# Attack strategy of an ambush predator: which attributes of the prey trigger a pit-viper's strike?

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**Summary**

**1.** Why do larger predators generally consume larger prey items? Endemic pit-vipers (*Gloydius shedaoensis*) on a small island in north-eastern China ambush passerine birds, usually from the branches of small trees. Both minimum and maximum prey sizes increase with predator size.

**2.** To clarify the reasons for this ontogenetic shift, 251 snakes in ambush postures were approached and offered potential prey items (dead birds, or models covered in feathers) to clarify the cues that trigger a foraging strike.

**3.** The snakes struck at the prey item in 101 of these trials, and this 'decision' was influenced by the size, movement and temperature of the prey item. A pit-viper's body size influenced its prey-size selectivity, with larger snakes refusing to strike at smaller prey items. Larger snakes also scavenge dead birds too large for smaller snakes to ingest, but do not ignore live birds: even the largest snakes use prey movement and prey temperature as cues to elicit feeding strikes.

**4.** The ontogenetic shift in prey size thus reflects a combination of processes. The absence of large prey from the diet of small snakes is due to gape-limitation (these snakes strike and attempt to swallow much larger prey). The absence of small prey items from the diet of larger snakes is due to active refusal to strike at small prey, as well as a behavioural shift to scavenging and to terrestrial rather than arboreal ambush-sites (and thus, higher rates of encounter with large prey items) by larger pit-vipers.

*Key-words*: Foraging, predator body size, prey size, snake, thermoreception

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## Introduction

Most animals feed selectively, and hence need to discriminate between objects that are or are not acceptable as food (Schoener 1971; Caraco & Gillespie 1986; Greene 1986; Arnold 1993; Nakano, Fausch & Kitano 1999). These dietary decisions define the trophic niche of the organism, and have significant implications for ecological processes at many levels (Holling 1966; Charnov 1976). For example, an animal's foraging decisions may affect not only its individual energy budget, but also the nature and outcomes (competitive exclusion, coexistence, etc.) of interactions between sympatric taxa (Stephens & Krebs 1986; Vitt 1987; Arnold 1993). Dietary composition can vary enormously even among individuals within a population, and among populations within a single species (e.g. Auffenberg 1981; Kephart & Arnold 1982; Nakano *et al*. 1999), but the reasons for this diversity remain unclear for most kinds of organisms. Mathematical

modelling of optimal feeding tactics has generated many predictions (Pyke, Pulliam & Charnov 1977), but also has stimulated considerable scepticism (Krebs & McCleery 1984; Greene 1986; Perry & Pianka 1997). An alternative way to gain insight into the foraging tactics of animals is to work at the mechanistic level. If we understand the proximate criteria that animals use in discriminating between 'accepted' and 'rejected' potential food items, we may then be able to clarify the ecological and evolutionary bases to those criteria.

One widespread pattern among predators is a trend for larger individuals to take larger prey items. This can be seen not only in comparisons among species, but also among populations of different mean body sizes within a single species, and even among individuals of different body sizes within a single area (Mushinsky 1987). Because populations of ectothermic vertebrates typically include individuals of a very wide range of body sizes (Pough 1980), they provide some of the best examples of intrapopulational correlations between prey size and predator size (e.g. Arnold 1993). Gape-limited organisms that feed on relatively large prey offer particularly good model

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systems for investigations of this topic, because juvenile predators are physically unable to ingest larger prey and, hence, ontogenetic shifts in prey size are the norm rather than the exception. For example, many studies on macrostomatan snakes have revealed strong ontogenetic shifts in prey size (Greene 1997). Such size-related shifts may have major ecological implications: for example, prey-size distributions can influence body-size distributions of predators (e.g. Madsen & Shine 1993) or the degree of sexual dimorphism in mean adult body size or feeding structures (Slatkin 1984; Houston & Shine 1993).

Although a correlation between predator body size and prey size has been reported in many taxa, the reasons for it generally remain untested. Gape-limitation offers an obvious possibility, but cannot explain cases in which minimum as well as maximum prey sizes increase with predator body size (Arnold 1993). Alternatively, ontogenetic shifts might reflect size-related changes in the predator's ability to capture, kill and digest prey of different sizes, rather than simply to ingest it. Another possibility is that larger predators actively select larger prey items and refuse (or fail to recognize) smaller ones, perhaps because optimal prey sizes increase for larger predators (Pyke *et al*. 1977). Lastly, predators may change their foraging tactics as they grow larger, perhaps relying on different methods of prey capture (e.g. mobile searching foraging *vs* ambush predation: Taylor 1984) or moving to different habitats where they encounter a different size spectrum of available prey (Houston & Shine 1993; Sinclair & Arcese 1995).

To test these hypotheses about the proximate behavioural and ultimate ecological reasons for prey size increase with predator body size, we need detailed information not only on the composition of the diet but also on predator behaviour and prey availability. For example, presentation of prey of different sizes to predators in natural foraging situations can directly test the proposition that larger predators actually ignore (or do not sense) small prey rather than simply not encountering them, or being unable to capture them. We can also quantify the cues used to elicit foraging strikes, and compare smaller and larger predators in this respect. Such studies are difficult to conduct with free-ranging vertebrates, for logistical reasons. However, we have worked with a terrestrial vertebrate that functions as a model research system for such studies: an ambush-foraging pit-viper that occurs in high densities on a small island and readily tolerates close approach by humans (Li 1995; Shine *et al*. 2002). Although laboratory-based studies have examined the types and intensities of cues used by captive pit-vipers during feeding episodes (e.g. Duvall, Scudder & Chiszar 1980; Kardong 1986; Kardong & Mackessy 1991), there have been no detailed studies of prey selection by free-ranging snakes (but see Hayes & Duvall 1991). Field data are essential to evaluate the validity of results from laboratory-based research (Chiszar, Smith & Radcliffe 1993).

