Flexibility in feeding behaviour may compensate for morphological
constraints of fossoriality in the amphisbaenian *Blanus cinereus*

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Abstract. Morphological adaptations for burrowing, such as an elongated body, and a small head may constrain feeding behaviour in fossorial reptiles. We experimentally examined the effect of prey type on prey capture and handling behaviour of the amphisbaenian *Blanus cinereus*. This amphisbaenian showed four different handling modes according to the characteristics of each prey type. When prey diameter was narrower than gape-size, prey were consumed without prey processing; when prey diameter was wider than gape-size, *B. cinereus* shifted handling mode to prey processing. Amphisbaenians scraped or tore off bite-sized pieces of large prey and showed longer handling times for some prey types than most epigeal saurians. Flexibility in feeding behaviour may allow amphisbaenians to exploit variable underground trophic resources, overcoming constraints of morphological adaptation to fossoriality.

Keywords: Prey preparation, handling mode, handling time, fossoriality, Amphisbaenia.

Several reptile lineages are adapted to live underground and all show morphological adaptations to fossoriality such as elongated bodies, reduced limbs and small narrow heads that enhanced burrowing capacity (Gans, 1974; Navas et al., 2004). However, these adaptations may restrict feeding capacity because, for example, bite performance will decrease in animals with narrow heads (Andrews et al., 1987; Vanhooydonck et al., 2011). Generalist predatory reptiles capture prey that differs in size, shape, hardness and defensive behaviour and mouth circumference (gape) may restrict the upper size limit of suitable prey (Demarco et al., 1985; Schwenk, 2000). Small prey can be swallowed whole, but larger prey or prey that is able to defend itself may require specific modes of prey reduction (Cooper, 1981; Jayne et al., 2002; Measey and Herrel, 2006).

Amphisbaenians are highly adapted to a burrowing life-style and information on feeding behaviour is based upon preliminary observations (Gans, 1974); there are no detailed analyses of prey-handling behaviour. The amphisbaenian *Blanus cinereus*, found in Mediterranean areas of the Iberian Peninsula (Busack, 1988; Salvador, 1981), is an opportunistic predator that feeds on soil invertebrates, mainly insect larvae and ants (López et al., 1991; Gil et al., 1993). We examined the effect of prey type on prey capture and handling behaviour of *B. cinereus* in the laboratory and specifically tested whether it demonstrates flexibility in feeding behaviour and whether prey type and prey size affect characteristics of its predatory behaviour.

We captured 14 adult male and 11 adult female *B. cinereus* near Torreldones (40° 35' N, 3° 56' W; Madrid Province, Spain) in March 2010. Amphisbaenians were housed individually at "El Ventorrillo" Field Station (Navacerrada, Madrid Prov.) in 5 l glass terraria containing sand substrate from the capture area. Ambient temperature was constant (20° C) and the photoperiod was natural. Individuals were fed a diet of live larvae, pupae and adult arthropods twice weekly and humidity was maintained by spraying the sand daily with a manual water spray. All animals were acclimatized to laboratory conditions and

experimenter's presence for at least one month before testing. To standardize hunger levels, individuals were not fed for one week prior to the experiment. All the amphisbaenians were healthy during the trials, and they were released at their exact point of capture at the end of the experiments.

Fossorial conditions were simulated by using transparent plastic tubes (30 cm length x 1.3 cm external diameter x 1.1 cm internal diameter) containing sand in the lower half and with the ends closed with cotton (one tube for each individual) (López and Salvador, 1992; López and Martín, 2001). The diameter of the tube was slightly wider than that of amphisbaenians (around 7 mm on average), so that tubes simulated soil galleries (i.e. the tube walls were in contact with the amphisbaenian's body) while allowed movements and feeding behaviour of amphisbaenians inside them. Individuals were kept in their tubes for six hours every day during the acclimatization period; during this period they showed normal behaviour (i.e. they stand still with their bellies resting on the substrate or walked with a continuous slow forward concertina movement from one end of the tube to the other) and were fed the same prey types used later in the experiment. The rest of the day, amphisbaenians were maintained in their house terraria.

