
Feeding behaviour in monitor lizards and snakes; does direction of prey ingestion influence prey handling time?

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ABSTRACT — Food ingestion was studied in Rat Snakes *Elaphe obsoleta*, Corn Snakes *E. guttata*, King Snakes *Lampropeltis getulus*, Hognose Snakes *Heterodon nasicus* and in monitor lizards (*Varanus* sp.). In most instances the prey items were ingested headfirst except in the Hognose Snake (*H. nasicus*) where direction of ingestion was more random. In all cases headfirst ingestion was shown to be the most efficient method in terms of the time taken to consume the prey item.

FEEDING dynamics in reptiles may be influenced by many factors, for example the size of the prey item, its shape, the body temperature of the reptile at the time of feeding and apparently even experience in prey handling (e.g. Halloy & Burghardt, 1990). One of the many similarities between snakes and monitor lizards is the development of cranial kinesis and subsequent capacity to swallow, proportional to their head and body size, large food items, particularly in snakes. However, feeding on large prey items is time consuming and fraught with problems in respect to risk of injury from predators or from the food animal itself. It might therefore be expected that evolutionary adaptation should have been in a direction that maximises rate of consumption whilst simultaneously minimising risk of injury. In this paper we give details of observations on prey handling in a group of captive snakes and monitor lizards. The study was designed to address the following questions: 1) what is the frequency of headfirst ingestion, and 2) does headfirst ingestion reduce prey-handling time? The results presented here were part of a first year Higher National Diploma research project at Huddersfield Technical College that was undertaken between September 2001 and June 2002.

METHODS AND MATERIALS

Three individual African monitor lizards of three species, *Varanus niloticus*, *V. albigularis* and *V. exanthematicus* were used in the project. All attain

large adult size feeding on any animal matter (including carrion) they can overpower (Bennett, 1998). The lizards were fed a series of dead rats and mice presented at right angles to the body of the lizard - in the sense that neither head nor tail was in closer proximity to the reptiles head. The snakes species used in the project were, with numbers of individuals in parenthesis, King Snakes *Lampropeltis getulus* ($n = 2$), Rat Snakes *Elaphe obsoleta* ($n = 4$), Corn Snakes *Elaphe guttata* ($n = 4$) and Hognose Snakes *Heterodon nasicus* ($n = 2$). All are North American forms (Conant, 1975). They were offered dead mice of varying sizes, again presented at right angles to the long body of the snake with both the direction and time taken for ingestion recorded using a stopwatch, which commenced when the subject seized the prey and ceased when the prey was swallowed and out of sight, including the rodent's tail. Direction of ingestion was recorded as either head or tail first. The results for the monitor lizards were recorded using the same method.

The food animals were weighed on digital scales with an error of + 0.1g. This was recorded just before being offered to the reptiles. The body masses of the food animals was: *Elaphe* sp. 10.1-39.7g (mean = 23.5g); *H. nasicus* 3.3-31.8g (mean = 8.9); *L. getulus* 16.30-24.5g (mean = 19.4g); *V. albigularis* 5.3-305g (mean = 165.9g); *V. exanthematicus* 15.3-47.6g (mean = 29.2g); *V. niloticus* 19.1-307.0g (mean = 193g).

Statistical analysis. Percentage frequencies of direction of ingestion in each reptile group were compared using an *h*-test of corresponding percentage *x* values by finding,

$$h = x_1 (n_1) - x_2 (n_2)$$

where x_1 and x_2 are the *x* values of the observed percentages of samples n_1 and n_2 . When the compared sample sizes were uneven, degrees of freedom (N') were found from,

$$N' = (2n_1n_2) / (n_1 + n_2)$$

where n_1 and n_2 are the sample sizes for the respective data sets. For N in even sample sizes degrees of freedom was simply obtained from, $N = (n_1 + n_2)/2$. To correct for different prey sizes on the time to ingest food the simple formula was applied,

$$C_{It} = (M_1 / (M_2)M_{2t})$$

where C_{It} the corrected ingestion time was calculated from M_1 the body mass of the largest prey item ingested in each sample, M_2 the body mass of the prey animal being consumed and M_{2t} the time taken to consume M_2 .

