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Arboreal ambush site selection by pit-vipers *Gloydius shedaoensis*

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For a sit-and-wait predator, the choice of ambush site may be a crucial determinant of foraging success. During fieldwork on a small island in northeastern China, we explored the availability and use of arboreal ambush sites (tree branches) selected by Shedao pit-vipers, *Gloydius shedaoensis*. The snakes were highly selective at a variety of spatial scales. For example, they displayed strong biases in terms of which tree species were used, which individual trees within each species were used and which branches were used within a tree. Snakes disproportionately used trees that were on the edge rather than the interior of thickets, and branches that faced out towards the clearing rather than back towards the thicket. Branches at an angle slightly above horizontal were preferred. The snakes used branches visited at high rates by potential prey, that provided effective camouflage, and with thermal and visual backgrounds (cool, bright) that contrasted strongly with avian prey items (hot, dark). The snakes used perches close to the ground (the area of greatest bird activity) despite suboptimal visual and thermal backgrounds. Use of thicker branches by larger snakes, and by snakes containing recently ingested prey items, may contribute to effective camouflage. Thermoregulation did not appear to influence foraging site selection.

Many species display consistent site selection in the course of their foraging activity. The most extreme examples of this phenomenon involve sit-and-wait foragers that lie in ambush in one place for long periods of time. The extreme site specificity of ambushers greatly simplifies identification of the criteria that predators use to select their foraging sites. Additionally, the central role of a suitable foraging site, used, in extreme cases, for almost all of an animal's lifetime, means that the availability of such sites may be crucial to individual foraging success (Morse & Stephens 1996). We thus expect intense selection for behaviours that optimize ambush site selection. On a broader level, reliance on specific habitat features may threaten the long-term persistence of populations of ambush predators if anthropogenic processes reduce the availability of those habitat features (Shine & Fitzgerald 1996; Webb & Shine 1998a).

Many crotaline snakes (pit-vipers) capture their prey from ambush sites, with individual snakes sometimes remaining in the same site for days or weeks (Greene 1983; Reinert et al. 1984). The ambush site may be chosen to maximize rates of prey encounter (Klauber 1956; Greene 1992), facilitate the effective use of sensory modalities important for the detection and capture of prey (Reinert et al. 1984) or both. In the case of crotaline snakes, such modalities include not only chemoreception, but also vision, heat-sensing (via the specialized heat receptors that give 'pit-vipers' their common name) and sensitivity to vibrational stimuli (de Cock Buning et al. 1981; de Cock Buning 1983). To clarify the cues that pit-vipers use to select ambush sites, we compared the array of available sites with those used by snakes in a study system that offered unique logistical advantages. We focused on cues potentially available from the wide range of these animals' sensory modalities.

METHODS

Study Area and Species

Shedao (literally, 'snake island') is a small (0.73 km^2) island in the Bohai Sea, 13 km off the Liaodong Peninsula in northeastern China (38°57′N, 120°59′E), lying on a major migratory route for birds that overwinter in southern Asia but breed in Siberia (Li 1995; Sun et al. 2001). Many thousands of birds visit Shedao in spring (May) and autumn (September–October). Shedao pit-vipers, *Gloydius shedaoensis*, are abundant on the island (ca. 20 000 snakes: Huang 1990). The adults feed exclusively on migrating birds (Li 1995), are inactive outside bird migration periods (Sun 1990; Sun et al. 1990, 2001), and have no natural enemies (Li 1995).

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Figure 1. Pit-viper, *Gloydius shedaoensis*, in typical ambush pose on the branch of a tree.

Shedao pit-vipers are ambush foragers, adopting a distinctive pose (with forebody in a concertina shape to allow rapid striking) and then remaining virtually motionless for hours. Some snakes lie in wait on the ground, but most select tree branches (Li 1995; see Fig. 1). Loreal 'pits' below the eyes are sensitive heat-detecting organs, and play an important role in prey recognition (de Cock Buning et al. 1981; Chiszar et al. 1986). Shedao pit-vipers spend the night on the ground, but return to the same foraging site every morning. They may remain in their arboreal perches until evening, or spend the hottest part of the day on the ground (Sun et al. 1990). Many snakes use the same branches as ambush sites throughout an entire bird migration period (Sun 1990; R. Shine, L. Sun, M. Fitzgerald & M. Kearney, unpublished data).

The trees used as ambush sites by Shedao pit-vipers comprise part of a complex mosaic of vegetation types on this small, windswept, steep-sided, rocky island. The flora includes a diverse assemblage of north Asian taxa (see Li 1995 for species list). The majority of trees are relatively small (<2 m high), and sometimes form dense thickets. Open grassy areas are also common, perhaps reflecting past fires (Huang 1990). During the spring bird migration period when we conducted our study, air temperatures were relatively low (mean maximum daily air temperature=18°C: Sun et al. 2001) and trees were just beginning to bud out their leaves.

Methods

Identifying ambush sites and snake orientation

On 3 successive days (6–8 May 2000), we walked the same 370-m path and captured all pit-vipers that we found within 2 m of the track. Each of these 149 snakes was measured (snout–vent length) and weighed (g). Sex was determined by hemipenial eversion. We also palpated the snake's abdomen to record whether it contained a recently ingested prey item. If so, we measured the maximum diameter of this bulge. Prior to release, we painted an individual identification number (Tana Shoe Colour, Tana Australia, Clayton, Victoria) on the snake's dorsal surface so that the animal could be identified without recapture on subsequent occasions.

Shedao pit-vipers typically rely on crypsis rather than escape when closely approached by humans in the field (Shine et al., in press). Thus, we could easily determine the exact ambush site used by each snake and could score the snake's orientation on its perch, that is, whether it was facing outwards (away from the main trunk of its tree) or inwards (towards the trunk). Each ambush site was given an identification number, and marked with flagging tape to identify the exact position. We recorded the height above ground, and perch diameter at the place the snake's midbody had been resting.

After the 3 days' marking (and 2 additional days to allow the snakes to recover from any stress), we walked the same track each morning for the next 7 days to record the locations of marked snakes. The 149 marked snakes were found in a total of 127 trees over the course of our study (some snakes used terrestrial not arboreal perches, and some trees contained more than one snake). The majority of snakes used only one tree during this period. Analyses based on the full data set yielded identical conclusions to those based on data from only the first tree used by each snake. Analyses in this paper are thus based on the complete data set (127 trees).

