

## Why do Juvenile Chinese Pit-Vipers (*Gloydius shedaoensis*) Select Arboreal Ambush Sites?

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### Abstract

Ontogenetic shifts in habitat use are widespread, especially in ectothermic taxa in which juveniles may be an order of magnitude smaller than large adult conspecifics. The factors that generate such habitat shifts are generally obscure, but we studied an unusual system that allowed us to compare consequences of habitat selection between adults and juveniles. Pit-vipers (*Gloydius shedaoensis*) on a small island in north-eastern China feed almost entirely on seasonally migrating birds. During the spring bird-migration period, individual snakes consistently re-used either arboreal or terrestrial ambush sites. Snakes in trees were smaller (and more philopatric) than snakes on the ground. This ontogenetic shift in habitat use may reflect the difficulty of capturing birds on the ground, especially by small snakes. In laboratory trials, large (adult) pit-vipers struck faster, further and more accurately than did small (juvenile) snakes. In experiments with free-ranging snakes, the proportion of strikes hitting the bird was lower for juveniles than for adults, and lower for terrestrial snakes than for arboreal snakes. Additionally, adult snakes generally seized the bird by the head whereas juveniles frequently struck the body or wings (and thus, obtained a less secure grip). Arboreal ambush sites may facilitate prey capture not only because they give access to smaller birds but also because they render the bird's location more predictable and, hence, enable the snake to position itself optimally prior to the prey's arrival. Because juvenile pit-vipers are less capable strikers, and are small relative to available prey items, they may benefit from the greater ease of prey capture from branches. Thus, the ontogenetic shift in habitat selection within this species may be because of ontogenetic shifts in the vipers' ability to capture and ingest large, mobile prey.

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## Introduction

A diverse array of habitat types can occur even within a small area, and animals use this diversity in complex ways. The organism's 'choice' of particular habitat attributes presumably relates to advantages and disadvantages associated with each alternative (Krebs and McCleery 1984). Although published work supports this prediction from optimality models (e.g. Christian et al. 1983; Adolph 1990; Downes and Shine 1998), there are few field data on the costs or benefits associated with facultative use of alternative habitat types (Asplund 1974; Bell et al. 1991).

Especially within ectothermic species, a single population can contain individuals over a wide range of body sizes. Size can influence an organism's interactions both with abiotic factors (e.g. rates of heating, cooling, and dehydration; ability to use various sizes of shelter sites) and biotic factors (e.g. prey sizes and types; vulnerability to predators). Body size can also affect physiological performance (e.g. locomotor speed, metabolic scope, time to exhaustion: Pough 1977; Arnold 1993). Often, such ontogenetic changes are accompanied by concurrent shifts in patterns of habitat use (Asplund 1974; Heatwole 1977).

Although ontogenetic shifts in habitat use within reptiles offer excellent systems in which to investigate the use of alternative habitat types, this opportunity has rarely been exploited. The obstacles are primarily logistical. Because juvenile reptiles are so much smaller than conspecific adults, it is difficult to study all age classes using the same methods. In any survey, juveniles are likely to be more difficult to find – not only because they are smaller and thus hide more easily, but also because their greater vulnerability to predators may favour secretive behaviour, and their higher rates of heating mean that they do not have to remain for long periods in exposed positions for behavioural thermoregulation (Asplund 1974; Sun et al. 2001). Quantifying relative usage of alternative habitats by adults and juveniles is also difficult, not only because different habitats provide different degrees of observability (Weatherhead and Charland 1985), but also because the magnitude of this bias is likely to be affected by body size. The end result of these problems is that field studies of habitat use have typically focused on adults rather than juveniles. For example, there are few field data on any ecological attributes of juveniles in most snake species (Gibbons and Semlitsch 1987; Seigel 1993).