## Materials and methods

### STUDY AREA AND SPECIES

Shedao is a small ($0.73$ km$^2$) island in the Bohai Sea, 13 km off the coast of the Liaodong Peninsula in north-eastern China (Li 1995). Shedao lies on one of the main migration routes for passerine birds that spend winter in southern Asia and summer in Siberia. Thus, many birds pass through Shedao during migration periods in spring and autumn. The endemic pit-viper *Gloydius shedaoensis* exploits this seasonal food resource, and attains high population densities (>1 snake/m$^2$ in some areas: Huang 1989; Li 1995). Adult Shedao Pit-vipers are relatively large (average snout–vent length, SVL = 65–70 cm) and have no natural predators (Li 1995). The snakes are inactive for most of the year, but during two brief bird-migration periods (May and September–October) they can be found in ambush postures over much of the island. Most snakes lie in wait on the branches of small trees, with the forebody coiled in a concertina fashion so that they can strike forward rapidly if a bird lands on the branch in front of them (Li 1995; Shine & Sun 2002; see Fig. 1). Other Shedao Pit-vipers utilize terrestrial ambush sites, and take birds that are active on the ground. Many birds that are struck by snakes escape before dying, and are scavenged by larger snakes (Li 1995).



**Fig. 1.** The experimenter presenting a dead bird to a Shedao Pit-viper (*Gloydius shedaoensis*) in typical ambush pose.

Pit-vipers can potentially detect endothermic prey with specialized infrared (thermal) receptors, as well as by other sensory modalities such as vision and chemoreception (de Cock Buning 1983).

### METHODS FOR DIETARY ANALYSIS

Adult Shedao Pit-vipers feed almost exclusively on passerine birds (Li 1995). All of the taxa consumed are broadly similar in overall body shape, facilitating comparison of prey sizes. Pit-vipers are gape-limited predators and, thus, the most important determinant of maximum ingestible prey size is likely to be the maximum chest diameter of the prey item (Cundall 1987; Greene 1997). Chest diameter is also highly correlated with prey mass, a measure of the nutritional benefit available from consuming a particular prey item (regression of chest diameter *vs* ln prey mass for 17 birds on Shedao: $r = 0.94$, $P < 0.0001$). To document prey species and sizes, we retrieved birds that we saw being seized by snakes (if a snake was disturbed, it commonly would release the bird). We also estimated chest diameters of birds that had been recently ingested by snakes. Recency of ingestion could be determined by palpation, and maximum diameter estimated from the diameter of the snake's swollen midbody. In five cases where we measured dead birds and then placed them out to be eaten by snakes, we could assess the accuracy of this technique. Bird diameters measured inside snake stomachs were always within 3 mm of the diameter recorded prior to ingestion.

### METHODS FOR IDENTIFYING FORAGING CUES

Because the snakes readily tolerate close approach, we could expose them to a range of prey stimuli by presenting objects to snakes in foraging poses in the field. The stimuli that we used were either dead birds (of a variety of species and sizes) or artificial models. Many natural strikes by pit-vipers on Shedao are unsuccessful, with the bird escaping after being struck (R. Shine & L.-X. Sun, personal observation). As a result, it is common to find freshly dead or dying birds on the island. We used this sample (supplemented by birds that we saw being struck by snakes, as above) as stimuli for our foraging trials. The artificial models were round in shape and 30 mm in diameter. Each model consisted of a water-filled balloon inside a short length of nylon material (the foot from a woman's stocking). Feathers from dead birds were glued to the stocking with craft glue, which was then allowed to dry overnight before use. Strikes by pit-vipers generally punctured the balloon, which was thus replaced between trials.

All behavioural trials were conducted between 07.00 and 16.00 hours over the period 3–16 May 2000, and on snakes that were located in foraging poses (stationary, with forebody in concertina shape). The same

observer (RS) presented the stimulus in each case (Fig. 1). The bird or model was attached to a 50-cm length of fishing line (3 kg test) on the end of a 1.9-m fibreglass fishing rod. The stimulus was brought towards the snake, and dangled 5–10 cm in front of the snake's head. Over the next 60 s, the 'target' was either held still, or moved about (one vertical up-and-down motion, approximately 3 cm in extent, every 1–2 s) to simulate a live bird. The observer recorded the number of tongue-flicks over that period (see Burghardt 1968), whether or not the snake struck at the 'target', and the latency to strike. To avoid pseudoreplication, we attempted to expose each snake to only a single trial. Because snakes were not individually marked, a few individuals may have been tested more than once. Given the extraordinary abundance of pit-vipers on Shedao, however, this inadvertent re-testing would have been very rare.

Using this simple technique, we examined the ways in which snakes responded to prey size and to prey movement and temperature.