Scoring attributes of ambush sites

We quantified several characteristics of each arboreal ambush site. These included tree species, the height of the tree, its maximum canopy diameter, its canopy cover (% shade at ground level), and its maximum trunk diameter at 1 m above ground. To provide an index of branch numbers on the tree, we counted all branches >10 mm in diameter coming off the main trunk. We also scored the distance from the nearest tree to the branch used and the distance to the nearest open clearing (>1 m^2 in area). We counted the number of trees within 5 m^2 of the focal tree. To quantify the ways in which the numbers of potential snake perches changed with tree height, we counted the number of branches >10 mm in diameter at various heights above ground (0.5, 1, 1.5, 2 m). These were counted through imaginary horizontal planes at those heights (i.e. all branches intersecting such planes were counted).

To characterize branch availability at the same height as that used by the snake within the focal tree, we counted the numbers of branches in each size category (<5, 5–10, 11–15, 16–20, >20 mm diameter) intersected by an imaginary horizontal plane at that height. We also measured the compass bearing from the 'used perch' to the nearest tree and to the nearest open area of >1 m^2. We did the same for an unused branch, choosing the branch >10 mm diameter that came off the main trunk closest to the 'used perch'. Based on these compass bearings, we could then determine whether (for example) used perches tended to face towards open areas rather than other trees, and compare used perches to randomly selected branches in this respect. The angle to the nearest tree could range from 0° (branch pointing straight at the nearest tree) to 180° (branch pointing directly away from nearest tree). Finally, we measured the angle from the horizontal of both used and the previously selected unused branches.

At the end of the study, we surveyed the entire study area within 10 m of the track, to count the numbers of trees of each species that were used versus unused by snakes over the study period. For each tree we also scored whether it was isolated (>1 m from nearest tree), on the edge of a thicket, or in the interior of a thicket.

'Edge of thicket' study

Our initial work (above) suggested that many snakes selected perches in trees on the edge (rather than the interior) of thickets. In such cases, the snakes tended to occur on branches facing outwards (towards the open area) rather than inwards (towards the centre of the thicket). To quantify this apparent pattern, and test competing explanations for it, we divided such trees in half (inwards facing versus outwards facing) and scored the number of used versus unused branches >10 mm thick in each half of the tree.

'Thermal backgrounds' study

One major set of criteria that snakes might use in selecting branches involves the background against which they would view a prey item (a bird) alighting in front of them. Given the importance of thermal cues (detected by their heat-sensitive facial pits) in prey capture (de Cock Buning et al. 1981; de Cock Buning 1983; Chiszar et al. 1986), we might expect snakes to select ambush sites with cold thermal backgrounds (so that hot birds offer a strong contrast). To characterize the thermal backgrounds that a snake would experience from alternative branches, we used a Raytek 3I-LRSCL2 infrared thermometer (Raynger, Santa Cruz, California, U.S.A.). This instrument measures infrared radiation over the range 8000–14 000 nm. The range of wavelengths detected by the pit organs of *G. shedaoensis* is not known, but studies on a closely related taxon (*G. halys*) revealed a range of ca. 1000–15 000 nm (Goris & Nomoto 1967), and more recent work on pythonid pit-organs showed peak sensitivity at 8000–12 000 nm (Grace et al. 1999). Thus, the instrument measures radiation over the same range as the snakes (and as emitted by avian prey, ca. 10 000 nm: Grace et al. 1999). The Raytek was laid along the branch pointing in the same direction as the snake had been. We depressed the trigger for 3 s, then used the Raytek's averaging function to determine background temperature over the measurement period. Equivalent readings were taken from a nearby unused branch, as above.

We used the same method to investigate the ways in which a branch's angle from the horizontal, and its height above ground, might influence the thermal background available to a snake. To test the effect of angle from the horizontal, we held the Raytek at the height above ground of the used branch and then rotated the Raytek through various angles (straight upwards=+90°; horizontal=0°, straight down= − 90°, through increments of 22.5°). We conducted these tests for both inwards-facing and outwards-facing branches of thicket edge trees (see above).

The effects of height above ground on thermal backgrounds were investigated in the same way as for branch angle, except that the angle was maintained at a constant 30° above horizontal (close to the mean angle of used branches: see below). The Raytek measured thermal backgrounds when held at 0, 20, 40, 60, 80, 100 and 120 cm above the ground. Trials for branch height and branch angle were carried out on 2 days differing in weather conditions: a fine warm day with no cloud (11 May) and a cold cloudy day (9 May). On both days, data were taken from 1330 to 1500 hours.

'Visual backgrounds' study

Pit-vipers use visual as well as thermal cues to identify prey items and guide the feeding strike (Radcliffe et al.

1986; Hayes & Duvall 1991). Thus, we might expect snakes to select branches that provide a clear, well-illuminated background against which their potential prey items can be viewed. To quantify the visual background, we measured light intensity using the automatic light meter within a Canon EOS 500 35 mm TTL camera (Canon Australia, Sydney). The camera's aperture was set to f 11, and we determined the shutter speed for correct exposure with ASA 64 film by pointing the camera out along the branch, at the same angle as the branch and in the same direction as the snake had pointed (i.e. either in towards the trunk or outwards). The shutter speed reading was converted to exposure values, and thence to illuminance (lx) following calibration trials against a Minolta flash meter 5 (Minolta, Osaka, Japan). We used this method to quantify the background illumination that a snake would experience from perches on inwards-facing versus outwards-facing branches of a tree at the edge of a thicket (see above). Both used and adjacent unused perches were assessed in the same way.

We also examined the influence of height above the ground on visual background, using the same methods as described above for thermal background tests but with the camera instead of the Raytek. The angle was kept at 30°, and we measured backgrounds at 0, 20, 40, 60, 80, 100 and 120 cm above the ground on 2 days of different weather conditions (as above).

'Operative temperatures' study

Plausibly, thermoregulatory biology might influence ambush site selection. To describe the body temperatures available to snakes using alternative perches, we adopted a simple method that obviated the need for physical models or mathematical calculations. The branches used by snakes were generally similar to snakes in colour and diameter, and snakes remain immobile in foraging poses for long periods (personal observation). Thus, the surface temperature of a branch might be similar to the body temperature of a snake using that branch. In other work, we found that the temperature of a pit-viper's dorsal surface offers a reliable indication of its cloacal temperature (as measured with an inserted probe: $r_{25}=0.95$, $P<0.0001$: R. Shine, L. Sun, M. Fitzgerald & M. Kearney, unpublished data). Using surface rather than cloacal temperatures minimizes stress to the snakes, and danger to the investigators. We thus used the Raytek to measure dorsal temperatures of snakes in foraging poses, and surface temperatures of branches immediately adjacent to the snake. Branch temperature was highly correlated with snake temperature ($r_{32}=0.98$, $P=0.0001$; snake temperatures ranged from 10 to 27°C). Thus, we measured surface temperatures of branches and used these data to approximate the thermal regimes of snakes using the branches.

