Diet and foraging behaviour of the semi-aquatic *Varanus mertensi* (Reptilia : Varanidae)

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Abstract. We report on the aquatic and terrestrial foraging behaviour and diet of the semi-aquatic *Varanus mertensi*. Foraging behaviour of *V. mertensi* is similar to that of other large terrestrial varanids: slow, methodical forwards movement with the head swaying from side to side with regular tongue flicks. Both olfactory and visual cues are used to detect prey. Foraging in the water is remarkably similar to that in the terrestrial environment, with this species using both visual and olfactory cues. Like other varanids, this species is able to use previous experiences to maximise its chance of locating prey. *V. mertensi* consume a large number of freshwater crabs (*Holthuisana* sp.) and a variety of small invertebrate and vertebrate prey across their distribution. Dietary differences across geographic regions are minor. Its diet is sufficiently catholic to enable it to adapt to seasonal and spatial differences in prey availability, one reason for its widespread distribution in the wet–dry tropics of Australia. Stomach contents differ from those of scats, with soft-bodied prey items being absent from scat samples.

Introduction

After an extensive review of dietary and foraging data for 35 species of goannas, Losos and Greene (1988) described most goannas as dietary generalists. With the exception of *V. komodoensis* and *V. bengalensis* (Auffenberg 1981, 1994), most varanids consume large numbers of small prey items rather than few large items, although the body size and gape of many species indicates that they are capable of subduing and devouring large prey. Losos and Greene (1988) suggested that seasonal and geographic variations in diet were a common feature among varanid species. The ability to draw on previous prey-capture experience to maximise hunting efficiency is also well developed in varanids (Shine 1986; Thompson 1995; Sweet and Pianka 2003). Some species have also been found to display an area-concentrated foraging strategy, shifting from one area to the next when prey are depleted (Thompson 1992, Thompson 1995). Sweet (1999) also described a seasonal shift in foraging habitat used by the tropical *V. glebopalma*, ascribing the shift to changes in prey availability.

Foraging behaviours adopted by most large varanids are characterised by slow forwards movement, swinging the head from side to side and regular tongue flicking (Thompson 1995). Tongue flicking enables prey detection using olfactory cues (Auffenberg 1983; Cooper 1989; Garrett and Card 1993). Most varanids also have well developed vision that enables them to detect movement of potential prey within their immediate environment (Thompson 1995).

Most semi-aquatic varanids are active, wide-ranging, opportunistic foragers that adopt foraging behaviours similar to those of terrestrial varanids (Gaulke 1991; McCoid and Witteman 1993; Traeholt 1993, 1994*a*). Although most semi-aquatic species are known to consume various aquatic prey such as fish (*V. mitchelli*: Shine 1986; Vincent and Wilson 1999), crustaceans and arthropods (*V. mertensi*, *V. indicus* and *V. salvator*: Losos and Greene 1988; McCoid and Witteman 1993; Traeholt 1994*a*, 1994*b*), most still consume a variety of vertebrate and invertebrate species of terrestrial origin. Aquatic varanids show similar geographic and seasonal variation in diet to terrestrial species (Losos and Greene 1988; Gaulke 1991; Traeholt 1994*a*, 1994*b*).

Varanus mertensi is a semi-aquatic goanna with a distribution that includes most of tropical Australia (Cogger 1992). It inhabits many watercourses, billabongs, springs and soaks within its geographical distribution. These goannas also inhabit human-made water bodies such as dams and irrigation areas. Not surprisingly, large numbers of *V. mertensi* can be found in the various lakes and channels of the Ord River Irrigation Scheme in the East Kimberley region of Western Australia. Since their introduction in 1937 cane toads, *Bufo marinus*, have colonised many areas within the Australian distribution of *V. mertensi*, particularly in tropical north-east Australia. Sutherst *et al.* (1995) reported cane toads occupying about 50% of Queensland and small portions of New South Wales and the Northern Territory. Using a computer-based CLIMEX model, Sutherst *et al*. (1995) predicted cane toads may spread to colonise areas