These logistical impediments differ among systems. Although research on juveniles is difficult in many taxa, there are occasional situations where all size/age classes within a population are easily observed in the field. Such a situation occurs on a small island in north-eastern China, where pit-vipers (*Gloydus shedaensis*) occur in high densities in relatively open habitat (Sun 1990; Li 1995; Shine and Sun 2002; Shine et al. 2002a,b). Snakes of all size classes feed primarily on migrating birds, which they ambush from either arboreal or terrestrial sites. Snakes of all body sizes are equally observable in these exposed positions. We can thus quantify differences in habitat use between juvenile and adult snakes in a system where differential observability is not a problem, and where we can be confident of the biological significance of site selection (i.e. these sites are clearly

used for ambushing prey, and not for other functions: Li 1995; Shine and Sun 2002). Juvenile pit-vipers rely primarily upon arboreal ambush positions, whereas adults use both arboreal and terrestrial sites (Li 1995). Mark-recapture studies show that this is a real phenomenon, rather than an artefact of lower observability of juveniles in terrestrial locations (Sun et al. 2001). We examined these two types of ambush sites, with particular regard to factors that might generate an ontogenetic shift in their use.

## Methods

### Study Species and Area

Shedao pit-vipers (*G. shedaensis*) occur on one small island in the Bohai Sea and also in montane areas of the nearby Liaodong Peninsula in north-eastern China (Zhao and Adler 1993). Despite their large size [mean adult snout-vent length (SVL) 65–70 cm: Sun et al. 2001], the species attains remarkably high population densities on the island of Shedao (38°57' N, 120°59' E). Mark-recapture studies indicate a population of > 15 000 snakes within a total area of 0.73 km<sup>2</sup> (Huang 1989, 1990). In suitable habitats on the island, this translates into one pit-viper per square meter (Koba 1938; pers. obs.). Adult Shedao pit-vipers feed exclusively on birds, and these are the primary prey for juvenile snakes also (Li 1995). Adult pit-vipers are dangerously venomous and have no predators on the island, but hawks may occasionally take juvenile snakes (Li 1995). The snakes are inactive throughout most of the year, but emerge to lie in wait for prey during two bird-migration periods (May and Sept.: Sun 1990). During these periods the island is visited by many thousands of migratory birds, mainly passerines, on their way to or from breeding areas in Siberia (Li 1995).

The snakes capture birds from ambush, waiting with the forebody in a concertina shape. Some snakes in ambush postures contain two or three freshly ingested birds, showing that snakes continue to lie in wait for prey even after feeding (Li 1995). Some snakes use tree branches as ambush sites (Fig. 1), whereas others lie in wait on the ground (Fig. 2). Prey are also taken by scavenging rather than ambush: larger snakes frequently consume birds struck and killed by snakes too small to ingest them (Li 1995). The vegetation in our study area consists of a mosaic of trees, shrubs and grassland. Most trees and shrubs grow to < 2 m height, and most branches used by snakes are < 1 m above the ground. In another paper, we provide detail on the tree species present, structural aspects of the vegetation, and the characteristics of branches that were or were not used by foraging pit-vipers (Shine and Sun 2002). The present paper compares terrestrial vs. arboreal ambush sites.

### Timing of Study Relative to Feeding Season

We visited Shedao from 2 to 17 May 2000, at the peak of the spring feeding period. The snakes only feed for about 4 wk in spring (Li 1995; Sun et al. 2001).



*Fig. 1:* Shedao pit-viper in ambush posture in a tree

They commenced feeding in the week before we arrived (L. Sun, pers. obs.), so our study spanned most of the main feeding activity for spring 2000.

#### **Use of Arboreal and Terrestrial Ambush Sites**

On three successive days (6–8 May 2000) on Shedao, we walked the same 370-m path and captured all pit-vipers that we found in ambush postures within 2 m of the track. Each of these snakes was sexed (by hemipenial eversion) and measured (SVL). We also palpated the snake's abdomen to record whether or not it contained a prey item, and to measure the bolus diameters of recently ingested



*Fig. 2:* Shedao pit-viper in a terrestrial ambush site

items. Freshly ingested prey could be distinguished from partially digested birds by palpation. Trials in which we measured dead birds, and then fed them to free-ranging snakes, showed that bolus diameters provide valid indices of prey sizes (maximum error 3 mm from five prey items). We painted a number on each snake's dorsal surface so that the animal could be identified without recapture on subsequent occasions.