Bird abundance surveys

To quantify a snake's opportunities to ambush birds, we scored the numbers of birds perching on trees as a function of branch height above the ground, and inwards-facing versus outwards-facing halves of trees on the edge of thickets (see above). Each time a bird left a branch and hopped on to another one it was counted as a new usage, because it conferred a potential ambush opportunity for a snake sitting on that branch. Thus, a single bird sometimes provided multiple data points within a short space of time. We conducted 56 5-min observation periods, equally spaced during daylight hours over 3 successive days.

RESULTS

Strongly nonrandom selection of ambush sites was evident at several levels. We begin with the broadest spatial scale (tree species) and work down to increasingly finer levels of resolution.

Species of Tree

We scored a total of 1947 trees of 10 species on the site, of which 127 were used by snakes (Table 1). Shedao pit-vipers were found in ambush poses in all 10 taxa of trees, despite the marked interspecific diversity in structural traits (Table 1). For example, some species (e.g. *Ampelopsis*) never attained heights >0.7 m and had no branches >10 mm in diameter, whereas others (*Ulmus*) grew to >5 m and had over 50 such branches (Table 1). Some trees offered essentially no shade (e.g. *Amorpha*), whereas others (*Ulmus macrocarpa*) had almost 50% shade. Some were typically found in thickets (*Ulmus pumila*, *Amorpha, Koelreuteria*) whereas others were generally isolated in open areas (*Celtis*). We classified each tree as isolated (>1 m from nearest tree), or on the edge of a thicket, or in the interior of a thicket. The tree species differed in their relative distribution between these three categories ($\chi^2_{18}=608.59$, $P=0.0001$). Comparing the number of trees of each species within our study area to the numbers actually used by snakes, contingency table analysis confirms a highly nonrandom pattern ($\chi^2_9=258.19$, $P=0.0001$). Snakes used *Celtis*, *Securinega* and *Zanthoxylem* more often than expected, but avoided *Amorpha* and *U. pumila*.

Proximity to Other Trees

Why did pit-vipers use some tree species but avoid others? Interspecific differences in traits such as overall size, shape, shading and so forth all offer possible explanations (Table 1). However, one major correlate of snake distribution stands out: pit-vipers were found primarily on tree species that were often isolated (such as *Celtis*) rather than those that formed thickets (such as *U. pumilis*; proportion of trees in thickets versus proportion used by snakes: Spearman rank correlation: $r_S=-0.82$, $N=10$, $P=0.014$). Overall, snakes were recorded more often on isolated trees (>35% of these trees) and edge-of-thicket trees (13%) than on interior-of-thicket trees (<0.3%; numbers of used versus unused trees in each category: $\chi^2_2=342.75$, $P=0.0001$).

If the snakes' use of particular tree species is due to a preference for more isolated trees, we should see the same pattern within as well as between tree species. That is,

Table 1. Characteristics of trees used as foraging sites by Shedao pit-vipers, divided by tree species

	Amorpha fruticosa	*Ampelopsis brevipedunculata*	*Celtis bungeana*	*Koelreuteria paniculata*	*Quercus acutissima*	*Robina pseudoacacia*	*Securinega suffruticosa*	*Ulmus macrocarpa*	*Ulmus pumila*	*Zanthoxylem schinifolium*
Number of trees used by snakes										
Absolute numbers	18	3	39	16	1	1	23	5	10	11
Proportion of all available trees of that species	0.03	0.10	0.69	0.06	1.00	1.00	0.14	0.05	0.02	0.50
Proportion of all trees of that species										
Isolated	0.02	1.00	0.81	0.09	1.00	1.00	0.17	0.21	0.00	1.00
Edge of thickets	0.24	0.00	0.19	0.29	0.00	0.00	0.15	0.47	0.22	0.00
Interior of thickets	0.74	0.00	0.00	0.62	0.00	0.00	0.68	0.32	0.78	0.00
Characteristics of trees used by snakes										
Tree height (m)	1.94±0.84	0.70±0.00	2.16±1.28	1.68±0.81	2	2	2.23±0.75	4.60±0.55	1.17±0.40	1.26±0.25
Trunk diameter at 1 m (mm)	11.50±10.15	0.00±0.00	30.18±26.53	24.94±24.46	25	32	34.57±12.42	87.00±2.74	5.00±7.44	11.09±5.49
Canopy diameter (m)	1.55±0.84	1.20±0.00	2.11±1.37	1.57±0.84	5	1	2.58±0.99	3.70±0.27	0.69±0.21	1.59±0.30
Number of branches >10 mm	7.33±10.98	0.00±0.00	43.51±52.18	8.06±8.23	50	9	22.57±9.67	36.00±49.30	3.90±3.35	25.46±1.51
Percentage shade	0.00±0.00	0.00±0.00	18.72±13.91	22.63±14.73	0	0	12.96±5.06	42.00±2.74	18.50±7.84	1.82±4.05
Distance to nearest tree (m)	0.60±0.40	2.00±0.00	4.36±8.05	0.64±0.53	5	4	1.48±0.60	1.80±0.27	0.42±0.32	1.05±1.39
Distance to nearest open area (m)	0.03±0.12	0.00±0.00	0.05±0.22	1.06±1.44	0	0	0.07±0.31	0.00±0.00	0.00±0.00	0.00±0.00
Number of trees within 5 m^2	14.44±6.88	2.00±0.00	9.97±7.68	20.19±8.68	4	4	18.74±12.43	8.40±2.19	38.50±11.32	4.46±3.08
Percentage shade within 5 m^2	13.61±6.60	5.00±0.00	20.39±13.74	30.00±15.47	20	0	33.91±17.51	33.00±2.74	51.50±8.52	6.82±7.83
Number of branches >10 mm diameter at										
0.5 m above ground	3.89±5.23	0.00±0.00	10.26±18.11	2.87±2.07	10	1	6.17±2.82	17.00±2.74	2.40±1.96	1.82±1.94
1.0 m above ground	1.94±2.39	0.00±0.00	17.33±27.79	2.73±2.25	20	1	5.39±1.73	16.20±1.64	0.60±0.97	6.09±0.30
1.5 m above ground	0.61±2.36	0.00±0.00	19.90±40.97	1.44±2.56	3	4	4.65±4.42	21.60±7.67	0.20±0.42	0.60±1.90
2.0 m above ground	0.17±0.71	0.00±0.00	15.90±40.74	0.75±2.05	0	0	1.35±3.13	22.80±9.86	0	0