Observations were made between 0930 and 1730 h from April to September. We used seven prey types in feeding experiments; adult ants (*Pheidole pallidula*), ant pupae, coleopteran larvae and pupae, spiders, isopods, and earthworms (Table 1). We introduced each individual amphisbaenian into its tube 5 min before each trial. A prey item was then placed in a random relative orientation approximately 5 cm in front of the amphisbaenian's snout. We observed behaviour from about 50 cm distant, in a darkened laboratory illuminated by a 50-W red light. Ambient temperature was between 19.8 and 23.5 °C, within the activity range of this species (i.e. mean selected temperatures ranged between 17.8 and 23.6 °C; Martín et al., 1990; López et al., 1998). Each individual was tested only once with each prey type in random sequence and we conducted one trial per day for each

animal separating trials by at least a week. We ended trials after consumption of the prey had finished or after 30 min since the prey was introduced in the tube if no attempt of capture was observed. Thus, not all amphisbaenians ate all prey types, and the sample size for each prey type represented the number of different individual amphisbaenians that ate that particular prey type. For this reason, we were not able to obtain similar sample sizes of males and females for each treatment and we decided to pool observations of both sexes. Nevertheless, we did not expect to find large intersexual differences, if any, because sexual dimorphism in head size is very small in this species (Gil et al., 1993).

Using a ruler, we measured with snout-to-vent length (mean $\pm$ SE = 163 ± 5 mm), and with digital callipers measured, to the nearest 0.1 mm, jaw length (mean $\pm$ SE = 5.0 ± 0.1 mm) from tip of the snout to mouth commissure and jaw width (mean $\pm$ SE = 4.3 ± 0.1 mm) between the commissures. We measured prey size (maximum width, length and height), calculated prey width/amphisbaenian jaw width (relative prey size; 'RPS') (Mori, 1991) and calculated prey volume (approximation to the volume of an appropriate geometrical shape for each prey type; see López et al., 1991) for each trial.

We recorded: 1) 'Latency to first bite' to the nearest second; 2) 'capture position': (part of the prey's body initially bitten: anterior [head and neck], middle, posterior, total body, or extreme [for prey without differences between anterior and posterior portions; e.g., earthworms, ant pupae]); 3) 'direction of prey ingestion' (extreme first [anterior or posterior], midbody first, or total body; 4) 'number of bites'; 5) 'handling behaviour', including whether prey was consumed in one or several actions with pauses during which prey was released, whether prey was completely eaten, whether assistance was needed from the walls or substrate to strike or swallow prey, and whether or not prey was violently shaken. When prey was struck but not consumed, some data were not obtained.

We measured 'total handling time' as the time in seconds elapsed between the moment prey was successfully grasped and the instant when the amphisbaenian closed its

jaws completely for the first time after the prey had disappeared from view. Total handling time included all pauses occurring during the process while the prey was being handled. However, in some cases the amphisbaenian stopped handling, released temporally the prey in the middle of the handling process and returned later to continue ingestion. Then, we calculated 'partial handling time' excluding time when the prey was released and not handled. Statistical significance was assessed using tests described either in Siegel and Castellan (1988) or Sokal and Rohlf (1995); alpha was 0.05.

Four methods of prey-handling behaviour were defined based on these observations:

1. "*Single Swallow*" (*SS*): Amphisbaenians approach prey and direct a fast attack bite, capturing the whole prey into the mouth. Prey are ingested in one single action, violently shaken while being held in the mouth, and then rapidly swallowed.

2. "*Intermittent Swallow*" (*IS*): Amphisbaenians slowly consume whole prey with 0 to six pauses (mean $\pm$ SE = 0.8 ± 0.3 pauses) until the prey is completely swallowed. Largest prey items are killed by knocking them against the walls of the tube.

3. "*Cut and Swallow*" (*CS*): prey are crushed and divided with bites along the body. Then completely consumed piece by piece. In one case an amphisbaenian coiled around a prey item.

4. "*Scrape*" (*S*): Prey are bitten, the jaws inserted inside the prey's body, and the body contents ingested, leaving only the prey's exoskeleton as a remain. In some cases (24.5%), amphisbaenians ingested the exoskeleton at the end of the scraping process. In *IS*, *CS*, and *S* modes, amphisbaenians press prey against the tube walls with their heads.