RESULTS

Snakes – Rat and corn snake (*Elaphe* spp.) data were pooled on the basis that the species have similar lifestyles and feeding habits (Conant, 1975). Figure 1 shows that this group ingested prey items headfirst 82% and hognose snakes (*H. nasicus*) head first 30% of the time with the difference between the two highly significant ($h = 1.099$, $P < 0.01$, 31.7 d.f.). The king snakes *L. getulus*, showed a 57% head first ingestion which was not significantly different either from *Elaphe* spp. ($h = 0.5540$, $P > 0.05$, 11.6 d.f.) or *H. nasicus* ($h = 0.552$, $P > 0.05$).

Monitor lizards – Frequency of headfirst ingestion of prey in monitor lizards is also shown in Fig 1. Headfirst ingestion was observed in *V. albigularis* 50% ($n = 10$) and in *V. niloticus* 70% of the time ($n = 14$). The percentage difference between the two was not significant ($h = 0.4110$, $P > 0.05$, d.f. = 11.66). Bosc's monitor *V. exanthematicus*,

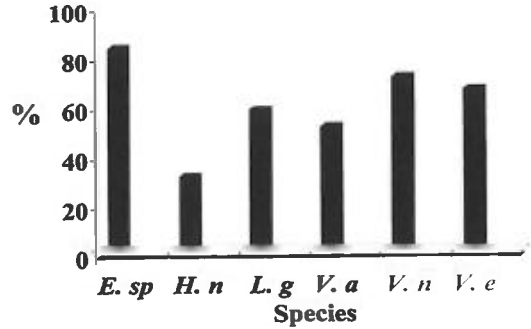


Figure 1. Histogram showing comparative frequencies of headfirst food ingestion in snakes and monitor lizards. The data are expressed as percentage frequencies of headfirst ingestion as opposed to either tail or mid body first ingestion. The x-axis labels are *E. sp* = *Elaphe obsoleta* and *E. guttata*, *H. n* = *Heterodon nasicus*, *L. g* = *Lampropeltis getulus*, *V. a* = *Varanus albigularis*, *V. n* = *Varanus niloticus* and *V. e* = *Varanus exanthematicus*. See text for further details.

swallowed headfirst 65% of the time ($n = 39$) which was not significantly different from either *V. albigularis* ($h = 0.304$, d.f. = 20.6) or *V. niloticus* ($h = 0.107$, d.f. = 15.9). A test for possible influences of Q_{10} effects on prey handling time in *V. niloticus* and *V. albigularis* using a multiple regression, with body temperature and prey size treated as independent variables and the time taken to consume the prey as the dependent variable, showed that in both species prey size was found to be of greater significance in determining handling time (*V. niloticus*, $P < 0.02$; *V. albigularis*, $P < 0.002$) than body temperature (*V. niloticus*, $P = 0.27$; *V. albigularis*, $P = 0.91$).

Comparing head and tail first ingestion

Snakes – When corrected for size effects the mean time taken to consume prey head first in *H. nasicus* was 32.5 seconds (SD = 47.1 seconds), with the tail first mean 139.1 (SD = 164.2) with the difference significant at the 90% interval ($F_{1,18} = 3.14$, $P = 0.09$). In *E. obsoleta* and *E. guttata* mean time taken to consume food head first was 158.1 seconds (SD = 113.9) with the

mean for tail first 290.4 seconds (SD = 288.5). The difference between means was significant at the 90% interval ($F_{1,27} = 2.91$, $P = 0.10$). Headfirst ingestion was quicker in *L. getulus* (mean = 32.5, SD = 47.1) than tail first (mean = 139.1, SD = 164.2) and significant at the 90% interval $F_{1,18} = 3.14$, $P = 0.093$.

