Memoirs of the Queensland Museum | **Nature**

56 (2)

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National Library of Australia card number
ISSN 0079-8835

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Arboreality, excavation, and active foraging: novel observations of radiotracked woma pythons *Aspidites ramsayi*

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Citation: Bruton, M. J. 2013 06 30. Arboreality, excavation, and active foraging: novel observations of radiotracked woma pythons *Aspidites ramsayi*. *Memoirs of the Queensland Museum – Nature* 56(2): 313–329. Brisbane. ISSN 0079-8835. Accepted: 23 August 2012.

ABSTRACT

Novel wild behaviours were observed during a 21 month intensive radiotracking study of the woma python *Aspidites ramsayi* (Macleay, 1882) in south-western Queensland, Australia. Arboreal behaviour was unexpected in this terrestrial and burrow-dwelling species, with no previous anecdotal or published reports. Arboreal activity occurred strictly at night during warm weather and was associated with sleeping reptile predation, particularly predation upon bearded dragons *Pogona barbata* (Cuvier, 1829). Excavation behaviour in wild womas was predicted from captive specimens in 1981, but has not been reported to date. Two observations of radiotracked womas excavating in alluvial clay soils are detailed with comments on the function of this behaviour. Finally, brief descriptions and a summary of all thirteen feeding observations are given. Bearded dragons *P. barbata*, sand goannas *Varanus gouldii* (Gray, 1838) and yakka skinks *Egernia rugosa* (De Vis, 1888) were the most commonly observed prey items; however predation and ingestion of one large mammal - an adult hare *Lepus capensis* (Linneaus, 1758) - was also observed. Pre- and post-feeding movements indicate an active foraging strategy predominates; however ambush behaviour was also observed. Here I outline and summarise these novel wild behavioural observations and discuss them in the context of known snake ecology and physiology. These observations greatly enhance the behavioural and ecological understanding of this large, yet elusive python. ❒ *Reptile, feeding, snake, radio-tracking, arid, temperature, caudal luring*

Aspidites ramsayi is a large (up to 2.5 m SVL) and rarely observed python found throughout arid and semi-arid central Australia (Wilson & Swan 2010). Sightings of this widely distributed species are rare due to a combination of sparse human population (Tobler, Deichmann *et al*. 1995; Australian Government 2006; Wilson & Swan 2010), fossorial and nocturnal habits (Bruton, unpub. data), and excellent camouflage (pers. obs.). Consequently the few published observations of wild woma behaviour are anecdotal and most pertain to sightings of disturbed pythons (e.g. Pearson 1993; Covacevich & Couper 1996; Maryan 2002; Borsboom 2008).

Despite a paucity of wild *A. ramsayi* behavioural observations, indigenous knowledge (Pearson 1993), information from research programs (Read 2010; Bruton, unpub. data; Dave Pearson pers. comm.) and observations of captive specimens (Richard Jackson pers. comm.) all indicate that the woma is a terrestrial/fossorial species that shelters predominately in underground burrows and occasionally moves overland between shelter sites. It is generally accepted that *A. ramsayi* is a terrestrial species with no previous reports or indications of arboreal behaviour, either in the wild or in captivity.

Aspidites ramsayi shelter in pre-excavated burrows created by varanids, rabbits *Oryctolagus cuniculus* (Linnaeus, 1758), hopping mice *Notomys alexis* (Thomas 1922), bilbies *Macrotis lagotis* (Reid 1837), and natural tunnel erosion (Covacevich & Couper 1996; Cogger 2000; Read 2010; Wilson & Swan 2010) in both sandy and clay soils. In captivity, womas have been observed using the head as a scoop to dig in sandy substrates (Fyfe & Harvey 1981; Richard Jackson pers. comm.), indicating they may be capable of burrow excavation in sandy areas. Womas are generally associated with sandy areas (Fyfe & Harvey 1981; Smith 1981; Pearson 1993; Maryan 2002; Read 2010) and in captivity they are rarely provided with finer clay substrates found in the east of their range. Although excavation behaviour has not been reported in the wild, Fyfe and Harvey (1981) predicted that '*...this technique would be used to enlarge existing burrows for shelter or while hunting*'.

Analysis of woma python stomach contents throughout Australia identified mammal and reptile prey items in approximately equal proportions (Slip & Shine 1990; Shine 1999). Specific reptile prey items include ring-tailed dragons *Ctenophorus caudicinctus* (Gunther 1875), dwarf bearded dragons *Pogona minor* (Sternfeld 1999), other agamids, gekkonids, blue tongue lizards *Tiliqua scincoides* (White 1790), other scincids, *V. gouldii*, other varanids, and 'snakes', whilst reported mammalian prey include rabbits *O. cuniculus*, hares *L. capensis*, bandicoots *Isodon spp.*, rats *Rattus spp.*, mice *Mus domesticus* (Rutty 1772), and other murids (Slip & Shine 1990; Covacevich & Couper 1996; Read 2010). The wide variety of both reptilian and mammalian prey items suggests a generalist diet but gives no indication of the hunting and prey capture strategies that wild womas employ.

In captivity, womas generally use typical boid coiling constriction when feeding (Fyfe & Harvey 1981; pers. obs.), indicative of a predominately ambush feeding strategy. However Fyfe and Harvey (1981) also describe a second 'most unusual' method in which womas do not utilise the mouth in a strike but instead squash prey against the side of the vivarium with the body. Similar squashing behaviour has also been observed in a captive woma population held at Australia Zoo (Richard Jackson pers. comm.). This 'squashing' method is likely to be effective in the confined spaces of the burrows *A. ramsayi* inhabit (Fyfe & Harvey 1981) and could be used in either active foraging or ambush prey capture situations. Another feeding strategy reported in captive womas is caudal (tail) luring (Fyfe & Harvey 1981); again indicative of an ambush hunting strategy. Whilst these captive behaviours give insight into potential hunting strategies, there are no known reports or descriptions of wild *A. ramsayi* foraging and food capture behaviours and it was not previously known if *A. ramsayi* is ambush predator or an active forager.

Here I report the first known observations of arboreal behaviour, wild burrow excavation, and wild prey capture and feeding behaviours in a population of eastern woodland inhabiting womas, and discuss these behaviours in the context of snake ecology and physiology.

METHODS

Twelve adult (5F:7M) eastern 'Brigalow' womas were radiotracked on a conservation reserve near the town of St George in southern Queensland. The location is sub-tropical semi-arid (rainfall ≈ 540 mm/year) with summer rain and generally dry winters. During this study, the mean ambient temperatures at the field site ranged from 1.7 - 18.6°C (July) to 18.8 - 30.8°C (January). Historic wool and beef production has resulted in a mosaic of remnant, cleared and regrowth woodland areas at the study site. Geology consists of low sedimentary rock ridges dominated by *Acacia catenulata* and *Acacia aneura* woodlands that slope down to clay alluvial soils dominated by open *Eucalyptus populnea* woodlands.