Means are given±SD. Number of branches >10 mm quantifies the number of points at which a branch of this size came off the main trunk of the tree. Number of branches at each height above ground refers to branches >10 mm diameter that were cut by an imaginary horizontal plane through the tree at each height.

within each tree species, the trees that contained snakes should be isolated or 'edge' trees rather than those inside thickets. As predicted, snakes generally selected isolated or edge trees (numbers of used versus unused trees, isolated versus edge versus thicket: for *Koelreuteria*: $\chi^2_2=38.24$, $P=0.0001$; for *Securinega*: $\chi^2_2=138.54$, $P=0.0001$; for *Amorpha*: $\chi^2_2=62.62$, $P=0.0001$). In summary, snakes were generally found in tree species that grow close to open areas, and, within those species, were more likely to be in individual trees that were closer to open areas.

Inward versus Outward-facing Branches

The branches used tended to point towards open areas (mean vector ± SD=146.15 ± 39.50°, $N=122$) whereas unused branches often pointed away from the clearing (98.61 ± 55.73°, $N=122$: $t_{121}=8.90$, $P=0.0001$). Similarly, used branches pointed away from other trees (118.15 ± 45.70°, $N=127$) whereas unused branches on the same trees did not (67.44 ± 48.69°, $N=127$; $t_{126}=9.83$, $P=0.0001$). We also tested the orientations of used branches against the null value of 90° expected if these branches are randomly distributed with respect to their proximity to other trees and to open areas. In both cases, a one-sample *t* test rejects the null hypothesis (direction to open area: $t_{121}=15.70$, $P=0.001$; direction to nearest tree: $t_{123}=7.06$, $P=0.0001$). Thus, snakes using trees on the edge of thickets were generally on branches that faced away from the thicket rather than towards it.

Although a three-factor ANOVA (with tree number, branch orientation and usage as the factors, and number of branches as the dependent variable) revealed that trees developed more branches in the outward-facing direction ($F_{1,34}=17.75$, $P=0.02$), it also detected a statistically significant interaction between orientation (inwards/outwards) and usage by snakes (used/unused: $F_{1,34}=17.75$, $P=0.02$; means ± SD of 2.86 ± 1.77 outward-facing branches not used by snakes, and 1.27 ± 0.73 used, versus 2.80 ± 2.45 inward-facing branches not used by snakes, 0.19 ± 0.40 used). That is, snakes actively selected outward-facing branches from among those available.

Height Above Ground

The majority of trees used by the Shedao pit-vipers had branches available over a substantial range of heights (Table 1). We have data on branch heights of 149 snakes (in 127 trees) and on branch heights from our overall tree survey ($N=3648$ branches). Comparison of these two data sets shows that the number of branches >10 mm in diameter is fairly constant with height above ground (measured at 0.5-m intervals) whereas the majority of snakes were found on lower perches (0.5 and 1.0 m) rather than higher levels (1.5 or 2 m; Fig. 2a). About 60% of snakes were on branches in our lowest category (<0.5 m above ground) whereas only 20% of available branches fell into this category overall (numbers of available versus used branches among the four height-above-ground categories: $\chi^2_3=144.39$, $P=0.0001$; Fig. 2a).

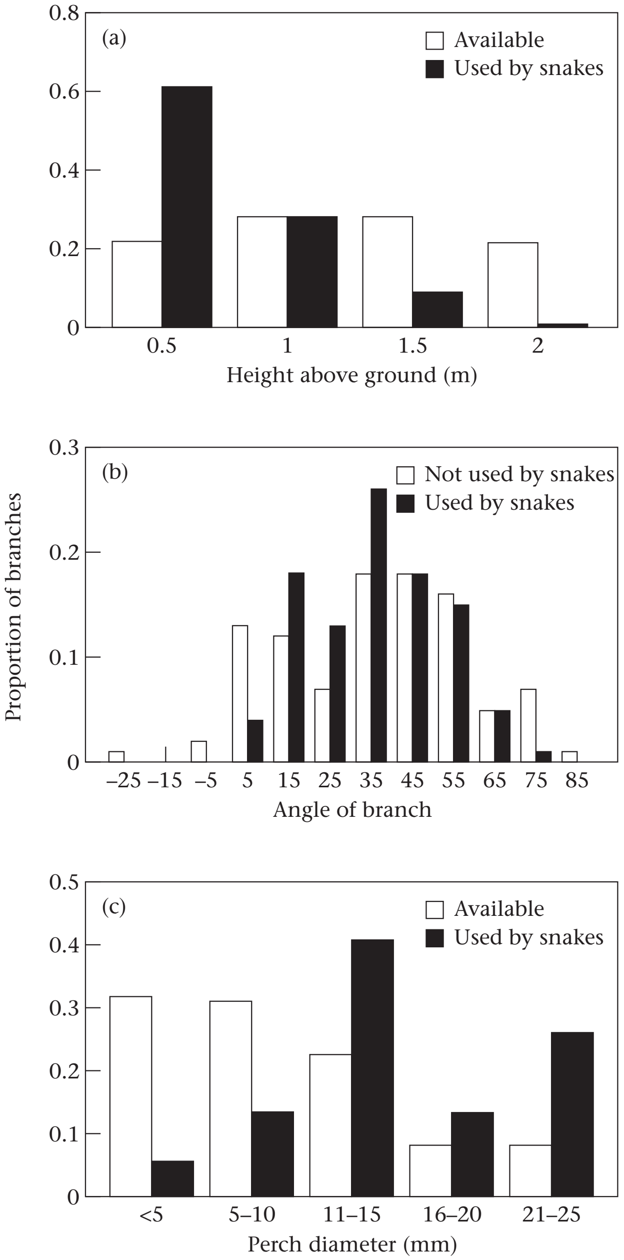

Figure 2. Availability of different perch (branch) attributes in trees used by Shedao pit-vipers, compared to the attributes of branches selected by the snakes. (a) Number of branches >10 mm in diameter at various heights above ground level, and the number of such branches used by snakes. (b) The same comparison in terms of the numbers of available versus used branches at different angles from the horizontal: (c) The same comparison for branch diameters. See text for statistical treatment of these data.