Perhaps because of a lack of natural predators, Shedao pit-vipers tolerate close approach by humans (< 1 m: Shine et al. 2002a). Hence, we could determine the ambush site used by each snake, and mark it with flagging tape. After the 3-d marking plus two additional days to let the snakes recover from any stress, we walked the same track each morning for the next 7 d to record the locations of marked snakes. This work generated a data set on successive locations of snakes, displacements between successive ambush sites, and the consistency with which individual animals used arboreal vs. terrestrial ambush sites. The snakes remain in their ambush sites for hours at a time, but return to sheltered terrestrial sites each evening, and sometimes during the middle of the day as well (Sun 1990; Sun et al. 1990). Thus, records of snakes in the same shelter sites on successive days represent a return to the site rather than continuous occupancy.

#### **Prey Mass and Snake Mass**

We recorded mass and chest diameter for a sample of 19 birds found dead or dying after being struck by pit-vipers. Mass was also recorded for 119 live vipers,

covering a wide range of body sizes. Using these data, we constructed polynomial regressions of linear dimensions to mass, so that we could then estimate masses of snakes and birds for which we only had records of SVL or chest diameter, respectively. All snakes containing freshly ingested prey items (obvious from distension of the snake's midbody) were captured, so that we could measure both the snake's SVL and the diameter of the bolus inside its stomach. We used data only from freshly ingested birds, easily recognizable by palpation. For birds, mass (g) =  $31.793 - [2.549 \times \text{chest diameter (mm)}] + [0.067 \times (\text{chest diameter})^2]$  ( $n = 19$ ,  $r^2 = 0.96$ ). For snakes, mass (g) =  $94.698 - [5.511 \times \text{SVL (cm)}] + [0.067 \times (\text{SVL})^2]$  ( $n = 119$ ,  $r^2 = 0.78$ ). Relative prey mass (bird mass relative to snake mass) could thus be estimated from bolus diameter and snake SVL.

### **Presentation of Prey Stimuli to Foraging Snakes**

To investigate whether attributes of the ambush site influence a snake's ability to launch a successful strike, we presented prey items to snakes in a standardized fashion. The items offered were either dead birds (that we found dead or dying, after they had been struck but lost by snakes) or artificial models (water-filled balloons inside feather-covered nylon bags 30 mm in diameter). All trials were conducted between 07:00 and 16:00 h 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 (R.S.) presented the stimulus in each case, and attempted to test each snake only once (a few animals may have been tested more than once, if they shifted ambush sites between days of testing). 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 to rest on the substrate (branch or ground) 5–10 cm in front of the snake's head. Over the next 60 s, the 'target' was moved about to simulate a live bird. This mode of presentation simulated as closely as possible the situation we observed prior to natural feeding strikes. We used multiple logistic regression to examine the ways in which a snake's size [juvenile (< 50 cm SVL) or adult (> 50 cm SVL): Li 1995] and location (tree or ground) affected whether or not its strike hit the target. We used size categories rather than measuring SVLs for these snakes, to minimize the amount of time spent handling these dangerously venomous animals in our remote study area. Whenever possible, the location of the strike (on the bird's head or body) was also scored for trials using dead birds as the stimulus.

### **Strike Speed, Distance and Accuracy**

We filmed snakes during natural encounters with prey, but could not obtain sufficient sample sizes or details to quantify attributes of the strike. Thus, we resorted to measuring defensive rather than foraging strikes, under the assumption that broad features of these responses would be similar. We used a Sony TRV 46E videocamera (25 frames per second) to film snakes < 30 min after they

were captured, in an open-topped plastic bin measuring 63 cm long  $\times$  40 cm wide  $\times$  40 cm high (see Shine et al. 2002a). Parallel lines at 2 cm intervals on the floor of the bin allowed us to measure strike distances and, thus, speeds. The snake was placed in one corner of the bin at the beginning of the trial, and harassed with a rolled-up cloth bag (approx. 3  $\times$  3 cm) tied to the end of a metal pole. The cloth stimulus was prodded against the snake's body repeatedly for a 60-s period. The stimulus was kept close to the floor of the bin, so that most strikes were parallel to the bin floor (hence reducing parallax error in scoring speeds). Body temperature of the snake was measured with a Raytek 31-LRSCL2 infrared thermometer (Raynger, Santa Cruz, CA, USA) immediately after the trial had concluded. From the videotapes, we scored the snake's strike distance, strike speed (i.e. rate of movement of the head during its forward progression) and accuracy. Each snake was used in only a single trial, to avoid pseudoreplication.