Each woma python was radiotracked for approximately one year (mean= 331 days, range = 199 - 480 days) from Oct 2010 - Jun 2012. The womas were radiotracked on foot approximately every 55 hrs (2 days + 7 hrs) during the summer active seasons and approximately every 79 hrs during the winter

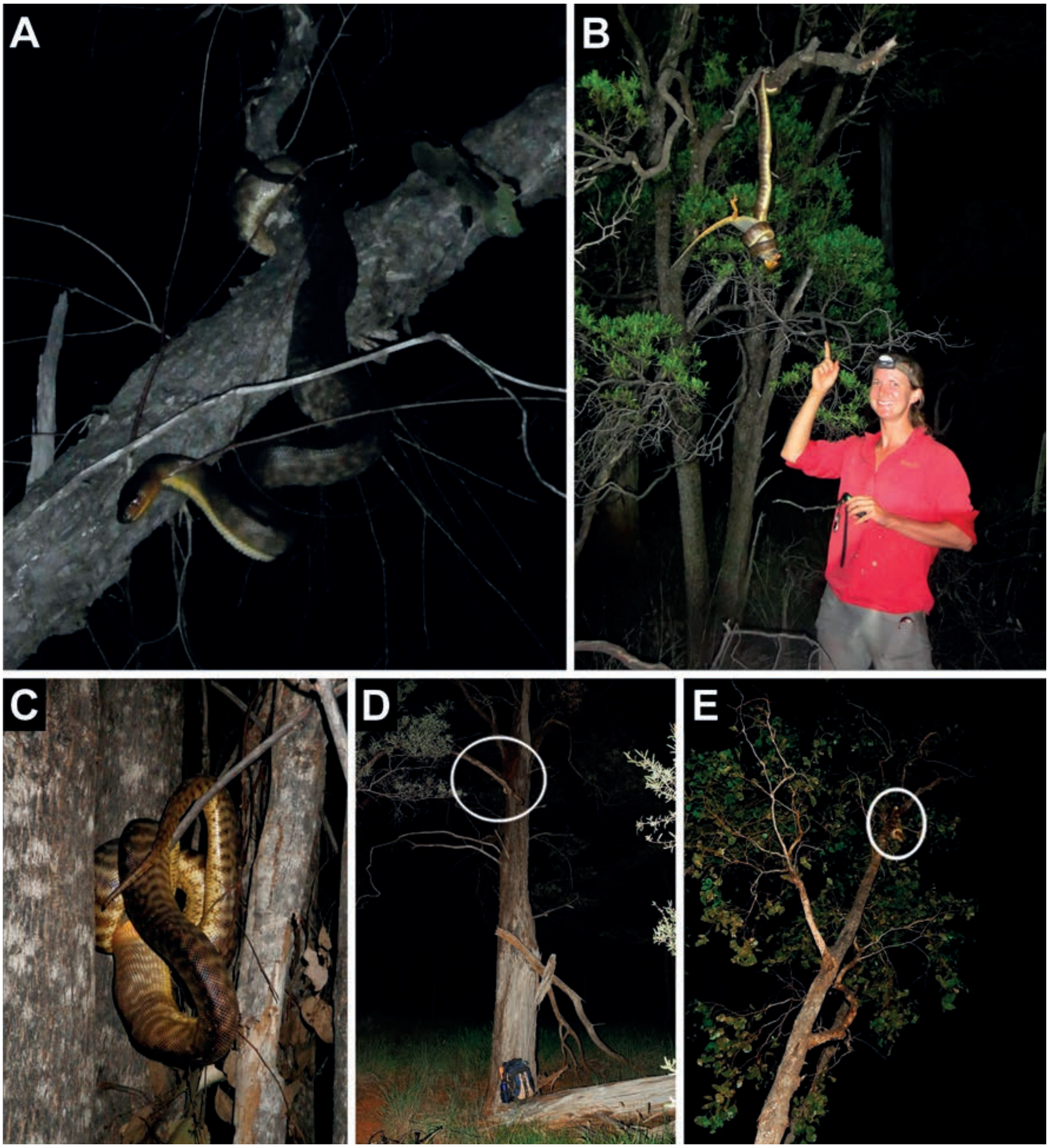

FIG. 1. Novel arboreal woma python *Aspidites ramsayi* behaviours: A, An adult male python pauses 5 m high in a poplar box *Eucalyptus populnea* tree. Coiling of the caudal section of the body indicates recent prey stalking/ingestion behaviour; **B**, An adult male python coils a bearded dragon *Pogona barbata* in a false sandalwood *Eremophila mitchelli* tree, the first observed arboreal behaviour; **C**, An adult male python hangs precariously 1.5 m high on a thin twig wedged between regrowth *E. populnea* trunks; **D**, A small female adult python 4 m high in a mulga *Acacia aneura* tree, hunting a sleeping *P. barbata* (not in frame); **E**, A small male adult python hangs from a branch 10 m high in a thin regrowth *E. populnea* tree whilst consuming an adult *P. barbata* captured in his coils.

TABLE 1: Summary of novel arboreal behaviours observed during a 21 month radiotracking program of twelve adult woma pythons *Aspidites ramsayi* in semi-arid Queensland, Australia.

*Radiotracking commencement date in parentheses. M = Male, F = Female

^Size at transmitter implantation (snout-vent length and mass)

#Height of python, height of prey (on arrival)

% Previous day maximum temperature and afternoon cloud cover

Python Id*	Size^	Date & Time	Observed Activity	Ht (M)#	Tree Species	T_b (°C)	T_a (°C)	Daily Max% (°C)	Notes
HU - M (27-10-11)	1.6 m 1.48 kg	28-10-11 23:12	Stalked, captured and ate a sleeping *P. barbata*	3, 3	*E. mitchelli*	24	24	29.3 patchy	Full cloud, 65% humidity, high winds
DC - M (15-3-11)	1.45 m 1.48 kg	14-11-11 03:11	Stationary, facing down trunk of tree	5, NA	*E. populnea*	24.5	23	33.5 patchy	No cloud, 55% humidity, light wind
DC - M (15-3-11)	1.45 m 1.48 kg	20-11-11 22:58	Stalked a sleeping sub-adult *P. barbata*	2, 1.8	*E. mitchelli*	25.5	24.5	35.7 clear	No cloud, 60% humidity, light wind
EL - F (27-4-11)	1.25 m 1.06 kg	22-11-11 23:05	Stalked a small adult *V. gouldii*	2, 4	*E. populnea* - dead	29	26.5	33.9 patchy	Min. cloud, 60% humidity, mod. winds
EL - F (27-4-11)	1.25 m 1.06 kg	6-1-12 21:34	Stalked a sleeping adult *P. barbata*	5, 4	*A. aneura*	30.5	27	35.4 clear	No cloud, 60% humidity, no wind
KT - F (4-1-11)	1.85 m 3.05 kg	6-1-12 23:36	Moved swiftly down trunk; head almost on ground on arrival	1, NA	*E. mitchelli*	26	24.5	35.4 clear	No cloud, 70% humidity, no wind
RM - M (23-5-11)	1.55 m 1.75 kg	11-2-12 2:11	Stalked, caught and ate a sleeping adult *P. barbata*	1.5, 1.5	*E. populnea*	20.5	19	32.9 clear	No cloud, 85% humidity, no wind
MX - M (20-3-11)	1.70 m 2.3 kg	20-2-12 3:52	Stalked, caught and ate a sleeping adult *P. barbata*	2, 3.5	*A. aneura*	23.5	23.2	36.8 clear	Minimum cloud, 70% humidity, no wind
KT - F (4-1-11)	1.85 m 3.05 kg	5-3-12 21:43	Stalked a sleeping adult *P. barbata*	3, 2	*A. aneura*	28	25.2	34.3 cloudy	Moderate cloud, 60% humidity, light wind
RM - M (23-5-11)	1.55 m 1.75 kg	5-3-12 23:00	Ate an adult *P. barbata*	10, 10	*E. populnea*	26.5	24.2	34.3 cloudy	Moderate cloud, 60% humidity, light wind

