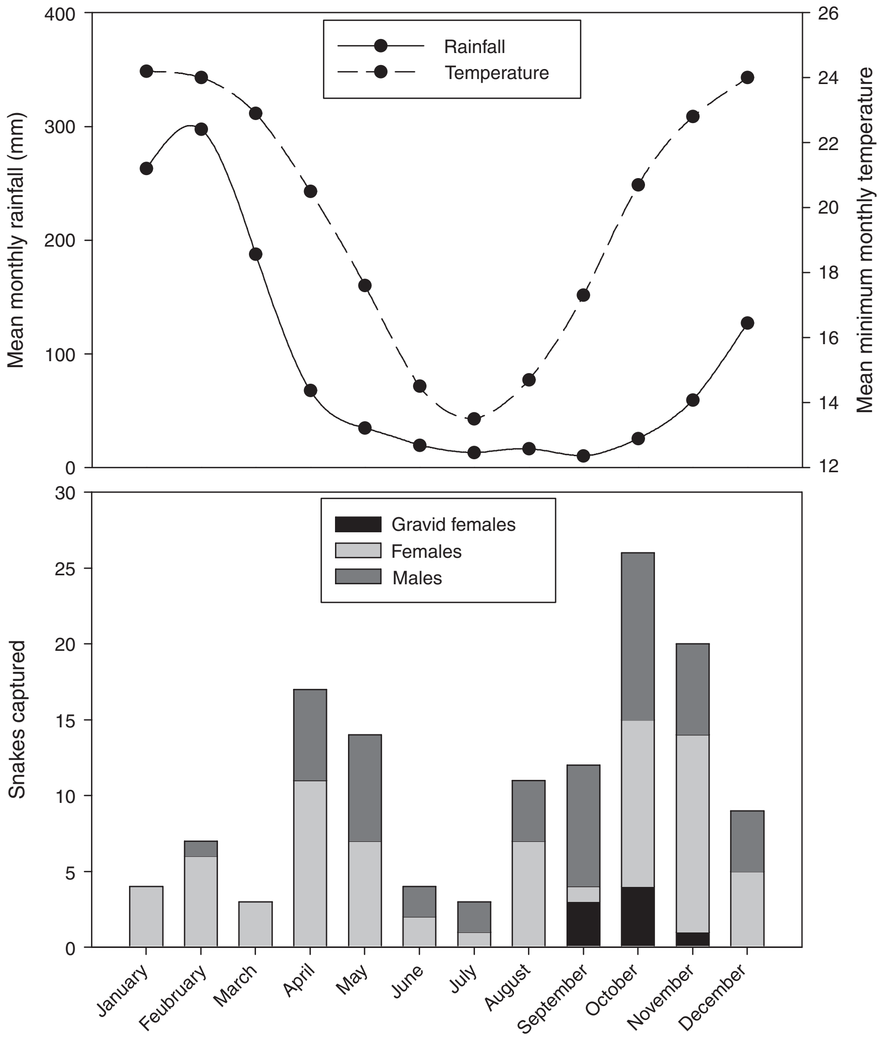

Fig. 2. Climatic data and activity patterns of *Dendrelaphis punctulatus* from the Townsville area based on specimens sampled from 1997 to 2006. Climatic data downloaded from Anon (2006).

Both sexes were encountered more frequently during the wetter and warmer times of the year (Fig. 2).

Body sizes, sexual size dimorphism and body condition

Female *D. punctulatus* grew larger on all parameters and attained greater mass than males (Table 1). Male and females also differed significantly in mean SVL (*t*-test: $F_{2,126} = -2.23$, $P = 0.027$) and mass (*t*-test: $F_{2,124} = -2.41$, $P < 0.017$). Females also had longer tails than males (Table 1), and tail length relative to SVL was significantly different between the sexes (ANCOVA with sex as factor, ln(SVL) as covariate, ln(TL) as dependent variable: interaction, $F_{2,98} = 158.21$, $P < 0.001$; intercepts, $F_{1,99} = 0.37$, $P = 0.54$) (Fig. 3). Head length and width relative to SVL also differed significantly between the sexes (ANCOVA with sex as factor, ln(SVL) as covariate, ln(HL) as dependent variable: interaction, $F_{2,41} = 56.23$, $P < 0.001$; intercepts, $F_{1,42} = 28.36$, $P < 0.001$) (ANCOVA with sex as factor, ln(SVL) as covariate, ln(HW) as dependent variable: interaction, $F_{2,40} = 18.54$, $P < 0.001$; intercepts, $F_{1,41} = 8.79$, $P = 0.005$)