across the tropical north of Australia as far west as Broome in the Kimberley of Western Australia. In recent years cane toads have spread well into the Northern Territory into areas such as Katherine Gorge and the Kakadu National park (Sam Sweet, Dan Holland, personal communications). Watson and Woinarski (2002) reported significant declines in populations of faunal species, including varanids, at sites invaded by cane toads in Kakadu National Park. It would seem probable that the semi-aquatic *V. mertensi* is one varanid that may encounter and consume toxic toads. The effect of invading cane toads on populations of *V. mertensi* is not certain; however, anecdotal reports from north-east Queensland suggest significant population declines in areas where toads are well established (Sam Sweet, personal communication). The importance of this study in the Kimberley region of Western Australia, an area currently devoid of cane toads, is crucial in developing our understanding of the possible effects of cane toads on populations of *V. mertensi*, particularly as cane toads are predicted to colonise the East Kimberley region. More widely, little is known of the ecology of *V. mertensi*. Christian and Weavers (1996) examined its active core body temperatures in the field and Shine (1986) reported on its diet. However, little data have been presented on its foraging strategy, either in the terrestrial or aquatic environment. We know of only one published report (Hermes 1981) describing an individual using its tail to 'herd' and then feed on trapped fish in a drying waterhole.

An understanding of diet and foraging behaviour can assist in understanding the daily spatial movements, thermoregulatory behaviour and reproductive behaviour of this species. This study examines foraging behaviour and diet of the semi-aquatic *V. mertensi* in irrigation areas and natural watercourses of the East Kimberley of Western Australia to provide insights into this species' ecology. We compare the diet of *V. mertensi* in the East Kimberley with that of the species near Jabiru in the Northern Territory and elsewhere in Western Australia to determine the extent of geographic variation in the diet of *V. mertensi*.

Reptile diets are often assessed on the basis of stomach contents collected from museum specimens (Greene 1986; Shine 1986; James *et al.* 1992), stomach flushing of live specimens (Legler and Sullivan 1979; Thompson 1996) and occasionally scat samples (Gaulke 1991; Traeholt 1994*a*, 1994*b*; Thompson and King 1995; Tsellarius *et al.* 1997; Sweet 1999). We compare the composition of flushed stomach contents with known *V. mertensi* scats to assess bias in using only scats to determine diet for this species of varanid.

Materials and methods

Foraging behaviour

Numerous observations of the foraging behaviour of *V. mertensi* were made for both radio-tagged and opportunistically encountered individuals during the course of a two-year field study. Temperature-sensitive radio transmitters (Model 2I-T, Holohil Systems) were

implanted into the abdomen of adult *V. mertensi* captured at various locations throughout the East Kimberley. Repeated locations and behavioural observations of radio-tagged *V. mertensi* were recorded for 49 individuals between January 2001 and January 2003. For seven goannas, their behaviour and location were recorded continuously from haul-out in the morning to haul-in in the late afternoon, to give a total of 20 full-day observations covering the entire activity period for one day. Data for these individuals included what the animal was doing (e.g. basking, swimming, etc), whether it was moving or stationary, its activity site (e.g. water, riparian vegetation), whether it was actively foraging, its foraging behaviour, and when and what prey it caught. Every effort was made to minimise observer interference on the lizard's behaviour by remaining in a vehicle or a considerable distance from the observed animal.

Stomach flushing

We sampled the stomach contents of 42 *V. mertensi* caught in the East Kimberley between January 2001 and January 2003. Most samples were recovered by flushing stomachs but our dataset also included the contents of several stomachs recovered from animals killed on local roads. The stomach of each goanna was flushed within 3 h of capture. This involved inserting a plastic tube (diameter 10 mm) down the oesophagus into the stomach. Fresh water (2–3 L) was then pumped into the stomach using a large syringe. Regurgitated water was filtered through 2-mm mesh. All material flushed from the stomach was collected and stored in 70% ethanol until examined. Stomach samples were subsequently dried in a controlled-temperature cabinet for 7 days at 35°C before being sorted into constituent groups. After sorting, the minimum number of each prey type was determined by counting each prey item or diagnostic part thereof. For example, the number of freshwater crabs was determined by dividing the number of claws by two. The dry weight of each prey group was recorded for each goanna. The proportion of the diet represented by each prey group was calculated as the percentage of the total biomass recovered from all stomachs.