inactive season. The time interval between radiotracking sessions resulted in alternating nocturnal and diurnal observations and allowed all periods of the day to be observed.

The pythons were located using conventional VHF signals from implanted temperature sensitive transmitters (Holohil SI-2T, 11g), using the method of Reinert and Cundall (1982). Locations were recorded using a global positioning system (Garmin E-trex) with 3 - 5 m accuracy. Body temperatures were calculated from a calibrated transmitter pulse rate recorded at each observation. Ambient temperature, humidity and wind speed were recorded using a portable weather meter (Kestrel 3000) suspended 1 - 1.5 m above the ground in the nearest shade. Daily ambient temperatures were recorded every ten minutes at a permanent weather meter (Kestrel 4500) installed at the field base; within six kilometres of all radiotracked woma python locations. The womas were radiotracked with minimal disturbance; however disturbance was occasionally unavoidable due to excellent

FIG. 2: An adult male woma python *Aspidites ramsayi* excavates a large burrow in alluvial clay soil.

camouflage. The observations reported here were all recorded on still camera and several behaviours were also captured on motion camera. A genetic tissue sample of each radiotracked woma python is held at the Queensland Museum.

RESULTS

Arboreal Behaviour. *Aspidites ramsayi* demonstrated ten arboreal behaviours out of 1680 radiotracking events during this study (Fig 1, Table 1, with further descriptions in Appendix 1). Six of the twelve radiotracked individuals demonstrated arboreal behaviour, including the smallest (EL – 125 cm SVL, 1.06 kg) and one of the largest (KT – 185 cm SVL, 3.05 kg). Both sexes demonstrated arboreal behaviour equally. The three most common tree species at the study site were utilised with equal frequency during arboreal activity – *E. populnea* (n = 4), *A. aneura* (n = 3), and *Eremophila mitchelli* (n = 3). Pythons were observed up to 10 m high in these trees, with 2 - 4 m being more common.

All arboreal observations commenced at night and were completed by dawn (range 21:30 to 04:00, mean observation time 24:00). Eight of ten arboreal observations were confirmed prey stalking behaviours and the remaining two observations occurred as the womas were descending the trees. Arboreal prey items consisted of *P. barbata* - the largest reptile species regularly sighted sleeping in trees and shrubs on warm nights at the study site (pers. obs.) - and one sleeping *V. gouldii*.

All arboreal observations occurred during warm weather in the austral summer seasons. During arboreal activity, woma body temperature was warmer than ambient air temperature during 9/10 observations (Table 1). Mean snake temperature on arrival at an arboreal observation was 25.8°C and ranged from 20.5 - 30.5°C, whilst mean ambient temperature on arrival was lower at 24.1°C, ranging from 19 - 27°C. The maximum daily temperature prior to a nocturnal arboreal sighting was higher than the midsummer mean maximum January

TABLE 2. Summary of novel observed feeding behaviours and subsequent movements of adult woma pythons *Aspidites ramsayi* during a 21 month radiotracking program in semi-arid southern Queensland, Australia.

*Radiotracking commencement date in parentheses. M = Male, F = Female

^Size at transmitter implantation (snout-vent length and mass)

$Time taken to ingest prey

#Distance from previous location, 55 hrs earlier

%Distance at next location, 55 hrs later.

Python Id*	Size^	Date, Time	Prey	Activity On Arrival	Time$	Dist. Prior#	Dist. After%	Immobile Period
1. CH - M (12-10-10)	1.8 m 1.45 kg	15-1-11 9:45	*V. gouldii* Adult	Head swallowed	35 mins	925 m	145 m	12 days
2. KT - F (11-1-11)	1.85 m 3.05 kg	15-3-11 10:07	*L. capensis* Adult	Capturing, killing	65 mins	70 m	60	8 days
3. GA - F (1-6-11)	1.35 m 1.3 kg	27-5-11 15:30	*E. rugosa* Adult	Basking. Regurgitated	NA	NA	NA	NA
4. HU - M (27-10-11)	1.6 m 1.48 kg	28-10-11 23:12	*P. barbata* Adult	Stalking 30 cm away	130 mins	430 m	420 m	6 days
5. DC - M (15-3-11)	1.45 m 1.48 kg	20-11-11 22:58	*P. barbata* Subadult	Stalking 20 cm away	NA	450 m	1,240 m	15 days
6. EL - F (27-4-11)	1.25 m 1.06 kg	22-11-11 23:05	*V. gouldii* Adult	Stalking 2 m away	NA	555 m	NA	NA
7. JA - M (20-4-11)	1.8 m 3.5 kg	13-12-11 19:50	*V. gouldii* Adult	Stalking 1 m away	>240 mins	1,160 m	400 m	12 days
8. EL - F (27-4-11)	1.25 m 1.06 kg	6-1-12 21:34	*P. barbata* Adult	Stalking 3.5 m away	NA	265 m	495 m	Nil
9. JA - M (20-4-11)	1.8 m 3.5 kg	18-1-12 12:25	*V. gouldii* Adult	Ensconced in hollow log	55 mins	0 m	325 m	10-15 days
10. RM - M (23-5-11)	1.55 m 1.75 kg	11-2-12 2:11	*P. barbata* Adult	Stalking 30 cm away	80 mins	165 m	60 m	15 days
11. MX - M (20-3-11)	1.70 m 2.3 kg	20-2-12 3:52	*P. barbata* Adult	Stalking 1.5 m away	70 mins	1,070 m	520 m	27 days
12. KT - F (11-1-11)	1.85 m 3.05 kg	5-3-12 21:43	*P. barbata* Adult	Stalking,15 m from tree	NA	475 m	50 m	Nil
13. RM - M (23-5-11)	1.55 m 1.75 kg	5-3-12 23:00	*P. barbata* Adult	Hanging, prey in coils	~50 mins	580 m	80 m	Nil

temperature (2012) of 30.8°C, and ranged from 29.3 - 36.8°C with a mean of 34.2°C.

