

## Correspondence

## Observations of feeding behaviour of an *Oxyrhopus melanogenys* (Serpentes: Dipsadidae): description of a novel prey-processing manoeuvre

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Being obligate predators of large-bodied prey, the vast majority of snakes share the same basic feeding mechanism: that of consuming prey whole, aided by the extreme kinesis skull bones (CUNDALL & GREENE 2000). This liberates snakes from the necessity of processing prey prior to ingestion, i.e., chewing, tearing, or breaking the prey item apart (GREENE 1997). In fact, examples of snakes employing any behaviour that could be interpreted as, or associated with, processing prey are extremely rare. *Storeria* (Natricidae) and *Pareas* (Pareatidae) forcibly extract snails from their shells in order to consume only the meaty part of the animal (ROSSMAN & MYER 1990, GÖTZ 2002), as is the case with tropical snail-eating snakes of the subfamilies Dipsadinae and Pseudoxyrhophiinae sensu ZÄHER et al. 2009 (SAZIMA 1989, ROSSMAN & MYER 1990). In the Asian crab-eating watersnakes *Fordonia* and *Gerarda* (Homalopsidae), the snakes tear the legs off crabs. This behavioural adaptation allows these homalopsid snakes to ingest prey of body sizes in excess of their own (JAYNE et al. 2002). It places Homalopsidae on par with large constrictors of the family Boidae, which have been documented to ingest prey of up to 160% of their own body mass (GREENE 1997). This capability is owed to the boas' method of prey capture/dispatch by means of constriction (GREENE 1997), which they share with approximately nine percent of genera in the Colubroidea (SHINE & SCHWANER 1985, ZÄHER et al. 2009). While prey-to-predator body ratios of this magnitude are thus known from the Boidae, if and when such ratios can be achieved by colubroid snake families remains understudied both in the wild and ex situ (GREENE 1997).

The genus *Oxyrhopus* is a fairly typical representative of the subfamily Xenodontinae (Dipsadidae) from the humid tropics of South America. These snakes have been docu-

mented as consuming a wide variety of prey, with a slight predilection for lizards, at least in seven Amazonian forest-dwelling species in the genus (ALENCAR et al. 2013). The by far most common taxon of this genus is *Oxyrhopus melanogenys* (TSCHUDI, 1845), and it has been shown to be amongst the most opportunistic species of *Oxyrhopus* (DUELLMAN 1978, 2005, ALENCAR et al. 2013).

On 01 July 2013, the herpetological monitoring team of Fauna Forever encountered an *O. melanogenys* in the process of ingesting a mouse (*Mus musculus*). This night walk was actually geared towards the protocols of the mammal monitoring team (PERES 1999), who were in want of extra data, but was derailed by the following observation, which took place between 21:01 h and 22:13 h at the Amazon Research and Conservation Center (ARCC), Las Piedras Province, Madre De Dios Department, Peru (12°03'8.2" S, 69°40'18.3" W, 230 m a.s.l.). Edited highlights of the videos taken of this event can be viewed online at <http://vimeo.com/amazonacademy/oxyrhopusmelanogenysfeeding/>.

Upon first encountering the snake, only part of the mouse's head had been ingested, indicating that the snake had only recently started to consume the mouse, and it was obvious that the mouse was dead, presumably having been killed by means of constriction. Deep folds and creases were visible on the mouse's body in the expected position for a constricted animal (Fig. 1A; GREENE & BURGHARDT 1978), although the snake's body was relaxed and nearly uncoiled, presumably having disengaged from the mouse's body after the initial feed response.

After three minutes had passed, during which the snake was nearly motionless except for the normal movements of the jaws (CUNDALL 1983), the snake began to shift its posture radically, possibly in response to feeling disturbed by the observers, but due to the coordinated and repeated

nature of the ensuing behaviour, we do not consider this a major factor. The snake would throw the entire posterior portion its body towards its head and form a coil around the prey item as it was now consuming it. Successive coils would be wrapped around the mouse until almost the entire body of the snake was involved in compressing the mouse to a smaller size (Fig. 1B). The movement of the coils indicated that they were exerting considerable pressure on the body of the subdued animal. The most obvious interpretation was that the snake was processing the mouse's body in order to fit it into its mouth, an action that turned an animal of great mass relative to the snake into a prey item that could be swallowed more readily.

It is very interesting to note how these coils were positioned. In general, the first coil would be made around the snake's head or even just posterior around the neck (Fig. 1C). As is shown in the video, there are even instances of the first coil being reinforced by a second (Fig. 2A) when even more pressure had to be exerted on the snake's head. While it seems that this pressure would be directed at the snake's feeding apparatus, it should be noted that the coils are not wrapped around the mouse's body (Fig. 1C).

Therefore these coils and the coiling behaviour are not an attempt to constrict the animal. Coils involved in constriction are aimed at mid-body and will also tend to roll the prey item over many times (GREENE & BURGHARDT 1978). In this instance, however, the mouse basically remained in the same position throughout.