### Prey size

We offered the snakes dead birds of a range of body sizes, divided into three classes. We used three warblers (two *Phylloscopus inornatus* and one *P. proregulus*) as 'small' birds (15–17 mm chest diameter, 5–6 g). A Great Tit (*Parus major*) and a Rufous-tailed Robin (*Erithacus sibilans*) were used as 'medium' birds (27–30 mm, 12–14 g). Only one 'large' bird was available (Gray Nightjar, *Caprimulgus indicus* 55 mm, 98 g). The smaller species are well within the size range of birds consumed by Shedao Pit-vipers, whereas the nightjar was too large to ingest (Table 1, Fig. 2). Initial analyses revealed no significant differences in snake responses to replicate individuals within each size class, and thus the data have been pooled for analysis (i.e. we report only size-class effects). We recorded snake size as a categorical variable (juvenile, <50 cm SVL, or adult, >50 cm SVL; Li 1995).

### Prey movement and temperature

Because scavenging is an important source of large birds for large pit-vipers (see below), an ontogenetic shift in prey sizes might reflect a trend for larger snakes to search for dead rather than live birds. If so, we might expect that cues indicating that a bird was alive (movement and warmth) would be less important in eliciting strikes from adult than from juvenile pit-vipers. To test this prediction, we manipulated both of these variables:

1. The prey item was either held still in front of the snake's head, or moved about throughout the 60-s observation period to mimic a bird's behaviour.
2. We filled the balloons with either warm (35 °C) or cold (10 °C) water. To maintain water temperature,

**Table 1.** Birds recorded to have been killed and/or eaten by Shedao Pit-vipers, during fieldwork in May 2000. In some cases the bird was recovered from the snake that was swallowing it, for identification. In other cases we found dead or dying birds that had escaped after being bitten. A few of these were too large to be ingested by snakes, but most of the others undoubtedly would have been consumed by scavenging snakes (as shown by trials where we placed some of these birds out and recorded their later consumption). Hence, we score them below as 'eaten'

| | | | Number of birds | |
| Common name | Scientific name | Mean chest diameter (mm) | Killed | Eaten |
| --- | --- | --- | --- | --- |
| Northern Sparrowhawk | *Accipiter nisus* | 58 | 4 (+1*) | 0 |
| Common Quail | *Coturnix coturnix* | 44 | 1 | 1 |
| Yellow-legged Button-Quail | *Turnix tanki* | 52 | 1* | 0 |
| Rock Pigeon | *Columba livia* | 50 | 1 | 0 |
| Gray Nightjar | *Caprimulgus indicus* | 55 | 1 | 0 |
| Brown Shrike | *Lanius cristatus* | 31 | 2 | 1 |
| Siberian Blue Robin | *Erithacus cyane* | 28·5 | 2 | 2 |
| Rufous-tailed Robin | *Erithacus sibilans* | 28 | 1 | 1 |
| Blue Rock Thrush | *Monticola solitaria* | 36 | 1 | 1 |
| Radde's Warbler | *Phylloscopus schwarzi* | 26 | 3 (+1*) | 4 |
| Inornate Warbler | *Phylloscopus inornatus* | 16·8 | 5 | 5 |
| Lemon-rumped Warbler | *Phylloscopus proregulus* | 18 | 2 | 2 |
| Great Tit | *Parus major* | 30 | 1 | 1 |
| Meadow Bunting | *Emberiza cioides* | 28 | 1 | 1 |
| Little Bunting | *Emberiza pusilla* | 26 | 5 | 5 |
| Yellow-breasted Bunting | *Emberiza aureola* | 33 | 5 | 5 |
| Black-faced Bunting | *Emberiza spodocephala* | 23 | 1 | 1 |
| Bunting spp. | *Emberiza* spp. | 30·3 | 3 | 3 |

*Bitten but not killed.
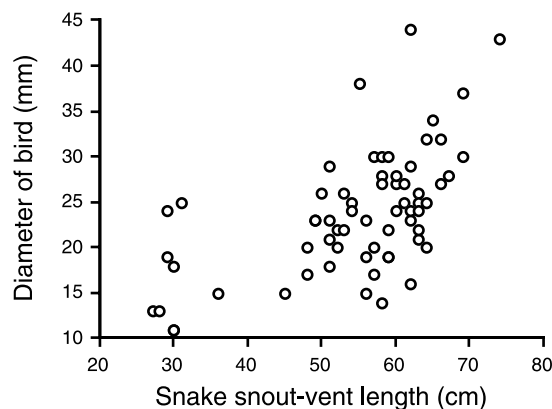


**Fig. 2.** The body sizes (chest diameter, mm) of birds ingested by Shedao Pit-vipers, relative to the body size (snout–vent length, cm) of the snake that consumed them.

the balloons were carried inside a folded hot-water-bottle in the field prior to use. Although the internal temperature of the 'warm' model was thus >30 °C, the insulating effect of the feathers substantially reduced external (surface) temperature. We used a Raytek 3I-LRSCL2 (Sauta Cruz, CA) infrared thermometer to measure surface temperatures of models and live birds (as captured in mist nets on Shedao). Bird (feather) temperatures ranged from 14·7 to 27 °C (mean ± SD = 18·65 ± 3·04 °C, *n* = 13), depending on local weather conditions. The surface temperature of the 'warm' model ranged from 18 to 22 °C, whereas the 'cold' model followed ambient air temperature (generally 10–15 °C).