Excavation Behaviour. *Aspidites ramsayi* were observed excavating soil twice during this study. The first digging observation occurred early in the afternoon (2pm, 18 Dec 2011) on a hot summer day with full cloud cover and storms developing (T_{max} = 35°C, T_a = 32.7°C, ground temp. = 34-39°C, *A. ramsayi* T_b = 36.6°C). An adult male python (160 cm SVL) was located with the anterior portion of his body approximately 30 cm inside a wide burrow entry. A pile of loose soil was present outside the burrow (Fig 2). Ten minutes after arrival the python began to scoop more soil out of the burrow with his head and continued to do this for approximately twelve scoops before reversing out of the burrow and investigating the loose soil. The python then braced against the base of a hopbush *Dodonaea viscosa* shrub located 30 cm from the burrow entry, using it to loosen soil deep in the burrow. After leveraging

FIG. 3. An adult female woma python *Aspidites ramsayi* enlarges an existing burrow entry close to a sand goanna *Varanus gouldii* (potential prey) sighting moments earlier.

against the shrub for a further five minutes, the python slowly moved down into the burrow entry and disappeared. This woma had moved 400 m from its last known burrow and 55 hours after the digging observation, had moved a further 260 m to shelter in a well-established ground burrow system.

The second digging observation was of a small adult female python (SVL = 135 cm) at sunset late in summer (24 Feb 2012). It was a warm day with some cloud present (T_{max} = 31.6°C, Ta = 27.4°C, ground temp. = 27-28oC, *A. ramsayi* Tb = 28.0°C). Whilst locating the python, an adult *V. gouldii* (a known prey item) was observed retreating from the top of a hollow log within one metre of the subsequently determined location of the python. On arrival the head of the python was deep inside a slender burrow and the tail was jerking erratically from side to side, a behaviour identical to that observed previously during a prey attack (Appendix 1: Feeding Observation 7). The python proceeded to scoop dirt out of the burrow using her head in the same manner as described by Fyfe and Harvey (1981) and observed in the earlier *A. ramsayi* excavation. The scooping movement exposed a small amount of loose soil at the burrow entry, indicating the woma had just commenced digging (Fig 3). The python continued to scoop out dirt for another two minutes before (without being disturbed) abandoning the excavation to enter a very small burrow 1 m away and underneath the log from which the *V. gouldii* had retreated. Eight minutes later, the python slowly exited this same burrow, stopping intermittently, and then moved back past the excavated burrow before exiting the area. This python had moved 125 m from her previous (exposed) location and 55 hrs later she had moved 250 m further to a hollow log shelter.

Feeding Behaviour. Twelve feeding behaviours from nine individual *A. ramsayi* and one occurrence of a regurgitated prey item were recorded during the radiotracking program (Fig 2, Table 2, with descriptions in Appendix 1). Feeding behaviours occurred both night and day, but occurred more often at night (9/12 observations). The nine ingested prey items included three adult *V. gouldii*, one adult *L. capensis*, four *P. barbata*, and a regurgitated adult *E. rugosa*. Stalking (without

TABLE 3. Radiotracked adult woma python *Aspidites ramsayi* body temperatures and weather conditions during thirteen feeding observations (semi-arid southwest Queensland, Australia). * M = Male, F = Female

Python Id*	Date & Time	T_b (Oc) Start	T_b (Oc) End	T_a (Oc) Start	T_a (Oc) End	Weather
1. CH - M	15-1-11 9:45	36.5 sun	41.8 sun	27	30	Minimal cloud, 60% humidity, light wind
2. KT - F	15-3-11 10:07	33 shade	31.7 shade	29.3	32.3	No cloud, 50% humidity, light wind
3. GA - F	27-5-11 15:30	NA sun	NA	19	NA	No cloud, 45% humidity, light wind
4. HU - M	28-10-11 23:12	24 night	23.4 night	24	24	Full cloud, 65% humidity, high winds
5. DC - M	20-11-11 22:58	25.5 night	NA	24.5	NA	No cloud, 60% humidity, light wind
6. EL - F	22-11-11 23:05	29 night	NA	26.5	NA	Min. cloud, 60% humidity, mod. winds
7. JA - M	13-12-11 19:50	26 night	32 night	23.9	16.2	No cloud, 65-90% humidity, no wind
8. EL - F	6-1-12 21:34	30.5 night	NA	26.9 night	NA	No cloud, 60% humidity, light wind
9. JA - M	18-1-12 12:25	26 log	35.5 shade	32.3	33.5	Minimal cloud, 50% humidity, light wind
10. RM - M	11-2-12 2:11	20.5 night	19.8 night	18.9	18.9	No cloud, 85% humidity, no wind
11. MX - M	20-2-12 3:52	23.5 night	23.9 night	23.2	22.5	Minimal cloud, 70% humidity, no wind
12. KT - F	5-3-12 21:43	28 night	NA	25.2 night	NA	Moderate cloud, 60% humidity, light wind
13. RM - M	5-3-12 23:00	26.5 night	NA	24.2 night	NA	Moderate cloud, 60% humidity, light wind

prey capture) of a further three *P. barbata* and a *V. gouldii* were observed. Eight prey stalking behaviours were observed, though not all were successful. Seven of the eight observed prey stalking behaviours occurred in trees at night and prey included five adult *P. barbata*, a subadult *P. barbata*, and a small adult *V. gouldii*. The thirteen feeding records were dominated by reptilian prey (92%).

The pythons travelled an average of 506 m (range 70 – 1160 m) from their last recorded position to capture prey (Table 2). Following successful ingestion of prey (n = 8), the womas moved an average of 250 m (range 60–520 m) to a shelter and remained immobile for an average of 11.3 (range = 0–27) days before departing the shelter (Table 2).

All feeding observations occurred during the austral warm season, between October and March. However, regurgitation of the *E. rugosa* occurred in late autumn (Table 2, Appendix 1: Feeding Observation 3). Mean *A. ramsayi* body temperature on arrival at a feeding observation (27.4°C, range 20.5–36.5°C) was higher than mean ambient temperature (25.5°C, range 18.9 –32.3°C, Table 3). On most occasions, body temperature either increased or decreased according to the trend in ambient temperature during prey capture and ingestion (Table 3).