There was no clear association between snake body size (SVL) and perch height ($r_{146}=0.05$, $P=0.57$; Fig. 3a), but snakes that contained recently ingested prey items tended to be found on branches closer to the ground (mean height above ground ± SD=46.00 ± 14.71 cm, $N=13$) than snakes that had not fed recently (72.27 ± 36.03 cm, $N=135$; $F_{1,146}=6.77$, $P=0.01$).

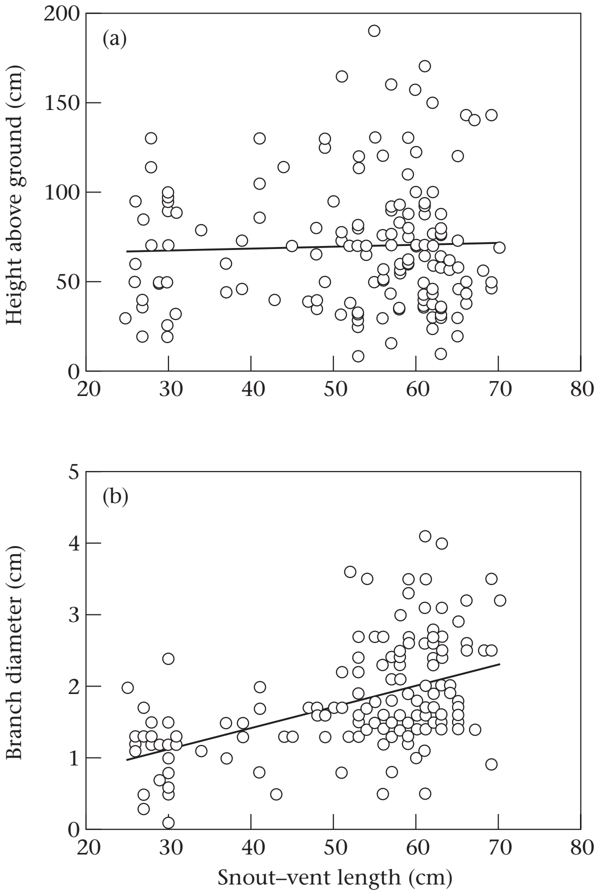

Figure 3. Snout–vent lengths of Shedao pit-vipers in comparison to the height above ground (a) and perch diameter (b) of the branches that they used as ambush sites. See text for statistical treatment of these data.

Angle of Branch

Average values of the angle of inclination (deviation from horizontal, where horizontal=0°) of each used branch and the closest unused branch in the same tree were almost identical (used branch: mean vector ± SD=32.34 ± 16.08°, N=122; unused branch: 33.39 ± 22.90°, N=122). However, the range of variation for used branches was lower than for unused branches. The majority of used branches were at angles of between 15 and 55°, whereas some of the unused branches were either more level, or steeper (Fig. 2b). A contingency table test (Batschelet 1981) indicated a significant difference between the two data sets (χ^2_8=38.29, P<0.0001) and an equality of variances test confirmed that the difference lay in the degree of dispersion (variance ratio=2.03, $F_{126,121}$=2.03, P=0.0001). That is, snakes selected branches close to the 'average' available angle, avoiding very steep branches and (especially) those close to or below horizontal (Fig. 2b).

Branch Diameter

Comparing the available size distribution with that of branches selected by snakes, Fig. 2c shows that snakes selected larger branches than those generally available. Contingency table analysis confirms active selection of branches >10 mm in diameter (comparing numbers of branches of each size class, used versus available: χ^2_4=125.26, P=0.001).

The branches selected were similar in diameter to the snakes that used them, and this similarity might make the snake more difficult for birds to detect (Fig. 1). If size matching is important for camouflage, we might expect to see a correlation between snake body size and branch diameter. Analysis shows that larger snakes were indeed found on thicker perches (SVL versus perch diameter: r_{147}=0.49, P=0.0001; Fig. 3b). An even stronger test is possible with recently fed snakes, because prey items cause visible distension of the snake's midbody. If size matching is facultative, we expect that snakes containing recently ingested prey items should select larger branches relative to their SVL. To test this proposition we conducted a heterogeneity of slopes test with SVL as the covariate, feeding status as the factor and branch diameter as the dependent variable. Slopes of the regressions between SVL and branch diameter were similar for fed versus unfed snakes (slopes $F_{1,145}$=1.36, P=0.25) so we deleted the interaction term and calculated the ANCOVA. As predicted, snakes containing food were found on thicker branches, relative to their SVL, than were snakes without food ($F_{1,146}$=4.17, P=0.043). Lastly, we can ask how the size of branch used by a recently fed snake compares to the snake's midbody diameter. As predicted from the 'size-matching' idea, snakes with larger prey items occupied larger branches (r_8=0.87, P=0.001). Diameters of both branches and snakes ranged from 10 to 35 mm, with a mean ± SD difference between the two of only 0.03 ± 0.44 mm (N=10). Thus, snakes were found on branches that closely matched their own midbody diameters.

Orientation of Snake on Branch

A snake could potentially lie either with its head facing outwards (away from the main trunk of the tree) or inwards (towards the main trunk). The latter position was recorded only once, in 184 records (including recaptures) of the 149 snakes. This sole exception involved an adult snake on a long, almost horizontal branch with a 1-m open area between the snake and the main trunk of the tree. Thus, this snake had a large open area in front of its head, despite being oriented towards rather than away from the main trunk.

Prey Abundance

The average number of bird-perching events ± SD on outward-facing branches was 2.04 ± 2.46 per trial, N=56, whereas the average number of perching events on inward-facing branches was much lower (0.66 ± 1.44 per trial, N=56; paired two-tailed t test: t_{55}=3.77, P=0.0004). Thus, birds perched more frequently on branches on the outward-facing rather than inward-facing side of tree.