Scat collection

A total of 25 field scats were collected between January 2001 and January 2003. *V. mertensi* scats were identified by both their location (proximity to a watercourse) and shape. Scats were collected only within the riparian zone at sites known to be inhabited by *V. mertensi*. Scats deposited by *V. mertensi* are cylindrical with a diameter of ~10 mm and length of ~100 mm. Scats were stored in 70% ethanol until examined. Scats were washed thoroughly through a 2-mm fine mesh with running water, after which they were dried in a controlled-temperature cabinet for 7 days at 35°C. Dried samples were sorted into constituent groups. After sorting, the minimum number of each prey type was estimated as above and the dry weight of each prey group recorded for each scat. The proportion represented by each prey group within each scat was calculated as above.

Density of Holthuisana *burrows*

Because freshwater crabs (*Holthuisana* sp.) were the predominant food source for *V. mertensi*, we estimated the relative abundance of these crabs on two occasions to gauge their prevalence as a prey source in the foraging areas of *V. mertensi*. These estimates were conducted during the late dry season (November 2002) and the beginning of the wet season (January 2003) at a site on the Main Irrigation Channel of the Ivanhoe Plains Irrigation Area just outside the township of Kununurra. The site was selected because it provided easy access to banks of the irrigation channel that contained crab burrows, particularly during the wet season when access to most water courses was difficult. The site was marked and the same location used for both the wet and dry season. Freshwater crab abundances were estimated by counting the number of active burrows in three sections (5 m × 1 m) of the bank for three con-

secutive days. Banks on either side of most irrigation channels have a raised berm with a slope to the irrigation channel of about 40°. *Holthuisana* dig their burrows into the slope of the berm facing the channel. These berms are ~1 m wide, depending on the water level in the channel. Initially, the surface of the bank was raked clear of excavated soil accumulated at the entrance to each burrow. A small pile of excavated mud at the entrance of the burrow after each night's activity was used to define an active burrow. The proportion of active burrows (active/total × 100) was calculated and averaged over three days for the three trials. Finally, the density of active crab burrows per metre of irrigation channel bank was calculated and presented as mean ± 1 standard error of the mean.

Herbicide injections

Throughout the field study, detailed records were kept of the effects on vertebrate and invertebrate fauna of water-plant-reducing herbicide injections (Acrolein: 2-Propenal; Magna Herbicide Division, Baker Performance Chemicals, Inc.) into irrigation channels within the Ord River Irrigation Area conducted by local water-regulatory authorities.

Results

Foraging behaviour

We provide an account of eight foraging and feeding sequences selected from many to demonstrate the typical foraging behaviour of the semi-aquatic *V. mertensi*.

Observation 1 – Main Irrigation Channel (M1) in the Ivanhoe Plains Irrigation Area during the wet season of 2003

This lizard was foraging while swimming along the bottom of the channel at a depth of ~2.5 m, moving its head from side to side while searching under rocks, tongue flicking approximately every 5–6 s. After investigating around the edge of three rocks the lizard forced its head under the edge of a fourth rock 3–4 times, to a depth of ~10–15 cm while repeatedly tongue flicking. On the final attempt a small freshwater crab (*Holthuisana*) shot out from under the rock and swam up through the water column. The crab had gained about 1.5–2 m on the lizard before it retracted its head from under the rock, and chased and caught the crab before returning to the surface. By this time the lizard had been underwater for several minutes. After 2–3 attempts to orientate the crab, the lizard swallowed it without any apparent chewing whilst swimming against an obvious current on the surface of the water. The lizard then returned to the bottom of the channel and continued its underwater foraging.