Over the course of 72 minutes, the snake repeatedly executed the same manoeuvre. Even though at least one coil was slung around the mouse most of the time, there were distinct periods in which the snake appeared essentially motionless, and some or all of its coils would relax in their positions. This happened at a rate of once every 2.0–2.5 minutes in a series of distinct movements punctuating what would otherwise appear as normal snake feeding behaviour and thus a process wholly separate from the normal faculties of a snake of the subfamily Xenodontinae (CUNDALL 1983, POUGH & GROVES 1983).

As the mouse was transported farther and farther down the snake's gullet, less and less of the snake's body was free to take part in the manoeuvre. In the earliest instance visible in the video, as many as four coils of the body can be seen to be aiding the ingestion of the mouse. In some of the



Figure 1. Prey-processing by *Oxyrhopus melanogenys*: (A) note the relaxed coil around the mouse's feet; (B) two coils midway through the manoeuvre; (C) note the coil position on the snake's neck. Photo C: ABBEY THIBEAULT.

last shots, only one coil is involved, with the entire tail lying to the side. After 53 minutes into the process, we saw the final instance, at which point the hind limbs of the mouse were inside the snake's mouth. At this point, the snake's normal deglutition took over, and no further assistance by the posterior portion of its body took place. In all, this prey-processing manoeuvre was repeated more than 20 times, although our initial observation of a single coil lying loosely around the mouse's feet (Fig. 1A) indicates that the snake might have been busy processing the prey prior to our discovering it.

Photographic documentation of this event was extensive and included the use of a tailor's tape as a scale for measuring the animals. One photo (Fig. 2B), taken with an Apple iPhone 4S built-in camera, depicts more than half the snake's body on the same plane as the scale object, and when viewed at 50% zoom, allows near-perfect one-to-one scaling. This somewhat inaccurate method suggests the snake to be 56 cm ( $\pm 2$  cm) and the mouse nearly 8 cm long, although its nose is not visible inside the snake's mouth. See Table 1 for all relevant measurements.

As far as the question of mass is concerned, that of the snake can be deduced from existing data for mass relative to length. *Oxyrhopus melanogenys* of similar sizes weigh around 37 g (Fig. 3, B. CRNOBRNA unpubl. data). For the

mass of the mouse, we are fortunate enough to have available a wealth of data recorded from the very same site by means of three pitfall traps that were set up on the same trail and run for a period of five months prior to the feeding event. *Mus musculus* was the second most frequent mammal caught in these traps ( $n = 34$ ), and the average weight of adult individuals was 26.7 g ( $n = 22$ ,  $SD = 6.73$ , range = 19–41). The frequency of *M. musculus* captures in this array was higher than at any other site investigated in Las Piedras ( $n = 7$ ) in which buckets of suitable dimensions (60 l) for catching small mammals were employed (H. WILLIAMS unpubl. data), perhaps owing to the abundance of food available at the site in the form of numerous *Astrocaryum* palm trees (the nuts of which can be seen in the video; see also CORNEJO & JANOVEC 2010). Thus, we can expect this mouse to have been in good physical condition, and based on its anogenital distance, it was most likely a female with an above-average weight (EMMONS 1997).

Given these figures we can see that in this instance an *Oxyrhopus melanogenys* consumed a prey item of 75% or more of its own mass. The ingested mouse would come to occupy 10 cm, or 18% of the snake's total length (Fig. 2C). At 10 cm it was not "stretched" to a great extent (2 cm), but we cannot say if this was a result of the snake "compressing" the mouse's body mass. A soft-bodied prey item like



Figure 2. Initial and final relative positions of the animals observed at ARCC on 01 July 2013: (A) doubled coil; (B) 20% reduction; (C) "stretched" mouse in the snake's stomach compared to its total length. Photo A: ABBEY THIBEAULT; B, C: CORA CHAN.

Table 1. Measurements of animals observed at ARCC on 01 July 2013.

	Measurements
<i>Oxyrhopus melanogenys</i>	
Snout–vent length (cm)	46
Total body length (cm)	56
Approximate weight (g, see Fig. 3)	37
<i>Mus musculus</i>	
Head and body length (cm)	7.7
Hind foot length (cm)	2.8
Tail length (cm)	6.6
Ear length (cm)	0.9
Average weight ARCC pitfalls (g)	26.7

this would escape the “durophagy” category proposed by SAVITSKY (1983). Whether or not this manoeuvre would have a similar effect on the more solid musculature and tough skin of a lizard – the other more commonly consumed *O. melanogenys* prey type – is unclear.