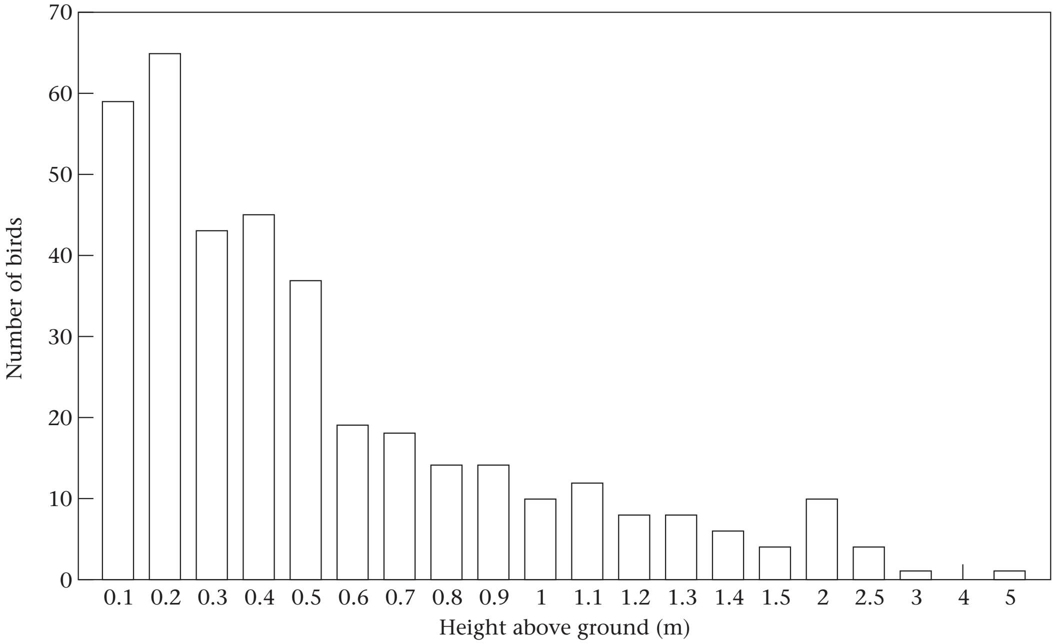

Figure 4. The heights above ground at which free-ranging passerine birds (mostly warblers and buntings) were recorded to perch on Shedao. A single bird may have contributed several data points to these histograms, because we scored the number of perching events (and, thus, ambush opportunities for snakes) rather than the number of birds.

We scored 564 bird-perching events over 4 days, mostly during the morning and evening when birds were most active. The data reveal a clear trend for birds to move about on branches close to the ground (Fig. 4). Many of the birds spent a great deal of time on the ground itself, and fed on terrestrial food items during most observation periods.

Thermal and Visual 'Backgrounds' to Ambush Sites

Both illumination levels and thermal backgrounds varied considerably between alternative ambush sites. Mean illumination levels varied fivefold as a function of attributes such as the height of the branch above the ground (see below), and thermal backgrounds varied from >30°C (when the branch faced towards sun-heated ground on a hot day) to < − 30°C (when the branch faced directly towards the open sky).

Restricting attention to trees at the edge of thickets, we used two-factor ANOVA to look at effects of branch orientation (inward- versus outward-facing) and usage (used versus unused) on the thermal and visual backgrounds available to pit-vipers. Branches facing outwards had higher illumination levels than those facing inwards ($F_{1,245}=14.39$, $P=0.0002$). Also, branches used by snakes had brighter backgrounds than those not used by snakes ($F_{1,245}=6.09$, $P=0.014$), with no significant interaction between the two factors ($F_{1,245}=1.33$, $P=0.25$; Fig. 5a). The end result is that perches selected by snakes had well-lit backgrounds, both because snakes selected outward-facing branches and because the particular branches selected were those with higher illumination.

Similarly, branches facing outwards (towards open areas) had cooler backgrounds than those facing inwards towards other trees ($F_{1,65}=8.09$, $P=0.006$). Thermal backgrounds of used branches were similar to those of unused branches ($F_{1,65}=0.55$, $P=0.46$; Fig. 5b), and no interaction was evident between usage and orientation ($F_{1,65}=0.0003$, $P=0.99$).

A randomized complete block ANOVA with day and branch height as factors (and tree number as the blocking factor) shows that light levels increased for higher perches ($F_{6,116}=8.67$, $P=0.0001$; Fig. 6a). The analysis also detected a difference in overall light levels between the 2 days of data collection ($F_{1,116}=11.19$, $P=0.001$) with no significant interaction between weather conditions (day) and height above ground in determining levels of illumination ($F_{6,116}=0.47$, $P=0.83$; Fig. 6a).

Higher perches had cooler thermal backgrounds ($F_{6,126}=4.59$, $P=0.0003$), but this relationship differed significantly between the 2 days on which we gathered these data (interaction: $F_{6,126}=2.92$, $P=0.01$). On a day with cool cloudy weather, height above ground had less effect on thermal background than on a fine sunny day (Fig. 6b). Cloud and soil temperatures were relatively similar on the cool day, but the (cold) open sky and (hot) landscape were very different on a sunny day. Overall, an increase in perch height resulted in a brighter, cooler background.

A randomized complete block ANOVA (with day and branch angle as the factors, tree number as the blocking factor and thermal background as the dependent variable) showed that the angle of a branch strongly affected its thermal background (Fig. 7). Branches that pointed upwards (and, thus, faced the sky and not the ground)

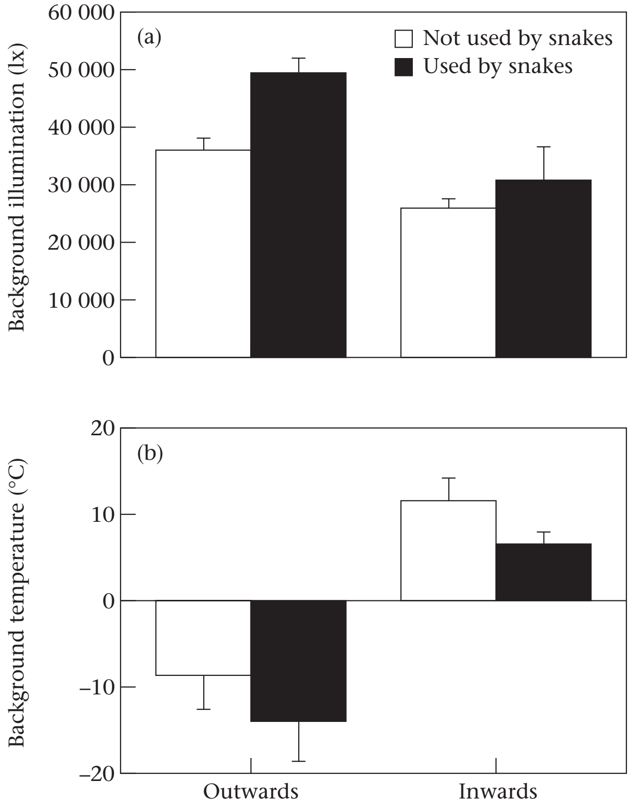

Figure 5. Visual and thermal backgrounds to foraging sites used by Shedao pit-vipers, compared to backgrounds available from adjacent unused branches. All trees used for this comparison were growing at the edge of thickets. Each branch was scored as either facing outwards (towards an open area) or inwards (towards the centre of the thicket). (a) Level of illumination (as measured by a camera's light meter) when looking out along the branch. (b) Thermal background (as measured by an infrared thermometer). Means are given+SE. See text for statistical treatment of these data.