DISCUSSION

Arboreal Behaviour: These are the first recorded observations of arboreal behaviour in a species that has formerly been recorded as exhibiting only terrestrial and fossorial tendencies both in captivity and in the wild. Whilst there are records of *A. ramsayi* from sparsely treed habitats, including mulga *A. aneura* and desert sheoak *Allocasuarina decaisneana* sand dunes near Uluru (Fyfe & Harvey 1981), the eastern woma population is the only population known to inhabit an area where large stands and continuous tracts of woodlands create a tall and semi-closed canopy. Other reported habitats include shrubby myrtaceous heath, (Smith 1981), shrubby Banksia heathland (Maryan 2002), cleared farmland (Maryan 2002), hummock grass and spinifex (Fyfe & Harvey 1981; Pearson 1993), and chenopod vegetation (Read 2010); all associated with more western *A. ramsayi* populations in South Australia, Western Australia and the Northern Territory. Therefore it is likely that for the majority of *A. ramsayi* populations, arboreal activity is restricted by an absence or scarcity of trees, and arboreality may be behaviour specific to eastern woma populations. Further reporting of wild woma sightings (including habitat and behaviour) in western locations is necessary to confirm this.

Although arboreal behaviour has not been reported in western *A. ramsayi* populations, captive raised womas from northern South Australia demonstrated that all womas may have at least some capacity to climb. Read (2010) reports that during a trial woma soft-release program, all four of the 5 year old pythons breached the 900 mm high netting fence within two months. No other examples of woma climbing behaviour either in the wild or in captivity have been reported.

Arboreal snakes have evolved physiological adaptations to withstand gravitational pressure in the circulatory system (Lillywhite & Henderson 1993). Therefore it is remarkable that the terrestrial *A. ramsayi* is not only capable of climbing to reasonable heights but is also able to spend over an hour consuming prey whilst hanging vertically from a tree limb (see Appendix 1: Feeding Observations 11 & 13), all without demonstrating adverse effects. Arboreal behaviour in adult womas is even more unusual considering they possess none of the typical arboreal snake external body shape adaptations of slenderness, a laterally compressed cross section, and a long tail (Lillywhite & Henderson 1993). However it is interesting to note that juvenile womas are more slender and laterally compressed in cross section than adults (pers. obs.) and may also be quite capable climbers. Further investigation into the physiological capacity of eastern womas for arboreal activity may uncover cardiovascular and/or other physiological adaptations to assist in coping with short-term gravitational stress.

Arboreal behaviour in *A. ramsayi* was observed exclusively at night during warm months and was strongly linked to feeding activity (Table 1). Behavioural observations of the most commonly recorded woma python prey items at the study site help explain this behaviour. On warm nights *P. barbata* were regularly observed sleeping horizontally on exposed tree and shrub limbs, as well as vertically on tree trunks. These 'roosting' adult *P. barbata* are a bountiful summer food supply that adult woodland inhabiting eastern woma pythons are able to exploit through an arboreal behavioural adaptation.

Two smaller agamids *Amphibolurus burnsi* (Wells & Wellington, 1985) and *Diporiphora nobbi* (Witten 1972) were also regularly observed sleeping on limbs of trees and shrubs on warm nights at the study site. *Amphibolurus burnsi* and *D. nobbi* 'roosted' in greater densities than *P. barbata* (pers. obs.), however they were not observed prey for adult womas. Based on movements from this radiotracking program and typical observed prey size, actively searching for and ingesting small agamids may result in a net energy loss for larger womas (see Arnold 1993 for snake predator-prey size and energy discussion), making such prey items

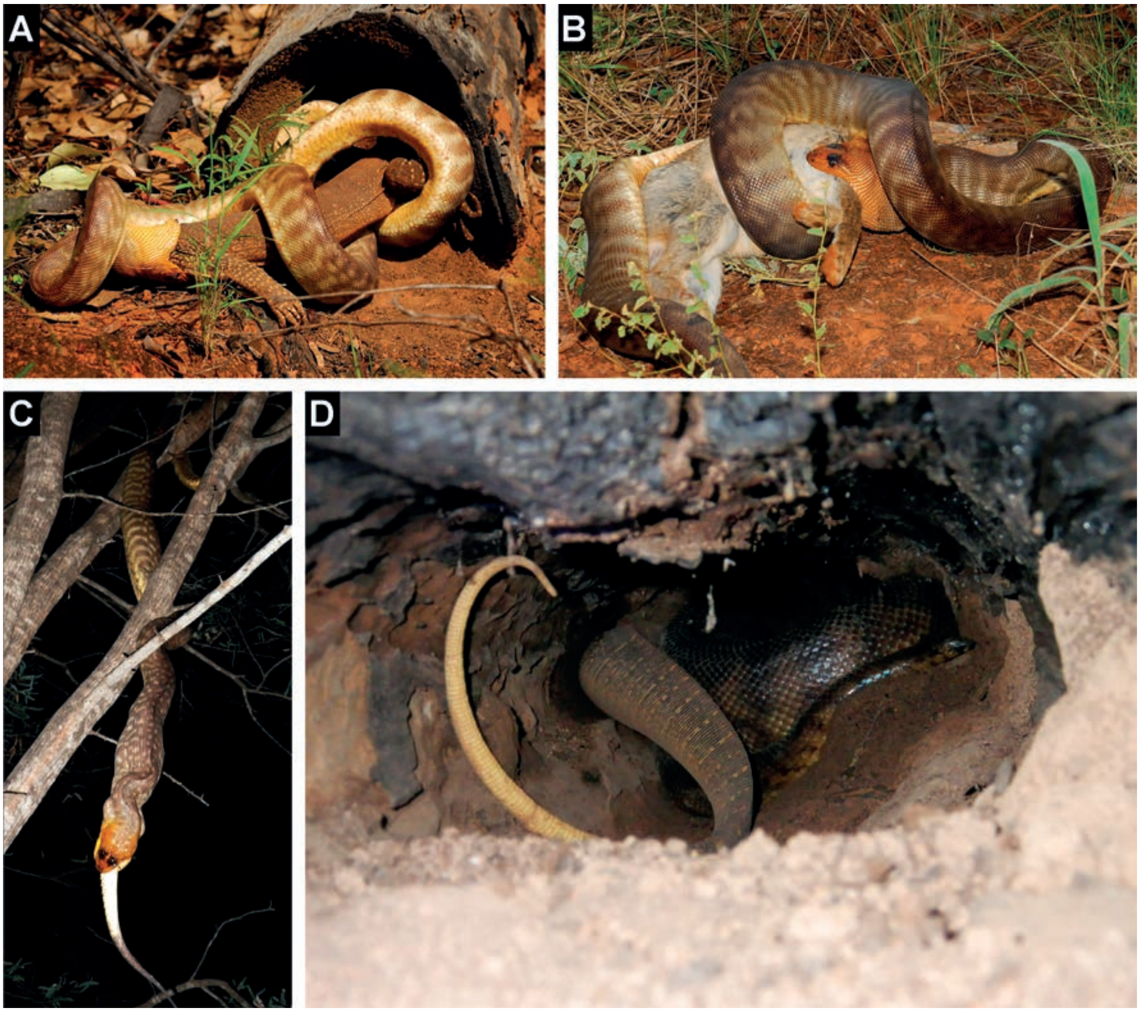

FIG. 4. Novel *Aspidites ramsayi* feeding behaviours and prey: A, An adult male python ingests an adult sand goanna *Varanus gouldii,* captured inside a single-ended hollow log; B, An adult female python consumes an adult hare *Lepus capensis* captured in long grass; C, An adult male python swallows a bearded dragon *Pogona barbata* whilst hanging vertically from a 4 m high mulga *Acacia aneura* tree limb; D, An adult male python traps and 'squashes' an adult *V. gouldii* inside a single-ended hollow log.

unviable. However, if juvenile womas are also capable of arboreal behaviour, it is conceivable that they would prey on 'roosting' *A. burnsi* and *D. nobbi*. Juvenile woma pythons were not radiotracked during this study and were rarely sighted at the study site.