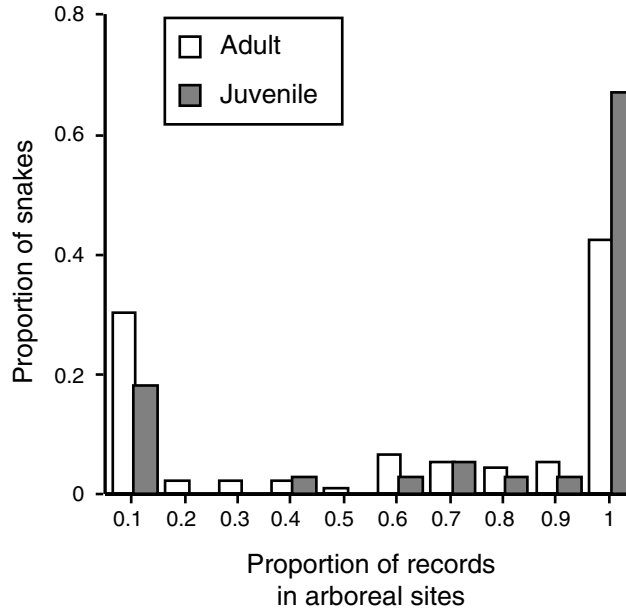
## Results

### Use of Arboreal and Terrestrial Ambush Sites

The 179 snakes that we captured and marked over the first 3 d of study were re-sighted a total of 340 times over the following 9 d. One hundred and one of the 179 initial captures (56%) were in arboreal perches, as were 238 (70%) of the re-sightings. Overall, the marked snakes were highly philopatric. Of 339 records of movement by 110 different snakes, 279 of these displacements (82%) were  $<$  5 m. In 176 of these cases (52%), the snake was in exactly the same place as it had been seen on the previous occasion. The same pattern is evident if we express these numbers in terms of mean values per snake, to avoid pseudoreplication (i.e. multiple records from a single animal). Of the 110 snakes, 75 (68%) moved an average of  $<$  5 m between successive records; 84 animals (76%) moved an average of  $<$  10 m between sightings.

Individual snakes not only remained close to their original capture site, but also consistently selected either arboreal or terrestrial ambush sites. Because some snakes consistently used arboreal perches whereas others used terrestrial ambush sites, the overall distribution of usage of these two types of location was strongly bimodal in both juvenile and adult pit-vipers (Fig. 3). This bimodality was not simply because of re-use of the same specific sites by many snakes. Even if we omit all records of snakes that returned to exactly the same sites as they were last encountered, a snake that was last seen on a branch was more likely to be re-sighted on another branch than on the ground (63 of 99, 64%). Similarly, a snake that was last seen on the ground was more likely to be re-sighted in another terrestrial site than in a tree (41 of 64 cases, 64%; even after deleting all records of re-use of previous sites,  $\chi^2 = 10.89$ , 1 df,  $p = 0.001$ ). The proportion of snakes found in the same type of ambush site as their initial location was higher for juveniles (70 of 80, 87%) than adults (198 of 259, 77%;  $\chi^2 = 3.87$ , 1 df,  $p < 0.05$ ).

A snake's ambush site also affected its movements between successive locations. Snakes that were initially sighted on a tree and later re-sighted on a tree,



*Fig. 3:* The consistency with which individual pit-vipers utilized either arboreal or terrestrial ambush sites, calculated as the proportion of re-sighting records in either type of site. Each snake ( $n = 39$  juveniles, 140 adults) provides a single data point for this histogram: for example, a record of 0.6 represents a snake for which 60% of sightings were in trees and 40% on the ground. The graph shows that most snakes were found consistently either in trees or on the ground, rather than moving between these two types of ambush sites

generally had moved only a short distance (displacement,  $n = 194$ ). Indeed, most of these snakes had returned to their original ambush site. All other categories of habitat usage (snakes recorded on trees and then re-sighted on the ground; or snakes recorded on the ground and later re-sighted either in trees or on the ground) had longer displacements ( $7.80 \pm 16.44$  m,  $n = 28$ ;  $6.93 \pm 11.59$  m,  $n = 43$ ;  $5.64 \pm 12.95$  m,  $n = 74$ ). A two-factor ANOVA with habitat type (arboreal/terrestrial) in the two successive locations as factors showed the distance moved was affected by a significant interaction between the habitat types of the successive locations ( $F_{1,335} = 4.15$ ,  $p = 0.043$ ).