Prey size varied with prey-handling mode; RPS (Kruskal-Wallis test, $H = 32.71$, $P < 0.01$) and prey volume ($H = 35.84$, $P < 0.01$) differed significantly between prey-handling modes. *S* and *CS* prey handling modes were used with significantly larger prey (*S*: RPS, mean $\pm$ SE = 1.01 ± 0.09 ; volume = 172 ± 31 mm³; $n = 11$; *CS*: RPS = $0.89 \pm$

0.15; volume = $199 \pm 52 \text{ mm}^3$, $n = 7$) (pairwise multiple comparison, $P < 0.01$) than with other modes (*IS*: RPS = 0.64 ± 0.04 ; volume = $89 \pm 13 \text{ mm}^3$; $n = 30$; *SS*: RPS = 0.22 ± 0.04 ; volume = $2 \pm 1 \text{ mm}^3$, $n = 14$). *SS*-handled prey had both the lowest RPS and volume ($P < 0.01$).

Prey type also influenced prey-handling mode (Table 1). Amphisbaenians employed single-swallow with only ants and spiders, whereas earthworms were always eaten with the intermittent swallow technique. Other prey types were consumed using more than one prey-handling mode. *IS*-handled coleopteran larvae were significantly smaller than *CS*-handled larvae (RPS, 0.64 ± 0.05 vs. 0.97 ± 0.15 respectively; Mann-Whitney U-test, $U = 1.92$, $P = 0.002$).

Capture positions differed with RPS ($H = 30.23$, $P < 0.001$) and prey volume ($H = 36.38$, $P < 0.001$). Prey struck interiorly were significantly larger (RPS = 1.05 ± 0.11 ; volume = $246 \pm 28 \text{ mm}^3$; $n = 5$) than those grasped at other positions (pairwise tests, $P < 0.05$ in all cases). Prey which were ingested in a single bite had the smallest size (RPS = 0.22 ± 0.04 ; volume = $2 \pm 1 \text{ mm}^3$; $n = 14$) ($P < 0.01$). There were no significant differences in the size of prey captured by other positions ($P > 0.05$) (middle: RPS = 0.78 ± 0.06 ; volume = $123 \pm 20 \text{ mm}^3$; $n = 28$; posterior: RPS = 0.62 ± 0.14 ; volume = $104 \pm 45 \text{ mm}^3$; $n = 5$; extreme: RPS = 0.64 ± 0.07 ; volume = $78 \pm 14 \text{ mm}^3$; $n = 10$).

Direction of ingestion varied with RPS ($H = 22.58$, $P < 0.001$) and prey volume ($H = 26.97$, $P < 0.001$). Midbody-ingested prey were significantly larger (RPS = 0.93 ± 0.11 ; volume = $170 \pm 30 \text{ mm}^3$; $n = 12$) than prey swallowed extreme first (RPS = 0.74 ± 0.05 ; volume = $114 \pm 18 \text{ mm}^3$; $n = 31$) or total body swallowed (RPS = 0.23 ± 0.05 ; volume = $2 \pm 1 \text{ mm}^3$; $n = 11$) (pairwise tests, $P < 0.01$). Total body swallowed prey had the smallest RPS ($P < 0.01$).

Bite number (Pearson's correlation, $r = 0.70$, $P < 0.0001$, $n = 54$) and partial handling time (excluding time spent in pauses) increased exponentially with prey volume

($r = 0.82$, $P < 0.0001$, $n = 54$) (fig. 1), as did total handling time ($r = 0.68$, $P < 0.0001$, $n = 54$). This relation was also obtained separately for prey types (excluding adult ants and spiders) with a wide volume range: ant pupae ($r = 0.63$, $P < 0.05$, $n = 10$), coleopteran larvae ($r = 0.78$, $P = 0.001$, $n = 17$) and pupae ($r = 0.52$, $P < 0.05$, $n = 8$), isopods ($r = 0.92$, $P < 0.05$, $n = 3$) and earthworms ($r = 0.79$, $P = 0.02$, $n = 8$).