## Results

### DIETARY COMPOSITION

We recorded 42 birds (belonging to 17 species of natural prey items) that were bitten by Shedao Pit-vipers (Table 1). Three of these birds survived until we ceased observing them, although they may have died subsequently. Some of the species that were killed (hawks, pigeons, nightjars) were too large for any Shedao Pit-Viper to swallow. These may have been killed by defensive rather than feeding strikes (see below). Of the remaining taxa, most were ingested by snakes, although not always by the snake that killed them. In several cases we saw small snakes kill birds but fail to swallow them because of gape-limitation. For example, the Common Quail listed in Table 1 was killed at 17.00 hours on 15 May 2000 by a 62-cm SVL snake that spent >60 min attempting to swallow it. We found the quail abandoned the next morning, and it was swallowed by a larger (74-cm SVL) snake later that day. Several of the larger birds found dead on the island had saliva covering their heads and necks, and clearly had been the subjects of unsuccessful swallowing attempts by snakes. Five dead birds that we placed out on the ground were swallowed by snakes over the next 12 h. Thus, scavenging of prey items too large for smaller snakes may be a significant food source for adult pit-vipers.

Although Shedao Pit-vipers of all size classes feed primarily or exclusively on birds (Li 1995), prey sizes increase substantially with snake body sizes. The birds

consumed by large snakes were much larger than those taken by juvenile conspecifics. Minimum prey sizes remained fairly constant until snakes reached sizes around 60 cm, but the largest snakes did not eat small birds (Fig. 2).

### FORAGING TRIALS

Our prey stimuli elicited strikes in 101 of 251 trials (40%). The latency to strike ranged from 1 to 59 s within the 60-s duration of each trial (mean = 18·36 ± 16·65 s, *n* = 101). Tongue-flick rates ranged from 0 to 3 per s (0·33 ± 0·40 flicks s⁻¹, *n* = 101), and the number of tongue-flicks prior to a strike ranged from 0 to 28 (4·74 ± 5·62, *n* = 101). Overall, 84 of the 101 strikes hit the target (83%). The snakes' behaviour confirmed that these were genuine foraging strikes rather than defensive strikes. In other studies where we exposed the snake to a threatening stimulus (close approach by a human or a predatory bird), the pit-vipers exhibited a stereotyped defensive display that involved rapid vibration of the tail-tip, flattening of the body, and snap-and-release strikes (Shine *et al.* 2002). Many snakes fled from these stimuli. In contrast, the snakes exposed to birds or models in the present study rarely tail-twitched, never flattened, never fled, and generally retained hold of the bird (but not the model) after the strike.

To identify cues that elicit the strike, we first performed an overall logistic regression with 'prey' attributes as independent variables and outcome of the trial (strike *vs* not strike) as the dependent variable. This analysis confirmed that all variables tested significantly influenced the snake's foraging decision. Log-likelihood ratio tests revealed that the snake was more likely to strike if the target was smaller rather than larger ($\chi^2 = 44\cdot75$, df = 3, $P < 0\cdot0001$), was warmer rather than colder ($\chi^2 = 10\cdot78$, df = 1, $P < 0\cdot001$), moved during the trial rather than remaining stationary ($\chi^2 = 57\cdot67$, df = 1, $P < 0\cdot0001$), and if the snake tongue-flicked in response to the item ($\chi^2 = 6\cdot48$, 1 df, $P < 0\cdot02$). In order to examine the nature of these effects, we now consider two sets of potential cues: prey size, and traits indicating that a prey item was alive rather than dead.
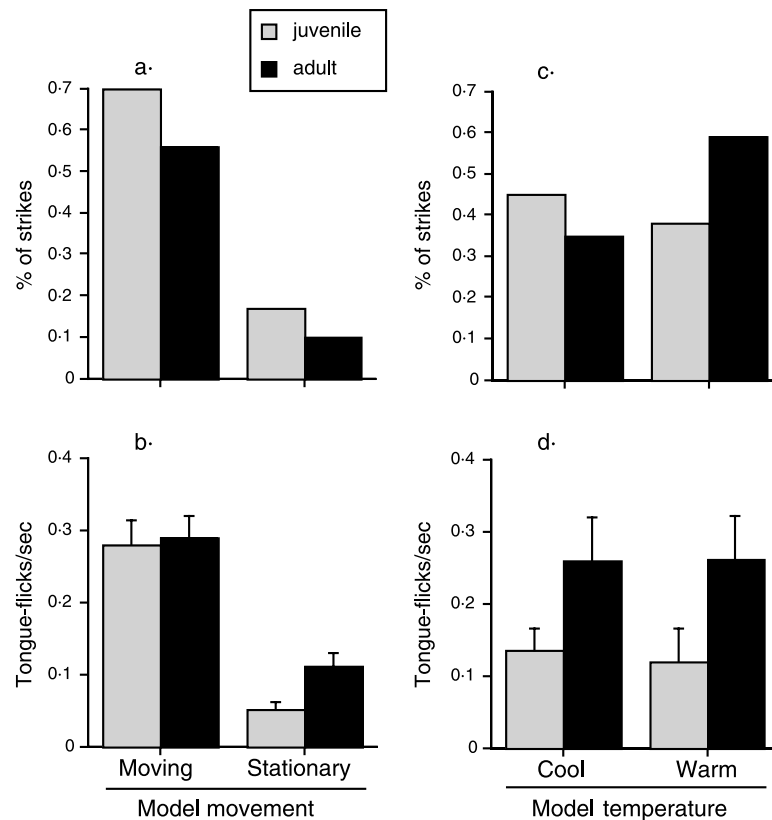
### *Prey size*