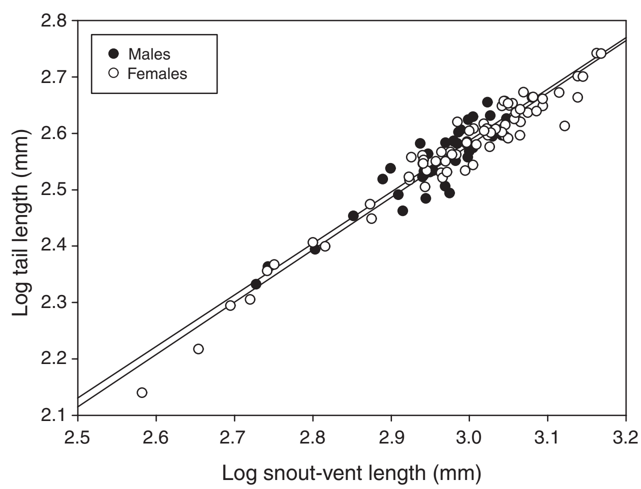

Fig. 3. Ln(TL) relative to SVL of male and female *Dendrelaphis punctulatus* from the Townsville area, Queensland.

(Fig. 4). Male and female *D. punctulatus* differed significantly in mass relative to SVL between the sexes (ANCOVA with sex as factor, ln(SVL) as covariate, ln(mass) as dependent variable: interaction, $F_{2,124} = 88.63$, $P < 0.001$; intercepts, $F_{1,125} = 140.93$, $P < 0.001$) (Fig. 5).

Food habits

The number of snakes containing prey or identifiable faecal samples in this study was low. Eleven snakes contained a single prey item and one contained two. Identifiable prey items included frogs (3), *Cylclorana alboguttata* (1), *Litoria caerulea* (5), *Opisthodon ornatus* (1), skinks (1), and acridid locusts (2).

Reproduction

Of the females sampled ($n = 81$), 9% ($n = 8$) were found to be gravid. The gravid females were collected during September, October, and November (Fig. 2). These females ranged in size from 920 to 1205 mm SVL (mean SVL = 1064 mm) (Fig. 6). Oviductal clutch sizes were found to range between 4 and 12 developing ova (mean clutch size = 7.8) and a significant correlation was found between clutch size and maternal SVL length ($r^2 = 0.60$, $n = 8$) (Fig. 6).

Discussion

The results of our study broadly agree with those of Shine (1991), the only other quantified research on Australian *D. punctulatus*. As all the specimens obtained for this study were found opportunistically as part of a larger study on the snakes of the Townsville region, we acknowledge that this method may have the potential to influence results, as discussed in Fearn *et al.* (2001). However, as our large dataset has originated from a single regional population over a relatively short temporal scale, we have been able to more precisely quantify aspects of daily and seasonal movements as well as apparent strongly seasonal trends in reproduction.

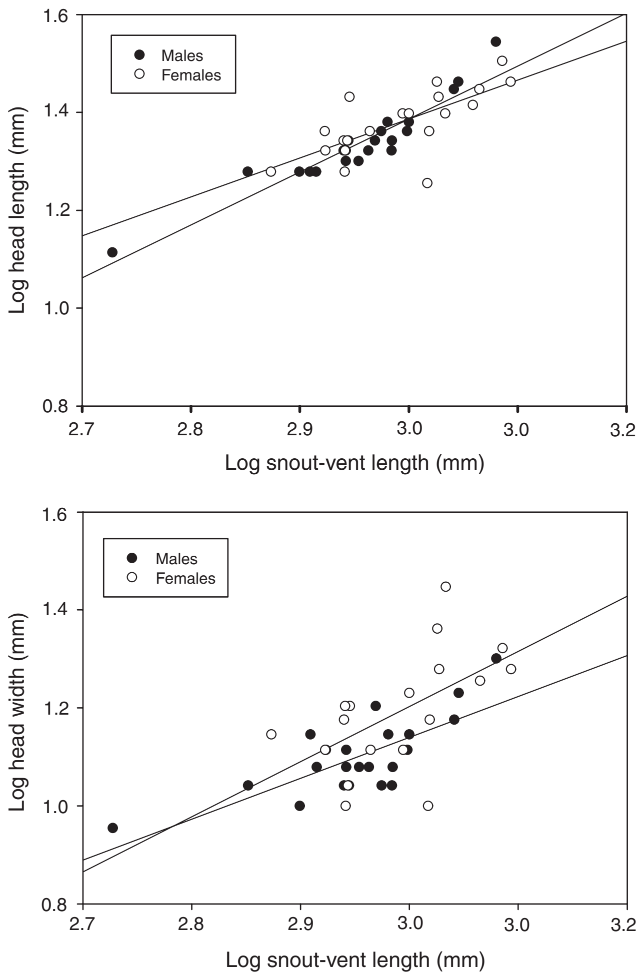

Fig. 4. Ln(HL) and ln(HW) relative to SVL of male and female *Dendrelaphis punctulatus* from the Townsville area, Queensland.