Monitor Lizards – When corrected for size, mean time to ingest food head first in *V. exanthematicus* was 0.24 ± 0.57 seconds and when taken tail first 0.26 ± 0.21 seconds. Analysis of variance showed no significant difference between the data sets $F_{1,37} = 0.03$, $P > 0.05$. In *V. albigularis* mean time to consume food headfirst was 0.62 ± 1.7 seconds and tail first 1.11 ± 1.0 seconds with the difference not significant $F_{1,9} = 0.20$, $P > 0.05$.

DISCUSSION

The results of this study have shown that in most of the animals under observation there was a strong preference for headfirst ingestion, which resulted in shorter handling time. The exception was in the Hognose Snake, *H. nasicus*, which appeared to ingest in a more random fashion but even in this species swallowing prey head first reduced handling time. Headfirst ingestion should be adaptive for several reasons, particularly if the prey is a mammal with fur or a bird with feathers, since swallowing headfirst must reduce resistance and hence energy cost. Faster ingestion should also render the animal less vulnerable in a chance encounter with a predator - a reptile with a large object in its mouth has little means of defence, and also reduce the risk of accidental damage with headfirst ingestion since the limbs of the prey species are at an angle less likely to cause damage. In general our results were in good agreement with Loop (1974) who found significantly shorter feeding times with headfirst ingestion at the 90% interval and with one of the few studies undertaken in the field, where the gopher snake (*Pituophis catenifer*) was observed to consume most prey items (88.5%) headfirst (Rodríguez-Robles, in press).

The direction of ingestion in snakes may be influenced by the direction of attack (Diefenbach & Emslie, 1971; Cooper, 1981) and vary with the

size and/or the age of the snake (Mori, 1996). The more random direction of ingestion in *H. nasicus* possibly involves a natural diet of frogs and toads, which are almost spherical in shape and may inflate with air in an attempt to prevent ingestion. Therefore there may be no pre-adapted behaviour for dealing with fur or feather direction in this species. Evolutionary considerations have been cited as an influence on feeding behaviour in other snake species. For example, Mori (1996) found that snakes that are generalist feeders are less efficient in rodent feeding than endothermic prey specialists. Mori further suggested that prey handling in young snakes is learnt and becomes more proficient as they grow to adulthood. Several studies have indicated that prey type may influence the way snakes consume their food (e.g. Loop & Bailey, 1972; de Queiroz, 1984) and have a cost benefit basis. In the Viperine Snake (*Natrix maura*), the cost of capturing and handling the prey – which increases exponentially with fish size, and the energy value of the prey – which increases linearly with fish size, results in prey with the highest profitability being selected (Davies et al., 1980). Direction of ingestion in some snakes may be related to prey type and the number of items consumed in succession (Stafford, in press) whilst the direction of scale overlap apparently acts as a cue for prey ingestion in ophiophagus snakes (Greene, 1976).

Prey handling time has been found to increase exponentially with decreasing body temperature in the lizard *Lacerta vivipara* (Avery & Mynott, 1990) and a similar relationship was observed in certain skinks (e.g. Andrews, et al., 1987; de Queiroz et al., 1987; de Queiroz & de Queiroz 1987) although interestingly not in *Chalcides chalcides* (de Queiroz et al., 1987). The somewhat limited body temperature ranges experienced by our monitor lizards during the project may explain the lack of a significant association between food consumption and temperature – a wider body temperature range might have produced different results. It is also important to remember that all prey items used in this project were dead when offered to the reptiles, live prey might have produced significantly different responses.

ACKNOWLEDGEMENTS

We thank Dr. Roger Avery, Peter Stafford, and Roger Meek our project supervisor for critical comments on the manuscript. Brenda Mills the Herpetological Unit's animal technician provided valuable support throughout the project work.

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