We cannot examine the effects of prey size without simultaneously considering the body size of the snake: a 'large' prey item for a small snake will be a 'small' prey item for a large snake. We analysed whether or not the snake struck at dead birds of a range of body sizes (chest diameters 16, 30 and 55 mm). We used only trials in which the dead birds were moved about in front of the snake, rather than remaining still. Trials using artificial models were excluded (these models were all of the same size). Logistic regression on the remaining 101 trials confirmed that smaller birds attracted more strikes ($\chi^2 = 44\cdot44$, df = 2, $P < 0\cdot0001$) and smaller
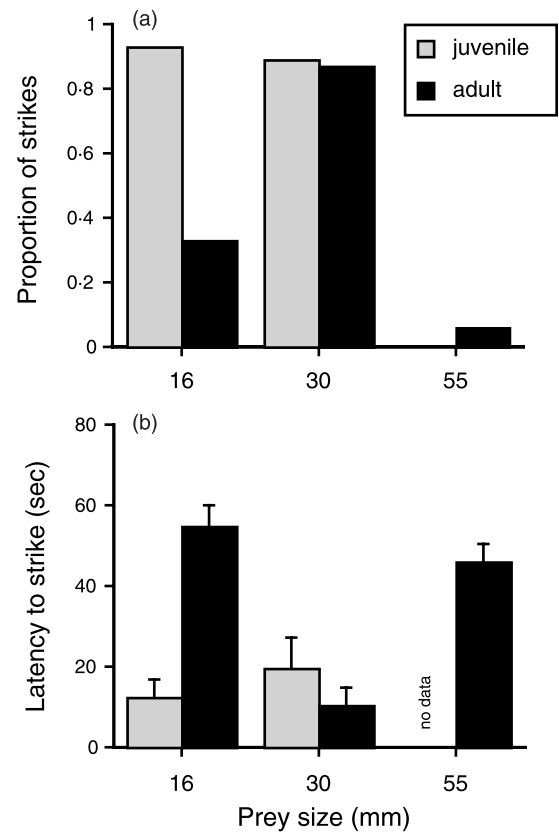
**Fig. 3.** Effects of prey size and snake body size (juvenile or adult) on (a) the proportion of trials resulting in the snake striking the prey item and (b) for those trials in which a strike occurred, the latency to strike since the beginning of the trial. Prey size is expressed in terms of chest diameter (mm). Data are restricted to trials involving dead birds rather than artificial models, and in which the prey item was moved about actively during the trial. See text for statistical analyses of these data. Sample sizes are 14, 24, 18, 23, 5 and 17 trials.

snakes struck more often ($\chi^2 = 8\cdot44$, df = 1, $P < 0\cdot004$). Two-factor analysis of variance (with bird size and snake size as the factors) showed that the latency to strike was also affected by the interaction between snake size and target size ($F_{2,87} = 11\cdot06$, $P < 0\cdot0001$). However, tongue-flick rates were not significantly affected by either variable or by the interaction between them (all *P*-values > 0·05).

Closer inspection reveals the reasons for these significant statistical results. Both juvenile and adult snakes struck in a high proportion of trials involving intermediate-sized (30 mm chest diameter) birds, but not in trials involving very large (55 mm) birds (Fig. 3). Juvenile pit-vipers, but not adults, frequently struck at small (16 mm) birds (Fig. 3). Latency to strike was related to the proportion of trials that resulted in strikes. Combinations of bird and snake sizes that resulted in high attack rates (% strikes) also involved brief latencies prior to the strike (regressing latency *vs* % strikes, *n* = 5, *r* = −0·97, *P* < 0·005). For example, on the rare occasions when large snakes struck at small birds, they did so only after a long delay (Fig. 3).

**Fig. 4.** Effects of snake body size (juvenile or adult), prey movement and prey temperature on the proportion of trials resulting in the snake striking the prey item (upper graphs) and rates of tongue-flicking during those trials, prior to the strike (lower graph). Graphs (a) and (b) show responses to prey that were moved or kept still; sample sizes are 76, 136, 28 and 52 trials. Graphs (c) and (d) show the effects of the temperature of an artificial bird model (a balloon filled with hot or cold water, inside a feather covering) on responses of juvenile and adult pit-vipers. The snakes were more likely to launch a strike if the model was warm rather than cool (c) and juveniles tongue-flicked less often than adults (d); sample sizes are 28, 82, 23 and 22 trials. See text for statistical analyses of these data.

*Prey movement and temperature*

We used logistic regression to evaluate whether the prey item's movement and temperature affected the probability that a snake would strike it. Log-likelihood ratio tests show that adult snakes were more likely to strike if the prey item was moved rather than remaining stationary ($\chi^2 = 41.83$, df = 1, $P < 0.0001$; Fig. 4) and if it was warm rather than cool ($\chi^2 = 6.96$, df = 1, $P < 0.009$; Fig. 4). Juvenile pit-vipers were also more likely to strike prey that was moving rather than stationary ($\chi^2 = 24.96$, df = 1, $P < 0.001$; Fig. 4) but the temperature of the prey item did not affect the snakes' response ($\chi^2 = 0.22$, df = 1, $P = 0.64$; Fig. 4). For those snakes that struck, the latency to strike was not affected by target movement or temperature (two-factor ANOVA, all $P > 0.05$).