To examine whether snakes using arboreal vs. terrestrial ambush sites differed in size or sex, we combined data from all of our studies during May 2000 on Shedao. Recaptures of marked snakes were omitted to avoid pseudoreplication, although some unmarked animals may have been recorded more than once (albeit, with at least 24 h between consecutive records). The relative proportion of snakes in trees vs. on the ground was lower in adult pit-vipers (291 of 494 adults, 59%), than in juvenile conspecifics (146 of 186 juveniles, 78%; see also Fig. 3;  $\chi^2 = 21.73$ , 1 df,  $p = 0.0001$ ). The proportion of snakes in trees vs. on the ground was similar in males (arboreality in 39 of 69 snakes known to be male, 57%) and females (62 of 94, 66%;  $\chi^2 = 1.13$ , 1 df,  $p = 0.29$ ).



### Foraging Success

Because snakes were consistent in their ambush-site selection, prey items inside arboreal snakes are likely to have been taken from arboreal perches and prey items inside terrestrial snakes from terrestrial ambush sites. Mean prey diameters (as estimated by bolus diameters inside snakes) were greater in terrestrial than in arboreal pit-vipers (25.4 vs. 21.7 mm;  $F_{1,52} = 4.86$ ,  $p < 0.04$ ). However, this difference is difficult to interpret because prey size depends on snake size and snakes in trees were generally smaller than those on the ground. Relative prey mass declined with snake size ( $r = -0.77$ ,  $n = 65$ ,  $p = 0.0001$ ); that is, the birds consumed by small snakes were much larger relative to snake size than were the birds taken by adult snakes. Relative to the snake that consumed them, birds in arboreal snakes were similar in size to those in terrestrial snakes (one-factor ANOVA,  $F_{1,63} = 0.07$ ,  $p = 0.80$ ). In summary, arboreal snakes contained birds that were smaller in absolute terms than were those in terrestrial snakes, but similar in size relative to the snake that consumed them.

### Presentation of Prey Stimuli to Foraging Snakes

We conducted 251 trials where we presented dead birds or artificial (feather covered) models to snakes in ambush poses. Of these trials, 101 resulted in strikes at the stimulus, and 84 of these strikes hit the target. We used multiple logistic regression to analyse these data, with independent variables that reflected attributes of the snake (adult/juvenile) and its location (tree/ground); the dependent variable was whether or not the strike hit the target. Strikes were more accurate if the snake was on a branch rather than on the ground (85 vs. 78%; log-likelihood ratio test  $\chi^2 = 4.33$ , 1 df,  $p = 0.037$ ), and more accurate from adults than from juveniles (90 vs. 74%;  $\chi^2 = 7.79$ , 1 df,  $p = 0.005$ ).

Juvenile and adult pit-vipers also differed in terms of where the bird was struck. Data on this topic were obtained in only a minority of trials, because of difficulty in scoring the strike's location if the bird was released immediately. Of eight birds struck by juveniles, two were seized by their heads, four by the midbody, and two by the wings. In contrast, 12 of 16 strikes by adult pit-vipers involved seizure of the bird's head; the other four strikes were directed to the bird's midbody (proportion of strikes to head: Fisher's exact test,  $p = 0.034$ ).