Observation 2 – Irrigation channel drain (D4) in the Ivanhoe Plains Irrigation Area during the late wet season of 2002

A lizard was observed standing on the edge of an artificial waterfall, snatching fish out of the air as they attempted to jump up through the waterfall. This *V. mertensi* was seen to catch three fish. After each successful capture the lizard would leave the waterfall and retreat ~5 m into the hinterland before orienting the fish head first in its mouth and swallowing it. Swallowing usually required 2–3 attempts and in one

instance the fish was dropped onto the ground where it was quickly retrieved before it could return to the water, and swallowed. Two fish were small *Leiopotherapon macrolepsis* (Kimberley Spangled Perch) and the other was a small *Amniataba percoides* (Stripy). Following consumption of these three fish, the lizard left the waterfall and began foraging along the edge of the irrigation channel, walking slowly along the bank moving its head from side to side, searching the fringing riparian vegetation with regular tongue flicking.

Observation 3 – Main Irrigation Channel (M1) in the Ivanhoe Plains Irrigation Area during the wet season of 2002

A lizard was observed probing numerous freshwater crab burrows, repeatedly tongue flicking when moving between burrows, on the bank of a completely drained main irrigation channel. After probing three burrows to a depth of 15–30 cm the lizard retracted its head from a fourth burrow with a freshwater crab (*Holthuisana*) in its mouth. It immediately arched its head back and swallowed the crab without any apparent orientation of the prey. After swallowing the crab this lizard sighted the observer and walked off, discontinuing its foraging.

Observation 4 – Main Irrigation Channel (M1) in the Ivanhoe Plains Irrigation Area during the dry season of 2002

A lizard was observed slowly walking through vegetation along the bank of the irrigation channel moving its head from side to side and regularly flicking its tongue. After no visible pursuit the lizard was seen grasping an unidentified frog in its mouth. It arched its head back and orientated the frog head first before struggling momentarily to swallow the frog. After a further 30–60 s of foraging amongst vegetation in which the first frog was captured the lizard was seen grasping a second frog in its mouth, which it swallowed the same way as the first.

Observation 5 – Packsaddle Plains main irrigation channel during an Acrolein injection in the dry season of 2002

After ~2–3 min of watching dead fish float past (a consequence of Acrolein injections into the channel) a *V. mertensi* was observed to swim out into the channel to capture a fish that was obviously distressed but not dead. This lizard returned to the bank and consumed the fish, head first, before returning to the observation point on the bank. It remained stationary on the bank basking for a further 10 min before being disturbed by a passing vehicle and leaving the area.

Observation 6 – Packsaddle Plains main irrigation channel during the dry season of 2002

A lizard was first observed slowly foraging along the bank/water interface, moving its head from side to side and

regularly tongue flicking, when its attention was attracted to the nearby riparian zone. After leaving the water, the lizard quickly pursued and caught a jumping grasshopper within the riparian vegetation. After consumption, which involved no apparent orientation of the insect, the individual returned to water–bank interface and resumed its slow-moving foraging behaviour along the interface.

Observation 7 – Packsaddle Plains main irrigation channel during the dry season of 2002

A lizard was observed slowly moving along the bank/water interface of the irrigation channel, moving its head from side to side and regularly tongue flicking. The lizard's attention was suddenly drawn to the nearby fringing vegetation and it promptly left the bank–water interface to investigate. Suddenly, the lizard began to pursue an unknown prey item in this vegetation. After an unobserved pursuit of ~3–4 m the animal raised its head to swallow a pygopodid (legless lizard) ~30 cm long. After consuming the pygopodid the lizard resumed searching the same fringing riparian vegetation for a further 1–2 min before returning to the water, where it resumed its slow-moving foraging behaviour.

Observation 8 – Natural waterhole at Salerno Gorge on El Questro Station during the late dry season of 2002

A lizard actively chased and caught two small live eel-tail catfish (*Neosilurus* sp.) in the main pool. Although not sighted during the actual capture sequence, owing to the depth of water, the lizard returned to the surface with these fish still struggling in its mouth. The lizard proceeded to consume both fish whilst swimming on the surface of the water after carefully orientating them into a head-first position.

Diet

The diet of *V. mertensi* consisted mainly of freshwater crabs (*Holthuisana*), which comprised 32.6% and 70.9% of the number of prey items in stomach and scats samples respectively (Table 1). This represented 29.0% and 83.7%, respectively, of prey biomass recovered from stomach and scat samples. In total, 45.0% of stomachs and 68.0% of scats contained *Holthuisana*.