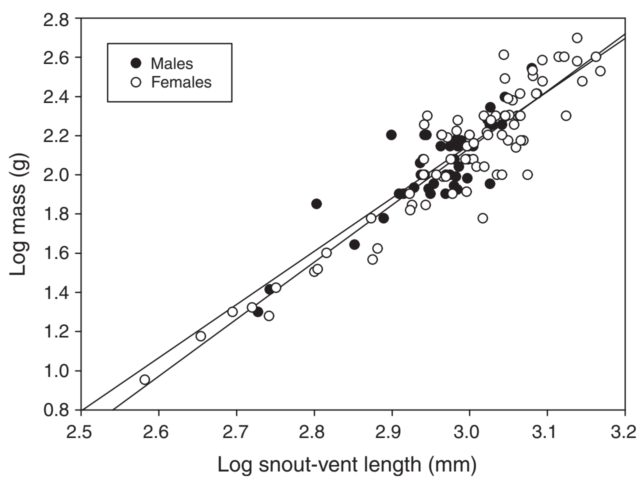

Fig. 5. Ln(mass) relative to ln(SVL) of male and female *Dendrelaphis punctulatus* from the Townsville area, Queensland.

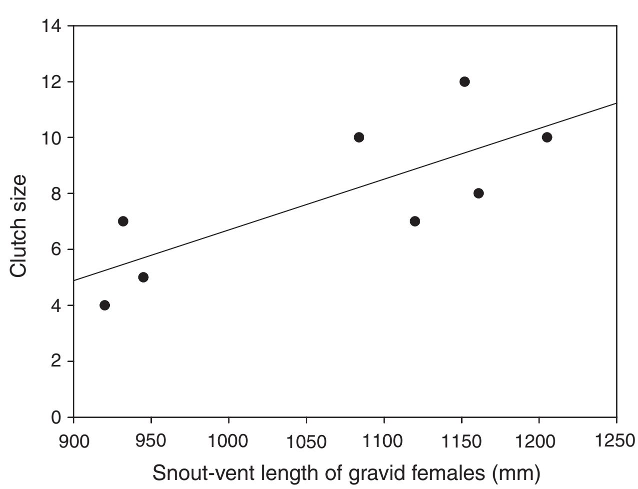

Fig. 6. Clutch sizes in relation to SVL of female *Dendrelaphis punctulatus* from north Queensland, Australia.

Seasonal activity and capture areas

D. punctulatus is universally described as arboreal (many anecdotal references summarised in Greer 1997), and while the frequency of arboreality is unknown in our study, it is clear that *D. punctulatus* spends enough time on or near the ground to be frequently encountered by people and killed on roads. This is further supported by the presence of burrowing, strictly terrestrial amphibians in the stomachs of Townsville *D. punctulatus*, as well as skinks and predominately grass- and low-herbage-eating locusts. Lillywhite and Henderson (1993) suggest that there are difficulties with attempts to classify snakes according to the degree of their arboreal habits because behaviours are often poorly quantified, which does not allow discrete categories of classification to be determined. One confounding factor in our study area is the predominantly open woodland habitat. Large eucalypts are relatively discrete and rarely display overlapping canopies. *D. punctulatus* in and around Townsville may therefore be forced to travel terrestrially in search of mates, food or shelter sites, much more so than for individuals in other populations, such as closed rainforests, where canopies are interlocked and more or less homogenous over large areas. Such a situation was apparent for the strongly arboreal Australian elapid *Hopolocephalus stephensi* in north-eastern New South Wales, where individuals in more open wet sclerophyll forests foraged close to ground level, in contrast to closed-rainforest-inhabiting specimens, which remained in the canopy (Fitzgerald and Shine 2002).

D. punctulatus is described as strictly diurnal (Greer 1997) but our results suggest that nocturnal activity may occasionally occur (Fig. 1). Only five specimens were collected nocturnally, as late as 2100 hours. This is not unexpected as nocturnal activity is common among snakes in the tropics (Greer 1997), where consistent high ambient and substrate temperatures allow snakes to be active while avoiding extreme diurnal temperatures, even occasionally among taxa considered to be entirely diurnal (Trembath 2004; Fearn and Trembath 2009). The *D. punctulatus* in our study displayed two broad peaks of activity: in the morning between 0900 and 1100 hours and in the late afternoon between 1430 and 1500 hours (Fig. 2). Such activity times appear to be typical for a wide variety of diurnally active Australian reptiles, both in the southern Australian summer and in the high tropics, apparently in avoidance of potentially harmful high temperatures in the middle of the day (Heatwole and Taylor 1987; Greer 1989, 1997).