Partial handling times of different prey types were significantly different, after correction for volume (ANCOVA, covariation handling time with volume: $F_{1,46} = 147.44$, $P < 0.0001$; prey effect: $F_{6,46} = 3.87$, $P = 0.002$). Coleopteran larvae and pupae required the longest handling times (Table 1). Also, the residuals of the regression between handling time and prey volume (see fig. 1) differed significantly between prey types ($F_{6,47} = 6.11$, $P = 0.0001$), suggesting that coleopteran larvae and pupae, isopods and adult ants required relatively longer handling times than expected by their volume, while ant pupae, earthworms and spiders required relatively shorter handling times than expected.

Partial handling times were also significantly different between prey-handling modes after correction for prey volume (ANCOVA, covariation handling time with volume: $F_{1,49} = 130.52$, $P < 0.0001$; prey-handling mode effect: $F_{3,49} = 4.93$, $P < 0.005$). CS-handled prey required the longest handling times, whereas SS-handled prey required the shortest handling times.

The amphisbaenian *B. cinereus* uses different prey-handling modes depending upon specific prey type characteristics and appears to follow the swallowing threshold model (Kaspari, 1990) that predicts prey will be reduced only when it is beyond the capacity of the forager to swallow it whole. If prey diameter is narrower than gape-size prey are consumed without reduction; prey may be ingested by a single swallow if short (ants and spiders) or swallowed with pauses if elongated (earthworms, coleopteran larvae). When prey diameter is wider than gape-size handling mode shifts to prey reduction.

Amphisbaenians show some mechanical adaptations allowing them to pierce and tear prey and most species have interlocking conical teeth at the tip of the snout. Occluding tooth rows enable biting pieces from larger prey (Gans, 1974; Malkmus, 1991; Goetz, 2007). Similarly, instead of swallowing a prey whole, crab-eating snakes tear off bite-sized pieces of crabs (Jayne et al., 2002). Many amphisbaenian species also twist to tear loose the grasped portion after achieving a bite (Gans, 1974), which is similar to the long-axis body rotations of caecilians when feeding underground (Measey and Herrel, 2006; Herrel and Measey, 2012).

The "scrape" feeding mode used by *B. cinereus* is not exclusively related to gape-size because ant pupae and isopods are narrower than the jaws of the amphisbaenian. The exoskeleton of these prey types is, however, hard and rigid (Herrel et al., 2001), and scraping may increase the nutrient concentration of the prey through removal of low-quality parts (Kaspari, 1990). This feeding method might be explained by the occluding tooth rows of amphisbaenians, which would enable to bite pieces off larger prey (Gans, 1974; Goetz, 2007), and extended chewing of food (Malkmus, 1991).

Headfirst capture by epigeal saurians may favour rapid prey ingestion with an apparent advantage in ingestion time (Diefenbach and Emslie, 1971). It may also prevent prey retaliation (Kardong, 1982), and could be advantageous in the capture of large and rapid prey items (Cooper, 1981). The observed variability in capture position by *B. cinereus* can be accounted for by adaptations for underground foraging, while we used experimental tunnels wider than the amphisbaenian diameter. Amphisbaenians and their prey were able to move in these galleries, but there was less space in these tunnels than normally available to epigeal saurians. When an amphisbaenian moves toward a prey, it will make first contact with the part of the prey facing it, which is likely randomly determined and selection of a specific part of prey item would require additional tunnelling cost. Similarly, for example, on first contact with a prey item, caecilians are unable to

determine their relative prey size, and may use spinning to estimate it based on the feedback on the amount of spin force required (Measey and Herrel, 2006). Also, semifossorial coral snakes *M. corallinus* capture and inject venom into any part of the body of their prey when they find them underground, but the snakes have to drag prey to the surface to better handle them and maximize head-first ingestion (Marques and Sazima, 1997).

Prey characteristics may also explain capture position. Many soil invertebrates in the diet of *B. cinereus* (López et al., 1991) have elongated bodies and little differentiation between front and rear. Invertebrates consumed are slow, and while headfirst capture in this case would not be particularly beneficial in most cases (Cooper, 1981), it would be beneficial if the prey is also potentially dangerous to the predator. Encounters between *B. cinereus* and elongated prey in narrow tunnels should favour capture position by extremes.