Aspidites ramsayi were not observed using trees for shelter. There were no womas observed in arboreal resting positions during this study. The only python observed stationary in a tree (Table 1: python DC 15-3-11) was facing down the main trunk with his posterior end coiled tightly around a branch - a characteristic boid post-prey ingestion position rather than a coiled resting boid position (Fig 1A, pers. obs.). All observed arboreal woma pythons immediately began to descend following prey ingestion; therefore it is likely that this python had just completed ingestion and was beginning to descend before 'freezing' after being disturbed by an initially fruitless and extensive search on the ground. *Aspidites ramsayi* appear to use trees exclusively for prey capture and ingestion and the limited amount of time that the pythons were observed in trees helps to explain why arboreal behaviour has not been previously reported for this species.

The two largest radiotracked womas were not observed engaging in arboreal activity. This includes the longest (Python BB – 210cm SVL) and the heaviest (Python JA – 180 cm, 3.5 kg). However large python KT (185cm, 3.05kg) was observed engaging in arboreal activity twice. Although it is reasonable to assume that the larger radiotracked womas may have engaged in unobserved arboreal activity, it is noteworthy that there may be a physiological size limit that restricts arboreal activity in very large woma pythons.

Despite greater thermal exposure of snakes in arboreal environments (Lillywhite & Henderson 1993), all except one of the womas were warmer than ambient temperature on arrival at an arboreal observation. Daily maximum temperatures preceding nocturnal arboreal activity were unusually hot on almost all occasions, indicating that either active basking or passive heat retention occurred prior to arboreal activity. Active basking cannot be presumed because warmer body temperatures during arboreal activity could be an artefact of faster ambient cooling rates than *A. ramsayi* body cooling rates at night (thermal hysteresis). Regardless of the mechanism, particularly warm days appear to stimulate active foraging activity, which increases the chance of woma pythons encountering prey scent trails leading to arboreal behaviour (for chemosensory perception discussion see Ford & Burghardt 1993).

Excavation Behaviour. Whilst womas have been observed excavating sandy soils in captivity, these are the first known observations of wild *A. ramsayi* digging behaviours, and they occurred in harder alluvial clay soils. Ehmann (1993) reports that python burrowing behaviour is unique to the *Aspidites* genus – *A. ramsayi* and the similarly sized, but more northerly distributed black-headed python *A. melanocephalus* (Krefft 1864). The digging descriptions for captive *A. ramsayi* (Fyfe & Harvey 1981), wild *A. ramsayi* (this study), and captive *A. melanocephalus* (Murphy, Lamoreaux *et al*. 1981) are all consistent – using the head as a scoop to excavate loose substrate. Murphy, Lamoreaux *et al.* (1981) reported four captive *A. melanocephalus* were able to excavate gravel using this technique, indicating that members of the *Aspidites* genus are capable of digging in a wide range of soil types.

Fyfe & Harvey (1981) were correct in surmising the digging behaviour they observed in captive *A. ramsayi* would likely be used for enlarging existing burrows for shelter or during hunting. In this study, the male excavating *A. ramsayi* (first observation) appeared to use the excavated burrow as a temporary shelter, and post-excavation behaviour indicates he was enlarging an existing burrow. The excavating female (second observation) also enlarged an existing burrow, as determined by a discrepancy between the amount of excavated soil and the burrow depth. The presence of known prey (*V. gouldii*) at this digging site combined with rapid caudal jerking motions consistent with a previous prey capture observation also indicate that she was actively hunting prey. Although we cannot rule out the possibility that *A. ramsayi* dig new burrows for shelter, it seems more likely that they modify existing burrows as a hunting, and possibly also as a sheltering strategy in all soil types.

Feeding Behaviour. *Aspidites ramsayi* are very secretive, spending 74 % of the time underground and 95% of the time in inaccessible shelters such as hollow logs, mounds of dirt, and large piles of woody debris (Bruton, unpub. data). Subsequently it is not surprising that wild *A. ramsayi* feeding observations have not been previously reported. It is likely that womas regularly feed in both underground and above ground shelters, and occasionally out in the open. Therefore it is important to note that the observed feeding behaviours presented here are only a brief glimpse of potential woma python foraging activity.

Museum records throughout Australia demonstrated that woma pythons consume mammals and reptiles in equal proportions, with birds also recorded (Shine 1999). Whilst it is unclear if ground-dwelling or flying birds were consumed, the observations of arboreal behaviour during this study indicate that roosting birds may be taken at night; however roosting birds are unlikely to leave a scent trail for the pythons to follow from the ground. Feeding observations indicate that prey for the eastern population of womas may be strongly biased towards reptiles; especially bearded dragons *P. barbata* and sand goannas *V. gouldii*. Whilst only one woma was observed feeding on a hare *L. capensis*, two other potential hare stalking behaviours were also observed. Unfortunately both hares were unwittingly disturbed whilst pinpointing the exact position of the python. No other mammalian prey foraging or feeding was observed despite the presence of numerous hares and rabbits *O. cuniculus* at the study site.

Although capture and ingestion of yakka skinks *E. rugosa* was not observed, it is likely that this species also constitutes a significant proportion of the diet of eastern woma python populations. *Aspidites ramsayi* utilised a high proportion of ground burrow systems at the study site that are confirmed or suspected yakka skink colonies (Bruton, unpublished data). In addition, the regurgitation of a yakka skink by a woma captured basking outside a known yakka skink colony (Appendix 1: Feeding Observation 3) confirms that *E. rugosa* are preyed upon within their colonial shelters. *Aspidites ramsayi* not only shelter in yakka skink colonies but also feed on the inhabitants.

Whilst it cannot be observed with current technology, it is feasible that many *E. rugosa* are captured within the confines of the communal burrow system tunnels using the prey 'squashing' method described by Fyfe and Harvey (1981). Whilst one radiotracked woma was observed using this 'squashing' method to capture a *V. gouldii* inside a hollow log (Appendix 1: Feeding Observation 7), no other 'squashing' behaviours were observed during this radiotracking program. However this was not unexpected due to the limited viewing opportunities in such confined spaces.