The remainder of the diet included many prey groups. Fish constituted 13.7% of all prey items and were in 14.3% of stomachs, which represented 11.5% of the prey biomass recovered from stomachs. Eggs represented a large proportion of the remaining diet (31.1% and 9.4% respectively of prey biomass from stomach and scat samples), but eggs were found in few stomachs (4.7%) and scats (12%), indicating that they were infrequently consumed but when eaten were a relatively large proportion of the diet. Frogs were infrequently consumed (7.1% of stomachs) but constituted a relatively large proportion of the diet (5.8% of all prey items and 11.1% of prey biomass). Spiders were frequently consumed, being found in 21.4% of stomachs (13.7% of all prey

items recovered) but represent a small proportion of the total diet biomass (1.0% of prey biomass). Similarly, water bugs and black beetles were consumed frequently but represent only a small proportion of diet biomass. The only other prey group that represented more than 5% of either the number of prey items or biomass recovered were mice (*Mus musculus*) (found in 1 stomach and 1 scat). Prey groups representing less than 5% included crickets, grasshoppers, unidentified insects, unidentified larvae (caterpillars), reptiles (Agamidae), carrion, fruit and the introduced freshwater crustacean 'red claw' (*Cherax quadricarinatus*).

Stomachs contained both soft- and hard-bodied prey (Table 1). Absent in scat samples were spiders, crickets, fish, frogs, dragon lizards, fruit and carrion. Water bugs were found at a much lower prevalence in scat samples than in stomachs. A 'red claw' was found in a scat but not in stomachs (Table 1).

Density of Holthuisana burrows

The average density of active *Holthuisana* sp. burrows was found to be 1.7 ± 0.27 burrows m^{-1} during the wet season and 1.3 ± 0.12 burrows m^{-1} during the dry season along the irrigation channel bank sampled.

Herbicide injections

Eleven injections of Acrolein into irrigation channels were recorded during the dry season (April–October) and three injections were recorded during the wet season (November–March). Acrolein injections resulted in almost all fish being killed downstream of the injection point in the irrigation channels. Four of five recordings of fish being consumed by *V. mertensi* in irrigation channels were immediately after herbicide injections into irrigation channels. Over the duration of our field study we recorded no short-term adverse effects on any *V. mertensi* observed consuming fish killed through application of herbicide into irrigation channels.

Discussion

Foraging behaviour

The foraging behaviour of *V. mertensi* incorporates slow, forwards movement with progressive swaying of the head from side to side and regular tongue flicking to detect the presence of prey. This search pattern, which is used both in the terrestrial and aquatic environment was also described for *V. gouldii* by Thompson (1995). The regular side-to-side movement of the head and flicking of the forked tongue presumably maximises the detection area for olfactory receptors located on the tongue (Auffenberg 1983; Cooper 1989; Garrett and Card 1993). Our data suggest that *V. mertensi* is capable of searching for and capturing prey underwater using olfactory cues. This has not been reported for other semi-aquatic varanids.

In addition to detecting prey using olfactory cues while foraging, *V. mertensi* also used their visual sense. Our obser-

Table 1. The diet of *V. mertensi*

Prey items consumed by *V. mertensi* found in the stomachs of museum specimens examined in the Northern Territory and Western Australian Museums by Shine (1986) and prey items found in the stomachs and scats of *V. mertensi* sampled throughout the East Kimberley during 2001–03 are shown. Numbers of prey items and combined mass of prey groups are shown in addition to the number of individual *V. mertensi* from which each prey item was recovered. Proportion of total diet constituted by each prey item is shown in parentheses