Blanus cinereus demonstrates handling times for some prey types than seem longer than for most epigeal saurians (Avery et al., 1982; Demarco et al., 1985; Paulissen, 1987; Herrel et al., 2001; Verwaijen et al., 2002), although at low body temperatures handling times for epigeal saurians can also be long (Avery and Mynott, 1990). Moreover, if we considered handling time in relation to head size, handling times for many prey types are similar to those of lacertid lizards (Herrel et al., 2001; Verwaijen et al., 2002).

Nevertheless, for some particular prey types, such as coleopteran larvae and pupae and isopods, handling times seem especially longer, which may be explained by the large size of these prey in relation to the amphisbaenian head size, by the high hardness of these prey types (Herrel et al., 2001), and by the elaborated feeding behaviour used that requires additional handling modes such as cutting and scraping the prey before swallowing.

The ability to detect potential predators is diminished during prey consumption and epigeal saurians, while feeding, can be detected visually or chemically by terrestrial or aerial predators and an increase in handling time would increase risk of predation. Predator

detection of, and access to, amphisbaenians is difficult underground and amphisbaenians may risk longer handling times for subduing prey. Pough and Andrews (1985) suggested that costs of subduing and swallowing for lizards can be ignored for most ecological purposes, but longer handling times observed in *B. cinereus* may reflect low metabolic requirements related to fossoriality (Withers, 1981; Kamel and Gatten, 1983) and suggests that handling costs in amphisbaenians should be re-examined.

Because unspecialized diet and behavioural flexibility *B. cinereus* can feed on a wide variety of invertebrates (López et al., 1991). This flexibility in feeding behaviour may allow amphisbaenians to exploit variable trophic underground resources, overcoming the constraints of morphological adaptation to fossoriality.

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Table 1. Size (mean $\pm$ SE; range between brackets) of prey eaten by *B. cinereus* ($n = 60$, including entirely and partially eaten prey), percentage of each prey type consumed by each prey-handling mode (SS, single swallow; IS, intermittent swallow; CS, cut and swallow; S, scrape) and partial handling time (s; mean $\pm$ SE) for prey entirely eaten.

Prey	n	Length (mm)	Width (mm)	Volume (mm ³)	Prey-handling mode				Handling time (s)
					SS	IS	CS	S	
Ants:									
Pupae	10	9 $\pm$ 1 (7-11)	3 $\pm$ 1 (2-4)	92 $\pm$ 14 (34-138)	-	70	-	30	95 $\pm$ 16
Adults	10	3 $\pm$ 1 (3-4)	1 $\pm$ 1 (1-2)	1 $\pm$ 1 (1-2)	100	-	-	-	35 $\pm$ 6
Coleoptera:									
Larvae	17	14 $\pm$ 1 (5-25)	3 $\pm$ 1 (1-5)	141 $\pm$ 30 (8-398)	-	65	35	-	725 $\pm$ 234
Pupae	8	14 $\pm$ 1 (10-18)	5 $\pm$ 1 (4-5)	241 $\pm$ 16 (196-314)	-	25	-	75	589 $\pm$ 119
Spiders	4	4 $\pm$ 1 (2-5)	2 $\pm$ 1 (1-2)	4 $\pm$ 1 (0.1-6.2)	100	-	-	-	35 $\pm$ 8
Isopods	3	7 $\pm$ 1 (5-8)	3 $\pm$ 1 (2-3)	21 $\pm$ 7 (8-28)	-	33	-	66	262 $\pm$ 38
Earthworms	8	29 $\pm$ 3 (18-40)	2 $\pm$ 1 (1-2)	73 $\pm$ 14 (19-126)	-	100	-	-	153 $\pm$ 62

341 **Figure 1.** Relationship between $\log_{10}$ transformed prey volume (mm^3) and partial handling
342 time (s) (excluding time spent in pauses) of the amphisbaenian *B. cinereus*. The different
343 symbols represent the different prey types (see legend).

344

345 Fig. 1

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