Aspidites ramsayi often travelled long distances both prior to and after prey capture (Table 2), indicating an active foraging mode. Supporting this, throughout the active season the womas regularly moved >300 m between shelter sites (49% of moves) and were capable of moving up to 2 700 m in 55 hrs (Bruton, unpub. data). However, one python demonstrated that womas are also opportunistic and will attack prey from an ambush position. In Feeding Observation 9 (Appendix 1), the sand goanna *V. gouldii* prey was familiar with the hollow log it sought refuge in and the python responded rapidly as it entered the log, indicating a set ambush. It is also likely that womas ambush yakka skinks in the tunnels of the ground burrow systems they shelter in. These observations suggest *A. ramsayi* are predominantly active foragers (intercepting and following prey scent trails), but are also capable of ambush tactics to capture prey.

Caudal luring is an ambush tactic employed by snakes from different phylogenetic lineages, e.g. Viperidae (Heatwole & Davison 1976), Elapidae (Carpenter, Murphy *et al*. 1978), Colubridae (Leal & Thomas 1994), and Boidae (Murphy, Carpenter *et al.* 1978). Caudal luring involves wriggling the slender and differentially marked tail tip like a grub to tempt prey within striking distance (Heatwole & Davison 1976; Carpenter, Murphy *et al*. 1978). The snake may make very rapid caudal movements once prey has been detected, as vividly described for the death adder (Carpenter, Murphy *et al*. 1978). Fyfe and Harvey (1981) report second hand observations of 'caudal luring' in captive womas, however this species lacks the differentiated tail tip and predominantly ambush foraging strategy typical of most species that employ this ambush technique (Heatwole & Davison 1976; but see Leal & Thomas 1994). During this study, erratic tail movements that could potentially be interpreted as caudal luring were observed twice: whilst digging near known prey and whilst 'rushing' forwards to capture cornered prey (see Results section and Appendix 1: Feeding Observation 7). These rapid caudal movements have also been observed in captive womas when they scent imminent food (pers. obs.). During burrow excavation, the rapid caudal tail movements occurred when the head of the python was deep inside the burrow (Fig 3), so luring prey within striking range could not be the purpose of these movements. The head of the python was also not within sensory range of the tail during Feeding Observation 7 (Appendix 1): this python attacked a cornered *V. gouldii* with his head inside a short single-ended log and his tail outside the log. The rapid caudal movements observed are best described as analogous to the tail wag or twitch of a stimulated dog or predatory cat. The stimulus for captive *A. ramsayi* is the scent of food, and imminent prey capture also appears to be the stimulus in the two wild observations. It is not clear if these tail movements have a purpose or are an artefact of hunting. Whilst superficially similar to caudal luring and associated with prey capture, the caudal behaviour observed in wild *A. ramsayi* during this study was not 'luring'.

CONCLUSION

As with all burrowing animals, *A. ramsayi* are very difficult to observe hence there is very limited information on basic ecology and behaviour of this species. This is accentuated by the fact that despite having a vast distribution, womas inhabit an area very sparsely populated by humans (Tobler, Deichmann *et al*. 1995): only 10 towns within the extensive woma python distribution have a population of >1000 people (Australian Government 2006). Therefore it is not surprising that information regarding the natural history and ecology of this elusive species is so limited. Reporting and description of the novel *A. ramsayi* behaviours encountered during this radiotracking study has increased our knowledge of woma python natural history and assisted in understanding python behaviour and ecology.

ACKNOWLEDGMENTS

The radiotracking study was established by Craig Franklin and Clive McAlpine at The University of Queensland with the partnership of Australia Zoo. Access to field site facilities, veterinary procedures, and captive woma expertise were provided by staff at Australia Zoo and the Australia Zoo Wildlife Hospital. Terri Irwin, Kelsey Mostyn, Dr Amber Gillett and Richard Jackson were pivotal in the co-ordination and implementation of this radiotracking program. Financial assistance was provided by the School of Geography, Planning and Environmental Management, and the School of Biology at the University of Queensland, Australian Geographic, The Wildlife Preservation Society of Queensland, Australia Zoo, Warroo-Balonne Landcare, Alan Mackenzie, Wendy Hodge, and Kerron Proctor. All procedures were carried out with approval from The University of Queensland Animal Ethics Committee (GPEM/187/10) and a Queensland Environment Protection Agency permit (WISP07547310).

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APPENDIX 1: BRIEF DESCRIPTIONS OF WOMA PYTHON *ASPIDITES RAMSAYI* FEEDING BEHAVIOUR OBSERVATIONS

Feeding Observation 1. A large woma swallowed an adult sand goanna *V. gouldii* (Fig 4A). On arrival, python CH was partially visible at the entrance to a single-ended fallen hollow log. An adult *V. gouldii* was trapped in his coils and the head was already swallowed. Python CH extricated himself and his prey from the hollow log during ingestion and finished swallowing whilst exposed to full sun on hot bare dirt, 1 m from the log entrance. Although the prey item was large, the ingestion time was short (Table 2). Python CH used typical snake 'jaw walking' motions to ingest the body of the *V. gouldii*, and oesophageal contractions only to swallow the long tail. Upon completion of the meal, python CH immediately returned to the hollow log.

Feeding Observation 2. A large woma caught, killed and swallowed an adult hare *L. capensis* (Fig 4B). On arrival, python KT was not visible in the long grass. After triangulating her position, a furtive attempt was made to observe her activity. However this approach startled the hare, which screamed and bounded away with python KT dragged along behind, clinging onto the hind foot with her mouth. Python KT overwhelmed and coiled the hare within 30 m. There was no movement from the hare after three minutes of constriction. Python KT found the head of the hare very quickly and began to swallow. Ingestion took an hour and occurred in the shade of a Dean's wattle *Acacia deanei*.

Feeding Observation 3. A small adult woma regurgitated an adult yakka skink *E. rugosa* two hours after her initial capture. Python GA was found basking outside a ground burrow system containing a radiotracked python (JA), with a large bulge in her stomach. Whilst every effort was made to gently capture her for transmitter implantation, she later regurgitated her meal in captivity. As this was the initial capture of python GA no snake temperatures are available. The prey item was easily identifiable with limited breakdown of the integument.

Feeding Observation 4. A medium-sized woma stalked, caught, killed and ate an adult bearded dragon *P. barbata* sleeping on an outer limb of a false sandalwood *E. mitchelli* tree (Fig 1B). This was the first arboreal observation, so a futile ground search took place over several minutes before the python and prey were located. On discovery python HU was stretched out from the trunk of the tree with his head 30 cm from the head of the sleeping *P. barbata*. The dragon did not respond despite the noise and light from the initial search. It took python HU 15 mins to stalk the final 30 cm along the branch to strike and capture the sleeping bearded dragon by the head in typical boid manner. The bearded dragon immediately inflated its body. Whilst capturing the prey, the cranial end of python HU fell from the branch, but he held on with the caudal end of his body to hang one metre below the branch. Python HU then coiled the prey upwards into his body and began consuming it whilst hanging vertically from the branch. After 20 mins python HU lost his grip and fell two metres to the ground with the *P. barbata* head already swallowed. He then re-coiled the prey in situ and continued to ingest it over the following 90 mins. The bearded dragon took a comparatively long time to ingest (Table 2), possibly due to its puffed-up profile. Python HU had been implanted with a transmitter only 4 days prior to this encounter and had been released only 37 hrs previously.