### Strike Speed and Accuracy in the Laboratory

We videotaped defensive responses of 66 snakes (49 adults, 17 juveniles) at body temperatures ranging from 8.4 to 30.1°C. Of these snakes, 45 struck at least once during the 60-s trial period ( $n = 393$  strikes). Because temperature affects strike speed in this species (Shine et al. 2002a), we used a one-factor ANCOVA with size class as the factor, body temperature as the covariate and strike speed as the dependent variable, to examine differences between adult and juvenile snakes. At the same body temperature, average strike speeds were quicker for adults than for

juveniles ( $0.98 \pm 0.20$  m/s for 32 adults vs.  $0.74 \pm 0.21$  m/s for 13 juveniles: slopes  $F_{1,41} = 0.08$ ,  $p = 0.77$ , intercepts  $F_{1,42} = 13.07$ ,  $p < 0.001$ ). Regardless of temperature, adult snakes struck further than juveniles ( $0.13 \pm 0.03$  m for 32 adults vs.  $0.08 \pm 0.03$  m for 13 juveniles: slopes  $F_{1,41} = 0.32$ ,  $p = 0.58$ , intercepts  $F_{1,42} = 31.45$ ,  $p = 0.0001$ ). Despite the shorter distances covered, defensive strikes by juveniles rarely hit the target (3 of 13, 23%) whereas adults were more accurate (21 of 32, 66%; from logistic regression, log-likelihood ratio test  $\chi^2 = 4.68$ , 1 df,  $p < 0.04$ ).

## Discussion

Although detailed studies are limited, ontogenetic shifts in habitat use by snakes seem to be widespread, and may often involve a greater reliance upon arboreal sites by juveniles than by conspecific adults (e.g. Heatwole 1977; Plummer 1981; Slip and Shine 1988; Lillywhite and Henderson 1993). The pit-vipers of Shedao offer an ideal system in which to examine these issues. The snakes are abundant, tolerate close approach, and have few if any natural predators (Li 1995). Although our field study was brief, it encompassed most of one of the two major annual feeding periods for the snakes. Our data confirm previous reports of an ontogenetic shift from arboreal to terrestrial ambush sites within *G. shedaoensis* (Li 1995).

Many kinds of explanations could be offered for such a difference, but most are inapplicable to the Shedao pit-vipers. For example, juvenile pit-vipers eat centipedes as well as birds, and may be more vulnerable to avian predators than are adult snakes (Li 1995). However, both of these ontogenetic changes should reduce rather than increase the proportion of arboreal activity by smaller snakes: the ground offers a better foraging area for centipedes, and a safer location against avian predation. Similarly, decreased reliance on arboreal perches by larger (adult) snakes might reflect physical constraint rather than optimality, if many perches are inaccessible to, or unable to support, a larger animal (e.g. Plummer 1981; Henderson 1993). Neither of these situations obtains on Shedao, with even the largest snakes easily and rapidly climbing into trees (pers. obs.) and resting even on slender branches (Fig. 1). Social interactions also drive ontogenetic shifts in habitat use by some reptiles, with adults excluding juveniles from some habitat types (Law and Bradley 1990). No such agonistic interactions were evident in Shedao pit-vipers, with animals ignoring each other's presence even when the snakes were in physical contact in ambush poses on the same or adjacent branches (see also Li 1995). We thus focus on factors that differ between arboreal and terrestrial ambush sites; for example, arboreal perches may give access to smaller birds, or facilitate the snake's attempts to capture prey.

Because we were unable to relocate all of the marked snakes, the mean dispersal distances from our data may underestimate real values because they omit animals that dispersed so far that we never saw them again. Despite this bias, it is clear that many of the snakes were highly philopatric. This was especially true for snakes from arboreal perches. The distance from one 'good' arboreal perch to

another is likely to be great enough to discourage migration (Shine and Sun 2002), whereas 'good' terrestrial ambush sites are common and hence their availability does not restrict displacements among alternative sites. A Shedao pit-viper's selection of an arboreal vs. terrestrial ambush site is likely to affect its foraging success in two main ways:

#### **Prey Encounter Rate**

All of the birds on Shedao are large relative to juvenile pit-vipers; indeed, this is one of the few snake species worldwide to feed mainly on birds from birth (Shine 1983; Luiselli and Rugiero 1993; Li 1995). Neonatal snakes can ingest only the smallest passerines (pers. obs.), and these very small birds may be more available from branches than from terrestrial sites. Most of the larger birds eaten by Shedao pit-vipers (*Erithacus*, *Emberiza*, *Luscinia*) forage on the ground more often than do the most abundant small taxa (*Phylloscopus* spp.) (Zhang et al. 1997). Some of the largest birds (notably quails, *Coturnix* spp.) are strongly terrestrial. In keeping with these inferences, mean prey sizes were larger for snakes on the ground than for snakes in the trees. The reliance of juvenile pit-vipers on very small birds may thus favour the use of arboreal perches.