Movement also stimulated tongue-flicking, in both adults and juveniles (two-factor ANOVA with snake size group and prey movement as factors; no significant interaction effect or main effect of snake body size; effect of movement, $F_{1,328} = 35.70$, $P < 0.0001$; see Fig. 4). When analysis was restricted to trials using artificial models, adult pit-vipers tongue-flicked more frequently than juveniles ($F_{1,152} = 11.87$, $P < 0.001$; see

Fig. 4) but warm models did not attract any more tongue-flicks than did cool models ($F_{1,152} = 0.03$, $P = 0.85$; interaction, $F_{1,152} = 0.05$, $P = 0.83$).

## Discussion

Both minimum and maximum prey sizes increased with predator body size in Shedao Pit-vipers (Fig. 2), as in many other snake species (Arnold 1993). This pattern raises two questions. First, why does maximum prey size increase in larger snakes: that is, why don't juvenile pit-vipers consume large birds? Second, why does minimum prey size increase: that is, why don't adult pit-vipers consume small birds? These questions can be asked in terms of either proximate or ultimate causation; our data primarily address the former level of explanation.

### WHY DOES MAXIMUM PREY SIZE INCREASE WITH PREDATOR BODY SIZE?

Small pit-vipers might be restricted to feeding on small birds either because of a physical inability to ingest larger prey (gape-limitation), because they actively select smaller birds, or because of ecological or

behavioural features that reduce their rate of encounter with larger birds. In practice, our data identify gape-limitation as the most important factor, because juvenile pit-vipers struck and attempted to ingest large birds. The common occurrence on Shedao of dead birds with their heads covered by saliva (Li 1995) clearly result from unsuccessful swallowing attempts by snakes. Similar behaviour has been reported in captive snakes of a variety of taxa (e.g. Kardong 1986; Forsman & Lindell 1993). Many of the juveniles in our foraging trials were <30 cm SVL, and hence could not ingest a bird >25 mm chest diameter (Fig. 2). Nonetheless, these juvenile snakes readily struck dead birds and artificial models 30 mm in diameter (Fig. 3). The same phenomenon is seen also in adult snakes, where at least three of the bird species that were killed (sparrowhawks, nightjars and pigeons; Table 1) could not have been swallowed by even the largest snake on the island.

Why do the snakes strike at birds that are too large to swallow? The answer probably lies in the difficulty of evaluating prey size precisely. The bird often alights only momentarily on the branch in front of the snake, and its critical dimension in terms of gape-limitation (chest diameter) may be difficult to predict from its silhouette (because birds may have wings partly outstretched, or feathers fluffed out for insulation). Under such circumstances, pit-vipers may benefit from striking at any bird that looks to be approximately the correct size. This phenomenon works only within a limited range of prey sizes, however. In our foraging trials, the snakes essentially ignored prey that were far larger (55 mm diameter) than could possibly be ingested.

### WHY DOES MINIMUM PREY SIZE INCREASE WITH PREDATOR BODY SIZE?

Gape-limitation provides an obvious reason for maximum prey size to increase with snake body size, but does not explain why large pit-vipers (>60 cm SVL) failed to consume small birds (Fig. 2). The answer to this question involves at least three processes:

1. Active selection of large prey. Small birds (16 mm diameter) were seized enthusiastically by juvenile pit-vipers, typically soon after the prey item was introduced to the snake (Fig. 3). In contrast, adult pit-vipers rarely struck at these small targets, and did so only after prolonged exposure (Fig. 3). Similar size-selectivity has been documented in at least one other study of pit-vipers (albeit in captive snakes). Large individuals of two rattlesnake species (*Crotalus atrox* and *C. scutulatus*) tended to reject small prey items, whereas smaller conspecifics did not (Reynolds & Scott 1982).

2. Ambush-site selection. Larger birds on Shedao (such as quails) are often found in terrestrial locations, whereas smaller birds (such as warblers) are usually seen on arboreal perches (R. Shine & L.-X. Sun, personal observation; Shine *et al.* 2002). Arboreal ambush-sites are preferred by juvenile Shedao Pit-vipers, whereas adult snakes more often utilize terrestrial sites (Li 1995; Sun *et al.* 2000; R. Shine & L.-X. Sun, personal observation). This pattern of habitat selection will thus bias encounter rates with birds of different body sizes, with adult snakes encountering small prey items less often than would otherwise be the case. However, this ambush-site selection bias cannot fully account for the absence of small prey items from the diet of large snakes because many small birds also forage on the ground, and because many adult snakes also use arboreal perches (Li 1995; Sun *et al.* 2000).

3. Scavenging. Many of the large birds consumed by adult pit-vipers are taken as carrion, having been killed earlier by snakes too small either to retain the bird until it ceased struggling, or to ingest the bird even if it was retained (Li 1995; R. Shine & L.-X. Sun, personal observation). The terrestrial sites selected by adult snakes may enhance their rates of encounter with dead and dying birds. Again, however, this factor cannot explain the absence of small birds from the diets of adult snakes. Some small as well as large birds escape from snakes before dying (R. Shine & L.-X. Sun, personal observation); and adult pit-vipers strike at cues (warmth and movement) characteristic of live rather than dead birds (Fig. 4). Snakes of many species utilize movement as a cue for attack (Burghardt 1968; Drummond 1979; Ross & Marzec 1990), and laboratory studies have shown that pit-vipers use thermal cues to enhance the accuracy of striking when visual cues are not available (Chiszar *et al.* 1986; Breidenbach 1990).