SAZIMA & MARTINS (1990) described the prey processing by a wild *Oxyrhopus guibei* that was fed a mouse of inordinate size. Although they lacked the detail afforded us by complete video documentation, they described a process not too dissimilar to what we documented at ARCC, and may well have witnessed first indications of prey processing just by presenting the mouse to the snake – one of the first clues that such behaviour exists (P. VENEGAS pers. comm., see GREENE 1997: 65). This is the first time this process has been described for *Oxyrhopus* almost completely, and may well be the first and only instance in which pre-ingestion processing of a mammalian prey item has been documented in any colubroid snake. The cases of snail-eating and the two homalopsid species mentioned above represent the only detailed accounts available, but our suspicion is that such processes are only awaiting description in other snakes as well.

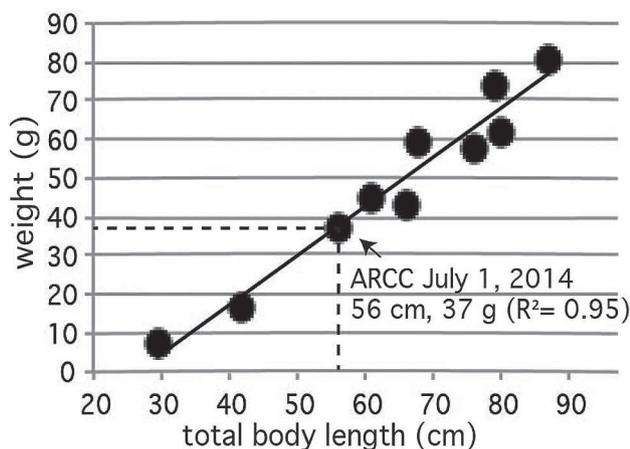


Figure 3. All *Oxyrhopus melanogenys* weight measurements taken by Fauna Forever 2009–2014 (B. CRNOBRNA unpubl. data;  $n = 9$ , SD 23.5, range 7–81).

This process, as it exists in the distantly related Boidae, is not so well defined due to the obvious problem of distinguishing it from normal feeding behaviour involving large prey. Although *Oxyrhopus* spp. are colubroids that constrict their prey (SAZIMA & MARTINS 1990, ANDRADE & SILVANO 1996) our observation is one of a facultative process that is separate from constriction as a means to dispatch prey, and different from the continuous process of striking, constricting, and ingesting that can readily be observed in any boid snake. We do not believe this to be merely a subtle difference. For one, the constriction process employed by colubroids has been inferred as having evolved separately from that of large constrictors according to the criteria assessed by WILLARD (1977). As can be seen in the photos, the ventral scales are orientated posteriorly to the mouse. The clarity in this instance of the manoeuvre being facultative is a second point. Had this particular snake captured a smaller prey item we can safely assume that it would not have engaged in this manoeuvre, considering the well-documented lack of this behaviour in Xenodontinae (MARTINS & OLIVEIRA 1998, DUELLMAN 2005, ALENCAR et al. 2013).

A full feeding behaviour study was performed by ANDRADE & SILVANO (1996) in which captive *Oxyrhopus guibei* were presented with suitable food items and their response behaviour was observed. From the outset, it is clear to see how such a study would be ill suited to reveal the behaviour we observed at ARCC. The study was aimed at clarifying whether *O. guibei* would consume the different types of prey items it was presented with. They made no reference to their mass, and the authors would be in a predicament testing the upper limit of prey mass that their *Oxyrhopus* would consume: a) the captive snakes would not necessarily strike and respond to a feed cue when faced with excessively large prey (DE VOSJOLI 2004) that could potentially be a risk for depredation on the snake; b) even if the captive snake attempted to feed on an oversized prey item, the energy required for ingesting and digesting it could result in multiple physiological problems that could ultimately result in the snake's death (see DE OLIVEIRA NOGUEIRA et al. 2014 for a most pertinent example). ANDRADE & SILVANO (1996) reported that *Oxyrhopus* of varying life stages use the body to assist with feeding, but did not describe the behaviour of adults or make any mention of the significance of such behaviour either.

The significance of this behaviour to the study of snakes is as follows:

The described behaviour allows *Oxyrhopus melanogenys* to ingest prey of inordinate body size, thus removing them from the category of “gape-limited” predators. The ramifications of this separation would extend to studies of morphology and the biomechanics of feeding (HAMPTON 2011) for all species capable of executing this manoeuvre.

This behaviour would allow *O. melanogenys* to access a wider variety of prey and enter the ecological niches of predators that would more readily and effortlessly take prey of such size (e.g., the Amazon tree boa, *Corallus hortulanus*), representing a concomitant increase in trophic

level. This should be observable in ecological data sets for any species capable of such manoeuvres.

The ability of *O. melanogenys* to ingest prey of this size would likely have to co-evolve with a suite of physiological traits that allow them to digest prey of excessive size. If not, then the existence of this behaviour may foil any arguments that prey size limitation should result in corresponding limitations to metabolic physiology (GILOOLY et al. 2001) in an ectotherm.

Because of these and other challenges to the path of herpetological study preceding this discovery, we implore on all those interested in studying snake feeding behaviour to take a closer look at this phenomenon in the lab and in the field, and in as many other species as possible.

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