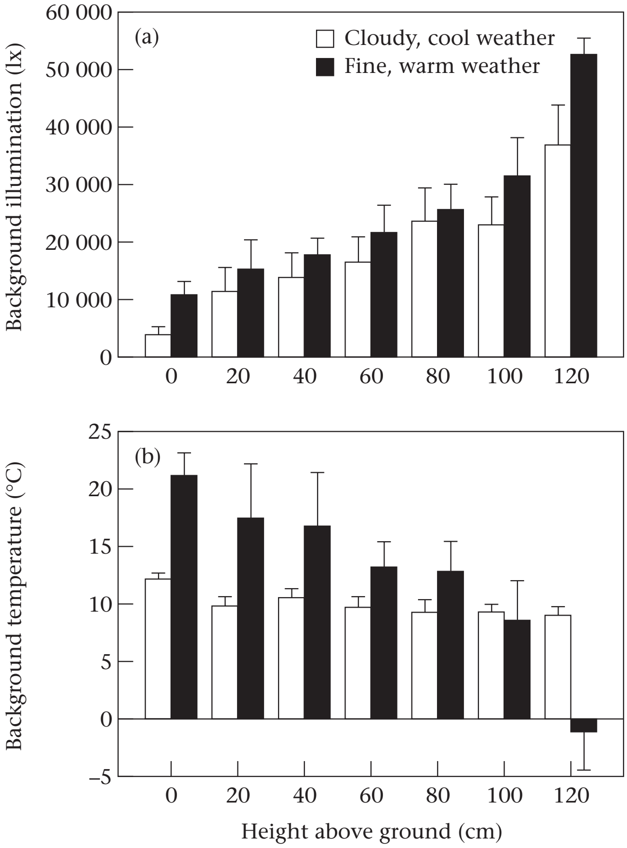

Figure 6. Effects of height above ground on the visual and thermal backgrounds of foraging sites used by Shedao pit-vipers. (a) Level of illumination (as measured by a camera's light meter) when looking out along the branch. (b) Thermal background (as measured by an infrared thermometer). These characteristics were measured on 2 days with different weather conditions. Means are shown+SE. See text for statistical treatment of these data.

had colder backgrounds, sometimes by as much as 60°C (i.e. +30 to −30°C: Fig. 7). The shift in background temperature with changing angle was abrupt, especially on the day with fine sunny conditions (i.e. when the sky was cold and the ground was hot). The ANOVA thus detected not only a significant effect of branch angle on background temperature ($F_{8,747}$=451.75, P=0.0001) but also a strong interaction between day (weather conditions) and branch angle in this respect ($F_{8,747}$=197.37, P=0.0001; Fig. 7).

Many of the branch angles that we evaluated for thermal background were outside the range that the snakes used as perch sites (compare Figs 2 and 7). None the less, the entire range of branch angles used in our trials are biologically realistic, because a snake that faced back towards the main trunk of the tree (rather than outwards away from the main trunk) would experience the thermal backgrounds that we measured. Thus, perches with a wide range of thermal backgrounds are available to the snakes, although they used only a small proportion of the available range.

Because the sky is bright and cold whereas the land is dark and hot, visual and thermal backgrounds to foraging sites tended to covary (e.g. Figs 5 and 6). Are these independent effects, or do the snakes react to one of these variables only? Analysis reveals a nonsignificant correlation between these two variables (r_{59}=0.17, P=0.19), suggesting that both may be causal influences on snake behaviour. To evaluate this situation further, we used multiple logistic regression. Our dependent variable was whether the branch was used by a snake, and our independent variables were the visual and thermal backgrounds of each branch. Log-likelihood ratio tests from the regression show that whether a branch was used as an ambush site was affected by both its visual background (χ^2_1=9.84, P=0.002) and its thermal background (χ^2_1=5.97, P=0.015). Thus, the sites used by snakes had backgrounds that were both cool and well lit.

Operative Temperatures

A two-factor ANOVA (with outwards/inwards and used/unused as factors, and branch temperature as dependent variable) did not detect any significant differences in branch temperature as a function of orientation to the thicket (inwards/outwards: $F_{1,65}$=0.94, P=0.34), whether

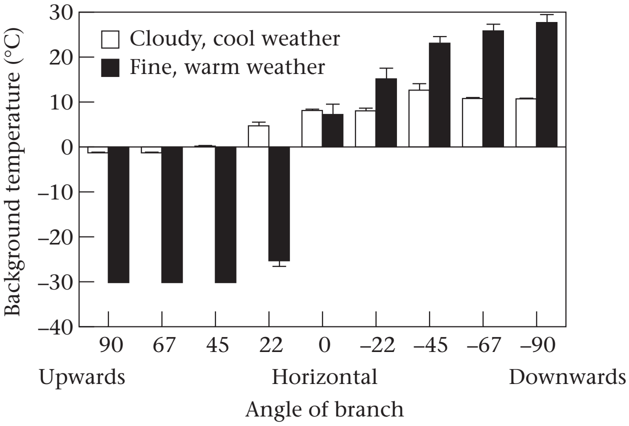

Figure 7. Effects of the angle of a branch (deviation from horizontal) on the thermal backgrounds of foraging sites used by Shedao pit-vipers (as measured by an infrared thermometer). Thermal backgrounds were measured on 2 days with different weather conditions. Means are shown+SE. See text for statistical treatment of these data.

the branch was used by a snake ($F_{1,65}$=1.76, P=0.19), or any interaction between these factors ($F_{1,65}$=0.68, P=0.41). This analysis suggests that the branches used by snakes are thermally similar to other branches.

DISCUSSION

A successful ambush site must have at least four characteristics: (1) it must be visited frequently by potential prey; (2) it must allow the predator to evade detection by the prey; (3) it must allow the predator to detect the prey item soon enough, and see it clearly enough, to allow an effective attack; and (4) it must facilitate prey capture. In addition, the ambush site must fulfil all of the other basic conditions required for any shelter site (such as protection from predators and environmental extremes) and, in some cases, provide a suitable opportunity for the predator to process (ingest, digest) the captured prey item. Our data provide an opportunity to explore the determinants of ambush site selection within this framework. Fortunately, the pit-vipers of Shedao provide a relatively simple system (one predator species, one major prey type, no higher-order predators or socially mediated site selection) which thus facilitates analysis. Such factors commonly influence foraging-site selection (Talbot 1979; Gotceitas & Godin 1992; Lens 1996).