Feeding Observation 5. An unsuccessful attempt by a medium-sized adult woma to capture a subadult bearded dragon *P. barbata* sleeping in a small *E. mitchelli* shrub. On arrival python DC was stretched vertically up the trunk of the tree with his head 20 cm from the tail of the sleeping bearded dragon. Five minutes later the bearded dragon unexpectedly jumped down to the ground and ran away, possibly due to disturbance. Python DC made no attempt to follow but continued to slowly stalk slowly up the shrub for another five minutes before observations were ceased.

Feeding Observation 6. An unsuccessful attempt by a small adult woma to capture a small adult sand goanna *V. gouldii* four metres high in a burnt eucalyptus *E. populnea* tree stump. On arrival python EL was two metres high on the smooth outer edge of the stump and beginning to disappear into the hollow inner trunk. The *V. gouldii* had not been sighted at this time and the correlation between arboreal behaviour and prey stalking had not yet been established. Python EL had not been sighted since her release six months earlier and it was vital that her transmitter implantation wound site be checked for infection and antenna protrusion. As she was being extricated from the hollow the torch beam illuminated the head of the sand goanna in a hollow two metres higher than python EL. It is likely that python EL had been stalking the sand goanna. A slightly protruding antenna necessitated a short stay in captivity so her next movements could not be observed.

Feeding Observation 7. A large woma attacked a large adult sand goanna *V. gouldii* ensconced in a single-ended hollow log (Fig 4E). On arrival, python JA had approximately 30 cm of his anterior end inside the log and was rapidly entering it. He appeared very animated with the posterior section of his body jerking erratically from side to side as he moved. Once inside, there was an audible scrabbling of claws and commotion. Several moments later the tip of a *V. gouldii* tail was visible twitching underneath the coils of python JA. Over the following four hours there was little movement from python JA as he squashed the sand goanna against the end, the bottom, and the sides of the log. At 01:00 the sand goanna was still alive and python JA showed no evidence of attempting to kill it but kept it pinned within the log. The following morning (09:40), python JA was sighted moving 340 m away from the attack site with a large goanna-shaped bulge in his stomach.

Feeding Observation 8. An attempt by a small woma to stalk and capture an adult bearded dragon *P. barbata* sleeping in a mulga tree *A. aneura* (Fig 1D). On arrival python EL was extended horizontally from the tree trunk with an adult bearded dragon sleeping 3.5 m away on the outer reaches of the same branch. Due to time constraints and fatigue, the stalking behaviour was not able to be observed and it is not known if the hunt was successful.

Feeding Observation 9. A large woma caught, killed, and swallowed an adult sand goanna *V. gouldii*. On arrival, the position of python JA was identified as approximately 1.5 m inside a slightly raised fallen hollow poplar box *E. populnea* log. Also noted was a sand goanna basking two metres away from the log. Despite slowly backing away, the sand goanna took fright and ran under the hollow log before doubling back to the log entry and pausing momentarily to scent it. The sand goanna then entered the log rapidly and was immediately attacked by python JA. The sand goanna then dragged python JA out of the log where he overpowered it in the shade of a mulga *A. aneura* tree, 1.5 m from the burrow entry. Python JA remained tightly coiled around the sand goanna for 20 mins before releasing his hold and locating the head for swallowing. Following ingestion, python JA immediately retreated back into the hollow log and settled in his original position.

Feeding Observation 10. A medium-sized woma caught, killed, and swallowed a bearded dragon *P. barbata* (Fig 1C). On arrival, python RM was stretched vertically up a multi-stemmed regrowth poplar box *E. populnea* tree. Whilst no prey item was initially located, python RM was observed continuously tongue flicking between a thick trunk of the tree and a nearby *E. mitchelli* shrub. Five minutes later python RM attacked and coiled the adult bearded dragon, along with a thin stick lodged horizontally 1.5 m above the ground in the midst of the multiple stems of the *E. populnea* tree (Fig 1C). The prey ceased moving within five minutes of capture and python RM proceeded to ingest it whilst hanging precariously in the tree. After 70 mins the stick slanted too far resulting in python RM sliding and tumbling 1.5 m to the ground with the head and body of the bearded dragon already swallowed. Python RM took a further 10 mins to complete ingestion and move away.

Feeding Observation 11. A large woma stalked, killed, and swallowed an adult bearded dragon *P. barbata* sleeping on an inner vertical stem of a mulga *A. aneura* tree (Fig 4C). On arrival python MX was climbing vertically up the tree with his head approximately 1.5 m below the tail of the sleeping bearded dragon. Over the following 30 mins python MX stalked up past the prey and attacked it directly on the head from above. Python MX then coiled the puffed up bearded dragon whilst suspended from a limb one metre higher than the original bearded dragon position. After 15 mins, python MX began to ingest the dragon whilst hanging vertically from one limb with his tail anchored down to a second limb, providing a stable position approximately four metres above the ground (Fig 4C). Python MX completely ingested the prey whilst hanging vertically. After ingestion, python MX immediately began to descend the tree.

Feeding Observation 12. A large woma stalked an adult bearded dragon *P. barbata* sleeping on a very slender outer twig of a three metre long horizontal mulga *A. aneura* branch. On arrival python KT was cruising slowly along the ground 15 m from the base of the mulga tree. The position of the sleeping bearded dragon was noted and it was realised that python KT may be following its scent trail. Five minutes after the initial location, a very dim light was used to locate python KT four metres from the base of the tree in a direct line from her previous position. She did not respond during either of the observations. Over the following 45 minutes the silhouette of python KT was followed using moonlight as she reached the base of the tree and proceeded to climb it. During the following 35 mins python KT explored the central trunk area up to a height of three metres. She did not attempt to climb out onto the limb containing the sleeping bearded dragon but spent much time exploring the trunk area. Observations were ceased at this point to radiotrack the remaining *A. ramsayi*.

Four hours later both woma python KT and the *P. barbata* were absent.

Feeding Observation 13. A medium-sized woma ate an adult bearded dragon *P. barbata* ten metres high in a thin regrowth poplar box *E. populnea* tree (Fig 1E). On arrival python RM could not be pinpointed. Eventually he was sighted hanging vertically down from a high limb of a straight trunked tree, anchored up and over a branch, with a bearded dragon in his coils, swallowing the head. To avoid disturbing him (and potentially a ten metre fall), RM was left alone to complete ingestion. Fifty minutes later python RM had just finished swallowing the bearded dragon and was lifting the anterior portion of his body up from a vertical hanging position. Over the following 25 mins python RM slowly descended the straight, narrow tree trunk using a concertina method typically employed by arboreal snakes. On descending to a height of 2.5 m, python RM was left to continue onto a shelter undisturbed.