Activity rates for *D. punctulatus* were highly seasonal, which is consistent with previously documented activity for a sympatric colubrid *Stegonotus cucullatus*, which inhabits the wet forests north of Townsville (Trembath *et al*. 2009). Increased detection rates by investigators are thought to occur through mate-searching activities by males when individuals cover large areas in pursuit of females (Brown *et al*. 2002), when females are seeking suitable oviposition sites, or when prey taxa display greater activity at such times (Brown and Shine 2002). In our study, encounter rates increased during the transition from the dry to the wet seasons (August–October), which coincided with the emergence of gravid females, showing that climatic categories appear to coincide with mating and oviposition for *D. punctulatus* in the Townsville area.

Body sizes and sexual size dimorphism

The low number of snakes in our sample containing identifiable prey items or ova in females prevents us from presenting compelling additional insights into the clear female-biased sexual size dimorphism (SSD) in this species. There is some evidence that trophic divergence between the sexes of *D. punctulatus* has led to females preying on larger prey items (Camilleri and Shine 1990) and thus presumably enhancing fecundity (Shine 1994). In addition, male combat, which appears to favour male-biased SSD in many snake taxa (Shine 1994), is unknown in *D. punctulatus* and multiple males have been observed attempting to mate with single females with no obvious aggression towards each other (S. Fearn, pers. obs.). The very low number of *D. punctulatus* containing prey in our study is reminiscent of a large dataset of the sympatric colubrid *Boiga irregularis* (brown tree snake) from north Queensland (Trembath and Fearn 2008). This phenomenon may be typical of field-collected samples of predominantly arboreal snakes, with Lillywhite and Henderson (1993) suggesting that the low mass of arboreal snakes is reinforced by short intervals between feeding and defaecation, as retention of faeces (common in terrestrial, heavy-bodied Boidae and Viperidae) is disadvantageous for arboreal taxa. Apart from labour-intensive and expensive telemetric studies involving large numbers of snakes, we can suggest no methods to improve the chances of obtaining quantifiable data on the trophic and reproductive ecology of *D. punctulatus*. Even relatively novel techniques such as the use of stable isotopes for assessing diet and trophic relationships (Dorcas and Willson 2009) will not enable researchers to detect differences in prey size that may, in part, be responsible for observed SSD.

Reproduction

Our results reinforce those of Shine (1991), who found spring and summer reproduction in east coast *D. punctulatus*, as well as increasing clutch size with maternal body size (Fig. 5). Ovulating and heavily gravid females were found in our sample from September to November. In addition, two males were discovered attempting to copulate with a single female in an air conditioning unit on the wall of a residential Townsville house in October. Spring mating aggregations may be typical for *D. punctulatus* in coastal Queensland as up to four males have been recorded simultaneously attempting copulation with a single female in Brisbane, south-east Queensland (S. Fearn, pers. obs.). The higher encounter rate of *D. punctulatus* with humans from August to November (Fig. 3) may reflect an increase in snake movements (particularly of males) associated with the reproductive period. The timing of oviposition for five female *D. punctulatus* captured from, and kept in, Townsville was the same as in our field-based data (Shine 1991), further indicating that mating and oviposition, at least in the Townsville region, is strongly seasonal. Female reproduction centred on the transition from the dry to the wet seasons (August–November) appears to be common among a range of snake taxa in the Townsville region (Fearn *et al.* 2005; Trembath and Fearn 2008; Fearn and Trembath 2009; Trembath *et al.* 2009; Fearn and Trembath, unpubl. data), possibly in response to the unpredictability of rainfall, both in timing and amount in the wet–dry tropics (even in the wet season). Female *D. punctulatus* may time neonate hatching to coincide with relatively high moisture and prey abundance (juvenile lizards and metamorphosing frogs) of the mid to late wet season; alternatively, purely abiotic factors such as relative substrate moisture of ovipostion sites may be driving the strongly seasonal reproduction seen in the Townsville area. Substrate moisture has been shown to be the major factor in deciding ovipostition times in the Northern Territory population of *Tropidonophis mairii* (Brown and Shine 2006). As north Queensland has a prolonged dry season, similar to that of the Northern Territory, this would make sense as the ground would be too hard to deposit eggs; however, the nesting sites of *D. punctulatus* remain unknown in the wild at this time. Intense studies documenting choice of nest site by *D. punctulatus* would be needed to explore this theory further.

The low number of reproductive females in our sample appears to be typical of field-collected datasets on tropical Queensland colubrids (Trembath and Fearn 2008; Trembath *et al.* 2009) and may be due to gravid females restricting their movements and staying close to suitable oviposition sites. An alternate hypothesis could be that *D. punctulatus* reproduces only every other year; however, this is unusual in tropical reptiles and is mostly shown to occur in animals that live in cool climates (Bull and Shine 1979).

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