Adult pit-vipers do not experience such severe problems with gape-limitation; most of the abundant passerine species can be ingested by an average-sized adult snake (pers. obs.). Thus, adults may benefit from the larger average size of birds captured from terrestrial sites. There is an additional source of very large birds on the ground also: prey items killed by snakes (either from trees or the ground) that either escaped before dying, or were too large for the predator to ingest. We found > 20 such birds over a 2-wk period on Shedao, and saw large snakes consuming prey that had been killed by other, smaller snakes. Five dead birds that we placed on the ground were consumed by large pit-vipers within 24 h. Hence, scavenging may also favour terrestrial activity by larger snakes.

#### **Ease of Prey Capture**

Many feeding strikes by pit-vipers on Shedao are unsuccessful, as evidenced by our experimental presentations of prey items, by observations of natural feeding events, and by the large number of dead and dying birds that we found on the island. Prey capture may be more difficult for juvenile pit-vipers than for adults, because (a) the prey are larger relative to snake size; and (b) juvenile pit-vipers strike more slowly, less accurately and over a shorter distance than do conspecific adults. The same lower accuracy was evident in our field trials, both in terms of the proportion of strikes hitting the bird, and the location on the bird's body where the snake struck. Observations of natural feeding strikes suggest that birds seized by the head were less likely to escape from the snake than were those seized by the body (R. Shine, pers. obs.).

Given this problem for juvenile pit-vipers, we expect them to select ambush sites that facilitate prey capture. The high rates of accurate strikes from snakes in

arboreal perches suggest that branches are better than terrestrial sites in this respect, possibly because of a greater predictability of prey location. The number of sites where a bird can alight is much lower in a tree than in a comparable area on the ground. A sample of 127 trees used as ambush sites by Shedao pit-vipers had an average of less than four potential ambush perches at 0.5 m above ground and less than two at 1.0 m above ground (Shine and Sun 2002). Almost all bird perching events occur at  $< 1$  m above ground (Shine and Sun 2002), so a given tree generally provided less than six potential perch-sites.

Because of the limited number of favourable perching sites in trees, the spatial location of birds (and thus, feeding opportunities for pit-vipers) is more predictable for arboreal sites than for terrestrial ones. A bird foraging on the ground will doubtless use different microhabitats non-randomly, but it may be more difficult to predict exactly where the bird will alight. Terrestrial ambush sites were typically close to features such as rocks or clear spaces that were frequently used by perching birds (see Fig. 2), and the same is true for terrestrial ambush sites used by at least one other species of avian-feeding pit-viper (Andren et al. 1994). Snakes in arboreal ambush sites may also face towards thermal and visual backgrounds that offer greater contrast against arriving prey (Shine et al. 2002b).

In summary, arboreal and terrestrial habitats on Shedao differ in ways that influence their suitability as ambush sites for pit-vipers. Some of these differences (such as in operative temperatures: Shine et al. 2002b) probably affect adult and juvenile snakes in similar ways, and thus do not favour ontogenetic shifts in habitat selection. Other traits will impact differentially on snakes of different body sizes. In particular, juvenile pit-vipers on Shedao may experience difficulty in capturing and retaining prey, because: (a) birds are fast-moving agile prey that pose problems for any snake; (b) birds are large relative to the size of juvenile pit-vipers; and (c) smaller snakes are slower, less accurate and strike over shorter distances than do larger conspecifics. In combination, these factors suggest that juvenile snakes should select ambush sites that facilitate prey capture and retention. For adult snakes, in contrast, rates of encounter with potential prey items may be more important. Hence, the outcome of the predator-prey interaction may be most sensitive to prey encounter rates for adult snakes, and to prey capture success for juveniles. The ontogenetic shift in habitat types thus may reflect these different priorities.

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