Thus, although ecological and behavioural shifts (especially, increasing reliance on terrestrial rather than arboreal ambush-sites) may contribute to the observed ontogenetic increase in minimum prey sizes in Shedao Pit-vipers (Fig. 2), the primary cause for this shift is an active refusal of large snakes to strike at small prey (Fig. 3). Optimal foraging theory suggests that such size-selectivity should evolve only if the 'cost' of striking at a small prey item outweighs the nutritional benefit likely to be obtained (Pyke *et al.* 1977; Arnold 1993). Such 'costs' are difficult to identify. Adult pit-vipers have no predators on Shedao (Li 1995). It is unlikely that a small bird could retaliate effectively against a large snake. A strike 'costs' energy and venom, but presumably only a trivial amount compared to the energy gain available from consuming even a small bird (Feder & Arnold 1982). Shedao Pit-vipers require <10 min to ingest small birds (R. Shine & L.-X. Sun, personal observation) and continue to ambush prey after feeding (some snakes in ambush postures contain multiple prey items: Li 1995). Thus, a

single successful strike aimed at a small bird should not impair the snake's ability to continue feeding during the period required for digestion of the first prey item.

One possible 'cost' involves the energy expenditure associated with rapid up-regulation of gut function. Sit-and-wait predatory snakes, which feed infrequently on large meals, typically down-regulate gut function (and thus, total metabolic expenditure) in periods between meals (Secor & Diamond 1995, 1997). The energy cost of rapid up-regulation after feeding, to enable digestion to occur, can exceed one-third of the energy in a meal, even for relatively large meal sizes (Secor & Diamond 1997). The energy content of a small bird may be high enough to warrant up-regulation by a small pit-viper, but too small to justify the same expenditure by a larger snake. Nonetheless, this scenario depends on quantitative aspects of costs relative to benefits, and intuition suggests that a bird in the fangs is always worth two on the branch. Also, many snakes take multiple prey items within a single season, so that any costs of up-regulation would be balanced by benefits from multiple meals.

In conclusion, Shedao Pit-vipers exhibit a strong trend for prey sizes to increase with the body size of the predator. Our data show that this correlation between prey size and predator size reflects a combination of at least three different factors. First, the inability of juvenile pit-vipers to physically ingest large birds generates an ontogenetic increase in maximum prey sizes. Second, the active refusal by adult snakes to strike at small birds means that minimum prey sizes also shift ontogenetically. Third, these processes are exaggerated by ontogenetic shifts in foraging behaviour, with larger snakes selecting ambush-sites that increase their probability of encountering large rather than small birds, and adopting an alternative foraging strategy (scavenging) that provides access mostly to large prey items. Our data also show that free-ranging pit-vipers use a variety of prey-associated cues (involving size, movement and temperature) when 'deciding' to launch a foraging strike, and suggest that information on the proximate determinants of such 'decisions' can clarify the reasons why larger predators consume larger prey.

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### References

Arnold, S.J. (1993) Foraging theory and prey-size–predator-size relations in snakes. *Snakes. Ecology and Behavior* (eds R.A. Seigel & J.T. Collins), pp. 87–116. McGraw-Hill, New York.

Auffenberg, W. (1981) *The Behavioral Ecology of the Komodo Monitor*. University Presses of Florida, Gainesville, FL.

Breidenbach, C.H. (1990) Thermal cues influence strikes in pitless vipers. *Journal of Herpetology* **24**, 448–450.

Burghardt, G.M. (1968) Chemical preference studies on newborn snakes of three sympatric species of *Natrix*. *Copeia* **1968**, 732–737.

Caraco, T. & Gillespie, R.G. (1986) Risk-sensitive foraging mode in an ambush predator. *Ecology* **67**, 1180–1185.

Charnov, E.L. (1976) Optimal foraging: attack strategy of a mantid. *American Naturalist* **110**, 141–151.

Chiszar, D., Castro, C.A., Smith, H.M. & Guyon, C. (1986) A behavioral method for assessing utilization of thermal cues by snakes during feeding episodes, with a comparison of crotaline and viperine species. *Annals of Zoology* **24**, 123–131.

Chiszar, D., Smith, H.M. & Radcliffe, C.W. (1993) Zoo and laboratory experiments on the behavior of snakes: assessments of competence in captive-raised animals. *American Zoologist* **33**, 109–116.

de Cock Buning, T. (1983) Thermal sensitivity as a specialization for prey capture and feeding in snakes. *American Zoologist* **23**, 363–375.

Cundall, D. (1987) Functional morphology. *Snakes: Ecology and Evolutionary Biology* (eds R.A. Seigel, J.T. Collins & S.S. Novak), pp. 106–142. MacMillan, New York.

Drummond, H. (1979) Stimulus control of amphibious predation in the northern water snake, *Nerodia s. sipedon*. *Zeitschrift Fur Tierpsychologie* **50**, 18–44.

Duvall, D., Scudder, K.M. & Chiszar, D. (1980) Rattlesnake predatory behavior: mediation of prey discrimination and release of swallowing by cues arising from envenomated mice. *Animal Behaviour* **28**, 674–683.

Feder, M.E. & Arnold, S.J. (1982) Anaerobic metabolism and behavior during predatory encounters between snakes (*Thamnophis elegans*) and salamanders (*Plethodon jordani*). *Oecologia* **53**, 93–97.

Forsman, A. & Lindell, L.E. (1993) The advantage of a big head: swallowing performance in adders, *Vipera berus*. *Functional Ecology* **7**, 183–189.