Prey Availability

Because an ambush site must provide the opportunity to capture prey, we expect predators to lie in wait in sites that receive frequent visits (Curio 1976). In the case of the Shedao pit-vipers, two attributes of perch selection by the snakes (outward-facing branches and branches close to the ground) mirror the distribution of prey capture opportunities (perching events by birds). The former bias is difficult to interpret, because outward-facing branches also offer suitable visual and thermal backgrounds for prey detection (Fig. 5, and below). However, the snakes' selection of relatively low perches (Fig. 2a) runs counter to background suitability (Fig. 6) but parallel with bird movements (Fig. 4). Chemoreception may be the primary mechanism by which rodent-feeding rattlesnakes 'decide' where to forage (Reinert et al. 1984; Duvall et al. 1985; Duvall & Chiszar 1990), but cannot offer useful cues to snake species that feed upon avian prey (because scent trails will not exist). Ambush-foraging pit-vipers (*Bothriechis schlegelii*) and pythons (*Morelia oenpelliensis*) that feed on birds as well as mammals are reported to lie in wait near trees that attract birds with flowers or fruit (Forsyth 1990; Barker & Barker 1994). Presumably, these taxa may resemble Shedao pit-vipers in relying upon nonchemical cues for ambush site selection.

Camouflage

Most sit-and-wait predators select sites where they are well hidden (Curio 1976). Shedao pit-vipers in terrestrial ambush sites hide themselves under leaf litter (Sun 1990; Li 1995), but must rely on camouflage in arboreal ambush sites. Their body colour and rugose scalation provide a close visual match to branches (personal observation; Fig. 1), a resemblance heightened by the snakes' use of branches that match their own midbody diameter (Fig. 3b). Certainly, we often failed to see pit-vipers in ambush poses until we had approached them far more closely than we desired. A shift in branch diameter selection after feeding suggests that this size matching is facultative. The size matching is not a secondary consequence of shifts in perch height with snake body size (Fig. 3a), nor can it be attributed to physical factors (i.e. thin branches can support large snakes: Fig. 3b).

Prey Detection

Birds on Shedao remain on any given perch only briefly (generally <2 s: unpublished data) and, thus, pit-vipers need to recognize potential prey items very quickly. Many strikes fail (personal observation). For pit-vipers, the eyes and heat-sensitive facial pits are the most important systems for prey recognition (Chiszar et al. 1986; Hayes & Duvall 1991). Thus, Shedao pit-vipers may select ambush sites that allow for a clear 'view' of the prey item both visually and thermally (Reinert et al. 1984). In keeping with this idea, preference for a bright, cool 'background' predicts patterns in ambush site selection by Shedao pit-vipers at several spatial scales. For example, this preference can explain the trend to use tree species that grow in clearings rather than in thickets; and within such species, to select individual trees within such clear areas. Within a single tree growing at the edge of a thicket, the side facing outwards rather than inwards was preferred; and even within the outward-facing side, snakes selected branches that offered particularly clear, cool backgrounds. Pit-vipers in ambush poses were almost always oriented with their heads facing outwards towards the nearest open area, and avoided branches near or below horizontal that would have offered a warmer, less well-lit background. All these biases plausibly reflect a preference for ambush sites that offer a clear, bright field of view. Similarly, ambush sites of angel sharks, *Squatina californica*, are consistently oriented upslope, possibly to facilitate the detection of prey (fish) silhouettes against downwelling light (Fouts 1999). Visual contrasts offer important prey recognition cues for a variety of birds and fish (Curio 1976; James & Heck 1994) and the same is probably true for many kinds of snakes (Czaplicki & Porter 1974).

Prey capture

Passerine birds are agile, fast-moving prey items that are difficult for snakes to capture. Shedao pit-vipers are one of very few snake species worldwide that feed primarily on birds (Shine 1983; Luiselli & Rugiero 1993). Not only does a snake have to seize the bird, but it has to hold on. If the snake loses its grip, the bird can fly so far before it dies that it will be lost. Given the pit-vipers' reliance on visual and thermal cues for accurate aiming of the strike, the clear backgrounds of selected ambush sites may enhance capture success. Other plausible determinants of success involve the speed of the snake's strike, the distance between the snake's head and the bird, and the availability of a stable platform from which to launch the strike (Lillywhite et al. 1998). Strike speed of Shedao pit-vipers is enhanced by higher body temperatures, but the restricted range of operative temperatures on suitable branches, combined with the need for immobility, may preclude thermoregulation in arboreal ambush sites (Shine et al., in press). Snakes generally select positions close enough to the tip of the branch that they can strike this distance. In the laboratory, some defensive strikes by Shedao pit-vipers covered >20 cm (more than one-quarter of the snake's body length). We have seen feeding strikes in the field where the snake has struck so vigorously that it has lost its position on the branch and flung its entire body (with bird in mouth) forward on to the ground below.

Branch angle, diameter and distance from the ground may influence the stability of the platform from which the snake launches its strike. Although very steep (almost vertical) branches are available and offer optimal backgrounds, they were rarely used. Striking straight upwards, past the birds' feet, may be more difficult than a sideways strike at a larger and more vulnerable target. Experimental studies on an ambush-foraging shark species have revealed that prey orientation relative to the predator has a dramatic effect on the frequency of attack (Fouts 1999). Thicker branches, or sites where the snake's hindbody can rest on the ground, may offer more stable platforms in the windy conditions that often prevail on Shedao. In very strong winds, snakes abandon their arboreal ambush sites (Li 1995).

In summary, our data are consistent with the hypotheses that sit-and-wait predators select ambush sites that enable them to encounter prey, to detect the prey easily whilst remaining undetected themselves, and to launch effective feeding strikes. The same general criteria may be widespread, but their relative importance will vary in response to factors such as the phase within the predator-prey interaction that engenders the greatest variance in foraging success. In a system with scarce prey, encounter rate may be the primary criterion for effective ambush site selection (Klauber 1956; Van Orsdol 1984). If prey are abundant but difficult to capture, predators may instead select sites that maximize ease of prey capture (Breier & Drennan 1997; Fouts 1999). In yet other situations, the optimal ambush sites may be those that facilitate detection of prey items (Reinert et al. 1984; Webb & Shine 1998b). Although such considerations will apply to many kinds of organisms, the pit-vipers of Shedao provide an unusually powerful opportunity to clarify the ways in which sit-and-wait predators select their foraging positions.

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