Prey group	Northern Territory (Shine 1986)			Western Australia (Shine 1986)			This study, Kimberley (stomachs)			This study, Kimberley (scats)		
	# Prey	Wet mass (g)	No.	# Prey	Wet mass (g)	No.	# Prey	Dry mass (g)	No.	# Prey	Dry mass (g)	No.
Arachnida	—	—	—	—	—	—	19 (0.14)	0.693 (0.01)	9	—	—	—
Lycosidae	4 (0.03)	0.37	4	2 (0.02)	0.2 (0.002)	2	—	—	—	—	—	—
Araneae	1 (0.007)	0.13	1	—	—	—	—	—	—	—	—	—
Hexapoda	—	—	—	—	—	—	—	—	—	—	—	—
Odonata	1 (0.007)	0.3	1	4 (0.04)	1.4 (0.014)	2	—	—	—	—	—	—
Orthoptera	3 (0.02)	0.64 (0.001)	3	4 (0.04)	2.65 (0.03)	4	—	—	—	—	—	—
Grylidae	1 (0.001)	0.3	1	2 (0.02)	1 (0.01)	1	3 (0.022)	0.18 (0.003)	2	2 (0.02)	0.41 (0.003)	1
Acrididae	—	—	—	1 (0.01)	1 (0.01)	1	3 (0.022)	0.62 (0.01)	3	—	—	—
Gryllotalpidae	1 (0.007)	0.5	1	—	—	—	—	—	—	—	—	—
Hemiptera	1 (0.007)	—	1	20 (0.20)	2.30 (0.02)	3	—	—	—	12 (0.1)	2.5 (0.02)	5
Nepidae	3 (0.02)	1.55 (0.002)	3	2 (0.020)	1.25 (0.01)	2	—	—	—	—	—	—
Nepiodea	—	—	—	—	—	—	7 (0.051)	0.19 (0.003)	4	1 (0.01)	0.02 (0.0001)	1
Coleoptera	—	—	—	—	—	—	—	—	—	—	—	—
Dytiscidae	24 (0.17)	9.05 (0.013)	2	3 (0.03)	4.8 (0.048)	3	—	—	—	—	—	—
Carabidae	1 (0.007)	—	1	9 (0.09)	6.4 (0.064)	5	8 (0.058)	1.35 (0.02)	5	12 (0.1)	2.5 (0.02)	5
Hymenoptera	—	—	—	—	—	—	—	—	—	—	—	—
Formicidae	1 (0.007)	0.08	1	—	—	—	—	—	—	—	—	~
Insects (unident.)	2 (0.014)	—	—	6 (0.061)	0.4 (0.004)	2	6 (0.043)	0.60 (0.01)	5	7 (0.05)	0.62 (0.004)	4
Insect larvae	—	—	—	—	—	—	5 (0.036)	0.51 (0.008)	4	—	—	—
Holthuisana	69 (0.49)	205.6 (0.29)	21	3 (0.03)	14 (0.14)	3	45 (0.33)	19.28 (0.29)	19	91 (0.71)	112.52 (0.84)	17
Decapoda	—	—	—	—	—	—	—	—	—	1 (0.008)	2.27 (0.017)	1
Caridae	10 (0.07)	5.07 (0.04)	1	19 (0.19)	10.8 (0.11)	3	—	—	—	—	—	—
Pisces	4 (0.03)	1.4 (0.002)	3	5 (0.05)	29.9 (0.3)	4	19 (0.137)	7.61 (0.115)	6	—	—	—
Anura	5 (0.036)	30.7 (0.043)	4	5 (0.05)	3.0 (0.03)	3	8 (0.06)	7.39 (0.11)	3	—	—	—
Reptilia (eggs)	6 (0.043)	420 (0.594)	1	2 (0.02)	20 (0.20)	1	11 (0.079)	20.68 (0.31)	2	10 (0.08)	12.64 (0.1)	3
Serpentes	1 (0.001)	30 (0.042)	1	—	—	—	—	—	—	—	—	—
Agamidae	—	—	—	—	—	—	1 (0.007)	0.36 (0.005)	1	—	—	—
Aves	1 (0.001)	—	1	1 (0.01)	—	1	—	—	—	—	—	—
Mammalia	1 (0.001)	1.8 (0.003)	1	1 (0.01)	—	1	—	—	—	—	—	—
Mus musculus	—	—	—	—	—	—	1 (0.007)	5.36 (0.08)	1	1 (0.008)	0.30 (0.002)	1
Carrion	—	—	—	—	—	—	1 (0.007)	0.44 (0.006)	1	—	—	—
Fruit	—	—	—	—	—	—	1 (0.007)	0.22 (0.003)	1	—	—	—
Other	—	—	—	—	—	—	(0.047)	0.90 (0.014)	7	—	3.21 (0.024)	8
Totals	140	707.49 (1)	31	99	99.65	34	138 (1)	66.39 (1)	42	128 (1)	134.5 (1)	25