Greene, C.H. (1986) Patterns of prey selection: implications of predator foraging tactics. *American Naturalist* **128**, 824–839.

Greene, H.W. (1997) *Snakes. The Evolution of Mystery in Nature*. University of California Press, Berkeley, CA.

Hayes, W.K. & Duvall, D. (1991) A field study of prairie rattlesnake predatory strikes. *Herpetologica* **47**, 78–81.

Holling, C.S. (1966) The functional response of invertebrate predators to prey density. *Memoirs of the Entomological Society of Canada* **48**, 1–86.

Houston, D.L. & Shine, R. (1993) Sexual dimorphism and niche divergence: feeding habits of the arafura filesnake. *Journal of Animal Ecology* **62**, 737–749.

Huang, M. (1989) Studies on *Agkistrodon shedaoensis* ecology. *Current Herpetology in East Asia* (eds M. Matsui, T. Hikida & R.C. Goris), pp. 381–383. Herpetological Society of Japan, Kyoto.

Kardong, K.V. (1986) The strike behavior of the rattlesnake, *Crotalus viridis oreganus*. *Journal of Comparative Psychology* **100**, 304–314.

Kardong, K.V. & Mackessy, S.P. (1991) The strike behavior of a congenitally blind rattlesnake. *Journal of Herpetology* **25**, 208–211.

Kephart, D.G. & Arnold, S.J. (1982) Garter snake diets in a fluctuating environment: a seven year study. *Ecology* **63**, 1232–1236.

Krebs, J.R. & McCleery, R.H. (1984) Optimization in behavioural ecology. *Behavioural Ecology: an Evolutionary Approach*, 2nd edn (eds J.R. Krebs & N.B. Davies), pp. 91–121. Blackwell Scientific, Oxford.

Li, J.-L. (1995) *China Snake Island*. Liaoning Science and Technology Press, Dalian.

Madsen, T. & Shine, R. (1993) Phenotypic plasticity in body sizes and sexual size dimorphism in European grass snakes. *Evolution* **47**, 321–325.

Mushinsky, H.R. (1987) Foraging ecology. *Snakes: Ecology and Evolutionary Biology* (eds R.A. Seigel, N.B. Ford, S.S. Novak), pp. 302–334. Macmillan, New York.

Nakano, S., Fausch, K. & Kitano, S. (1999) Flexible niche partitioning via a foraging mode shift: a proposed mechanism for coexistence in stream-dwelling charrs. *Journal of Animal Ecology* **68**, 1079–1092.

Perry, G. & Pianka, E.R. (1997) Animal foraging: past, present and future. *Trends in Ecology and Evolution* **12**, 360–364.

Pough, F.H. (1980) The advantages of ectothermy for tetrapods. *American Naturalist* **115**, 92–112.

Pyke, G.H., Pulliam, H.R. & Charnov, E.L. (1977) Optimal foraging: a selective review of theory and tests. *Quarterly Review of Biology* **52**, 137–154.

Reynolds, R.P. & Scott, N.J. Jr (1982) Use of a mammalian resource by a Chihuahuan desert snake community. *Herpetological Communities* (ed. N.J. Jr Scott), pp. 99–118. US Department of the Interior, Fish and Wildlife Service, Washington, DC.

Ross, R.A. & Marzec, G. (1990) *The Reproductive Biology of Pythons and Boas*. Institute for Herpetological Research, Stanford, CA.

Schoener, T.W. (1971) Theory of feeding strategies. *Annual Review of Ecology and Systematics* **2**, 369–404.

Secor, S.M. & Diamond, J. (1995) Adaptive responses to feeding in Burmese pythons: pay before pumping. *Journal of Experimental Biology* **198**, 1315–1325.

Secor, S.M. & Diamond, J. (1997) Effects of meal size on postprandial responses in juvenile Burmese pythons (*Python molurus*). *American Journal of Physiology* **272**, R902–R912.

Shine, R. & Sun, L. (2002) Arboreal ambush-site selection by pit-vipers (*Gloydius shedaoensis*). *Animal Behaviour* **53**, 565–576.

Shine, R., Sun, L., Fitzgerald, M. & Kearney, M. (2002) Behavioral responses of free-ranging pit-vipers (*Gloydius shedaoensis*, Viperidae) to approach by a human. *Copeia* **2002**, 843–850.

Sinclair, A.R.E. & Arcese, P. (1995) Population consequences of predation-sensitive foraging: the Serengeti wildebeest. *Ecology* **76**, 882–891.

Slatkin, M. (1984) Ecological causes of sexual dimorphism. *Evolution* **38**, 622–630.

Stephens, D.W. & Krebs, J.R. (1986) *Foraging Theory*. Princeton University Press, Princeton, NJ.

Sun, L., Shine, R., Zhao, D. & Tang, Z. (2000) Biotic and abiotic influences on activity patterns of insular pit-vipers (*Gloydius shedaoensis*, Viperidae) from north-eastern China. *Biological Conservation* **97**, 387–398.

Taylor, J.A. (1984) Ecology of the lizard *Ctenotus taeniolatus*: interaction of life history, energy storage and tail autotomy. PhD Dissertation, University of New England, Armidale, Australia.

Vitt, L.J. (1987) Communities. *Snakes: Ecology and Evolutionary Biology* (eds R.A. Seigel, J.T. Collins & S.S. Novak), pp. 335–365. Macmillan, New York.