vations of *V. mertensi* pursuing and capturing live grasshoppers, small lizards and fish jumping up a waterfall suggests that the species' eyesight is acute. Likewise, our observation of an individual capturing several live fish in a waterhole suggests that the eyesight of *V. mertensi* is equally effective underwater. Our observations of a submerged individual flushing an unsighted crab from under a rock and another catching crabs in their burrows suggests that *V. mertensi* is equally adept at seeking out unsighted prey. In a similar manner, Thompson (1995) described how *V. gouldii* was able to locate mole crickets and spiders hidden in burrows by means of olfactory cues. The use of both olfactory and visual cues to detect prey is common in terrestrial varanids (Traeholt 1993; Christian 1995; Thompson 1995) but *V. mertensi* seems to use these same senses very effectively in an aquatic environment.

Interestingly, *V. mertensi* was rarely observed pursuing and capturing healthy fish within the aquatic environment. Although we did observe *V. mertensi* on three occasions to catch fish, on only one occasion was an individual observed pursuing and capturing slow-moving healthy eel-tail catfish (*Neosilurus* sp.) within a waterhole. The other two observations were of fish that were either dying or had restricted movement (e.g. fish negotiating a waterfall or dying from the effects of herbicide). Hermes' (1981) observation of *V. mertensi* capturing fish confined within a small drying pool, when added to our data, indicates that *V. mertensi* is able to adapt its foraging strategies to take advantage of the various ways in which potential prey present themselves.

Very few of a large number of dying fish flowing down irrigation channels during herbicide injections were consumed by *V. mertensi*. Long-term decaying carrion baits used in treadle-activated traps also failed to attract *V. mertensi* (unpublished observations). Our data suggest that *V. mertensi* will eat live fish when they can be caught, but are reluctant to eat long-term decaying dead fish or carrion. In a captive situation or around areas of human activity (e.g. caravan parks, camping areas), *V. mertensi*, like other large goannas, will readily learn to eat dead fish and cooked meat scraps (authors' observations).

Our observations suggest that *V. mertensi* concentrates its foraging either in the water (usually along the benthos) or along the bank–water interface, but it will occasionally forage the riparian vegetation fringing irrigation channels or waterholes. The bank–water interface represents an area of high concentrations of active crab burrows along irrigation channels. *V. mertensi* foraging along this interface can search for freshwater crabs by probing active burrows while simultaneously remaining vigilant for potential prey movement in nearby vegetation.

Our observation of an individual successfully capturing numerous fish negotiating a waterfall combined with anecdotal evidence reporting similar foraging behaviour by *V. mertensi* on other occasions (P. Raftery, personal communication) suggests that these goannas are capable of drawing on previous prey capture success to increase their foraging efficiency. This capacity to recall previous feeding experiences was also shown during feeding trials conducted on *V. salvator* (Traeholt 1993). Sweet and Pianka (2003) provide a range of examples to demonstrate that the capacity of varanids to learn by prior experience is probably better than that for most reptiles and our examples provide additional supporting evidence of this ability.

Other than for a single example of using a 'sit-and-wait' strategy to catch fish negotiating a waterfall, which we believe was atypical of the foraging behaviour of *V. mertensi*, *V. mertensi* is predominately an active forager and, in this regard, is similar to many other aquatic and terrestrial varanids, the exceptions being several large species such as *V. komodoensis* (Auffenberg 1972, 1978), *V. bengalensis* (Auffenberg 1983) and *V. griseus* (Tsellarius *et al*. 1997) and the small saxicolous species *V. glebopalma* (Sweet 1999) that have been shown to use predominately 'sit-and-wait' foraging tactics to capture prey items.

Diet of *V.* mertensi

Varanus mertensi in the East Kimberley and the Northern Territory (Shine 1986) eat a diverse range of soft and hard-bodied items, most of which are found around the water's edge. There were minor differences in prey groups identified in the stomachs of *V. mertensi* in the East Kimberley and the Northern Territory (Shine 1986). Prey groups that were not found in the diet of *V. mertensi* in the East Kimberley included Hemiptera (bugs), Hymenoptera (ants), Brachyura (shrimps), Aves (birds) and Serpentes (snakes). Prey groups not reported by Shine (1986) that we found in the diet of *V. mertensi* in the East Kimberley included Decapoda (red claw), Nepoidea (water bugs), Agamidae (dragon lizards), caterpillars (unidentified larvae), carrion and fruit. These differences are probably an artefact of small sample sizes in both studies. These data suggest that *V. mertensi* is opportunistic, feeding on all available invertebrate and vertebrate prey that it can catch and subdue in its local environment. Owing to this opportunism we would anticipate that *V. mertensi* encountering cane toads would almost certainly prey upon small toads, a suggestion further supported by our findings and the findings of Shine (1986) which identified frogs in the diet of *V. mertensi*.

This study and that of Shine (1986) indicate that freshwater crabs (*Holthuisana*) are the predominant component of the diet of *V. mertensi*. The prevalence of freshwater crabs in the diet of *V. mertensi* in the East Kimberley probably reflects prey availability rather than selective feeding. Crab abundance along irrigation channel banks was as high as 1.7 ± 0.27 burrows m^{-1}. Given that individual goannas will forage up to 1 km along an irrigation channel during a day's activity (unpublished data), crabs on channel banks present a significant potential prey source. Angelici and Luiselli (1999) also

reported that the diet of the semi-aquatic *V. niloticus* consisted mainly of locally abundant crabs found throughout the Niger Delta. Interestingly, fewer crabs were consumed by *V. mertensi* examined from the Western Australian Museum collection (Shine 1986) than in specimens we examined from the East Kimberley (Table 1). This difference is probably due to the higher local abundance of freshwater crabs in areas where *V. mertensi* was captured in this study.

Most prey consumed by *V. mertensi* originate from either the aquatic or riparian zone. This is similar to that reported for other semi-aquatic varanids. For example, Shine (1986) reported that *V. mitchelli* fed predominately on fish in Northern Australia, *V. semiremex* fed predominately on crustaceans in Northern Australia (Bustard 1970; James *et al.* 1992), *V. salvator* fed predominately on crustaceans in undisturbed areas of Malaysia (Losos and Greene 1988; Gaulke 1991) and *V. niloticus* fed predominately on crabs (Angelici and Luiselli 1999) in the Niger Delta and molluscs in Cameroon (Lonnberg 1903).

Most prey items consumed by *V. mertensi* were relatively small in comparison with the body size of an adult, with the four largest individual prey items consumed by *V. mertensi* (decreasing in size) being a mouse, small fish, crabs and reptile eggs. Although the individual wet mass of each prey item was not measured, it would appear that a large prey item, such as a mouse, weighing approximately 15–20 g, would represent only 0.6% of the body mass of an average adult *V. mertensi* (~2 kg). This represents a much smaller proportion than that reported for single dietary items of some other varanids. For example, *V. panoptes* has been reported to consume *V. gouldii* totalling 11% of its body mass (Christian 1995), an adult *V. varius* (weighing 20.4 kg) was reported to regurgitate four fox cubs, three small rabbits and three large blue-tongued lizards (Fleay 1950). *V. giganteus* is capable of consuming large vertebrate prey (King *et al.* 1989) such as possums (*Trichosurus arnhemensis*), bandicoots (*Isoodon auratus*) and young euros (*Macropus robustus*), and *V. komodoensis* has been reported to consume large vertebrate prey including domestic animals such as goats and pigs (Auffenberg 1981, 1994).

Stomach contents and scat samples

Stomach contents samples provide a more comprehensive appreciation of the diet of *V. mertensi* than do scats. This is due to soft-bodied prey being more completely digested, and only hard indigestible prey fragments passing into the faeces. Despite this, scats are still a useful source of data on the diet of *V. mertensi* because of the ease of sampling compared with stomach flushing.

Acknowledgments

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