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Thermal correlates of foraging-site selection by Chinese pit-vipers (*Gloydius shedaoensis*, Viperidae)

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Abstract

1. Do thermal factors influence foraging-site selection by ectothermic predators? Snake species that obtain their prey from ambush must remain immobile for long periods, precluding overt behavioural thermoregulation; and some “ambush” snakes use thermal cues to detect endothermic prey. Plausibly, alternative ambush sites might differ either in equilibrated body temperatures available to snakes, or in the thermal “background” against which prey items must be detected.
2. We examined this topic with field data on pit-vipers (*Gloydius shedaoensis*) on a small island in northeastern China. Adult snakes feed only on migrating passerine birds. The snakes ambush birds both from arboreal perches (branches of small trees) and from the ground.
3. Arboreal versus terrestrial ambush sites differed both in operative temperatures and thermal “backgrounds” available to the snakes. Operative temperatures inside copper models were lower in trees than on the ground (because of wind), and snakes in arboreal ambush sites were cooler than those in terrestrial sites. Thermal backgrounds from arboreal perches were cooler (and thus, provided more contrast against prey items) than did backgrounds available from terrestrial ambush-sites.
4. Thermal factors thus modify the suitability of alternative ambush locations for these pit-vipers, but with a trade-off: a snake in a tree can “see” its prey more clearly, but may not be warm enough (and hence, able to strike fast enough) to capture it. Further work is required to determine whether or not snakes actually use such thermal differences as criteria for the selection of ambush sites. © 2002 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Many natural environments display substantial thermal heterogeneity. Especially when ambient temperatures are low but solar radiation is intense, an ectothermic animal can choose between adjacent sites with very different operative temperatures (e.g. Huey and Slatkin, 1976; Huey, 1991; Peterson et al., 1993).

Such sites may also differ in other ways relevant to the organism's biology: for example, an exposed site may offer better basking opportunities, but simultaneously increase vulnerability to predators and reduce rates of encounter with prey (Huey, 1974). Presumably, patterns of habitat selection reflect a compromise among these conflicting optima. The selection of an appropriate site is most important for sedentary animals, and especially for ambush (“sit-and-wait”) predators. Because they rely upon immobility for effective concealment, such animals cannot move about to track temporal shifts in weather conditions. They may thus need to forego precise

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thermoregulation (Hertz et al., 1993; Webb and Shine, 1998). In keeping with these ideas, previous studies have reported lower, more variable body temperatures in free-ranging pit-vipers than in sympatric active-foraging snakes (Secor and Nagy, 1994). Rattlesnakes selected higher, more stable temperatures after feeding (Beck, 1996), suggesting that they had tolerated lower more variable temperatures while waiting in ambush for prey.

The significance of this potential conflict between foraging and thermoregulation will depend upon the degree to which alternative potential ambush-sites do indeed constrain body temperatures in different ways. In a closed-canopy forest, for example, spatial heterogeneity in operative temperatures will usually be low, and hence most potential ambush-sites may be equivalent thermally. However, predators in many other habitat types may have to choose between alternative ambush sites that differ profoundly in their thermal consequences. We have studied such a system in insular pit-vipers on a small island in northeastern China.

The pit-vipers of Shedao are well-suited to analyse this topic for several reasons. First, the climate is cool. The snakes feed only at the beginning of spring and the end of autumn, immediately after and before the hibernation period respectively. Their prey—migrating passerine birds—also visit the island earlier in spring and later in autumn, but the snakes are inactive at these times (Sun et al., 1990; Li, 1995). Because ambient temperatures constrain the seasonal timing of feeding, we might expect thermal factors to play some role in foraging success. Laboratory trials confirm that hotter Shedao pit-vipers strike faster and further (Shine et al., 2002). Second, the snakes are sedentary and capture their prey from ambush (Li, 1995; Sun et al., 2000). Because the snake cannot move about to thermoregulate, its body temperature will be determined by its selection of an ambush site. Third, the two main alternative types of ambush site are in trees versus on the ground (Fig. 1), and biophysical modelling suggests that these alternatives may provide very different operative temperatures (Bakken and Gates, 1975). Fourth, pit-vipers localize prey items using specialized infrared detectors (loreal pits) that rely on thermal contrast between the prey item and the background (de Cock Buning et al., 1981; de Cock Buning, 1983). Hence, ambush sites may also differ in the ease with which snakes can detect prey using their loreal pits. To maximize the thermal contrast of prey versus background, a snake might forage in sites where a warm bird would stand out against a relatively cool background.

We visited Shedao for most of one spring feeding season to quantify the thermal attributes of arboreal versus terrestrial ambush sites, in terms of operative temperature regimes as well as thermal “backgrounds” for prey detection. We also measured body temperatures



Fig. 1. Shedao pit-vipers in ambush postures in a tree (a) and on the ground (b).

of snakes both in ambush positions in the field and when provided with a thermal gradient in captivity.

2. Material and methods

2.1. Study species and area

Shedao pit-vipers (*Gloydus shedaoensis*) occur on one small island in the Bohai Sea and also on montane areas of the nearby Liaodong Peninsula in northeastern China (Zhao and Adler, 1993). Despite their relatively large size (mean adult snout-vent length [SVL] 65–70 cm: Sun et al., 2000), 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 km² (Huang, 1989, 1990). In suitable habitats on the island, this translates into approximately one pit-viper per square meter (Koba, 1938; pers. obs.). Adult Shedao pit-vipers feed exclusively on birds (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 September–October: Sun et al., 1990). During

these periods the island is visited by thousands of migratory passerines, on their way to or from breeding areas in Siberia (de Schauensee, 1984; Li, 1995).

The snakes capture birds from ambush sites rather than by active searching. Typically, snakes remain immobile for hours at a time, only moving from their ambush positions at nightfall (Sun et al., 1990). Snakes lying in wait for prey adopt distinctive postures, with the fore-body in a concertina shape (Shine and Sun, 2002). Some snakes use tree branches as ambush sites, whereas others lie in wait on the ground (see Fig. 1). The vegetation in our study area consists of a mosaic of trees, shrubs and grassland. Most branches used by snakes are <1 m above the ground (Huang, 1989; Li, 1995; Shine and Sun, 2002). We stayed on Shedao from 2 to 17 May 2000, approximately 70% of the duration of the spring feeding season (Sun et al., 2000).

2.2. Operative temperatures

To characterize the range of body temperatures available to snakes in different microhabitats on Shedao, we used thermocouples inside physical (copper) models. These models were designed to estimate operative temperatures: that is, the body temperature that a snake would exhibit if exposed to that environment for long enough to attain thermal equilibrium (Peterson et al., 1993). Each model was 250 mm long and 31 mm in outside diameter, with walls 1 mm thick. They were sealed at each end with rubber stoppers, and spray-painted with Krylon all-purpose aluminium primer #1314 (reflectance 17.1%, total absorptivity 82.9%: Peterson et al., 1993). The probe from a Hobo-temp data-logger (Onset Computer Systems, Meadowbank, PA) was placed into the lumen of each model, and the logger was set to record temperatures at 15-min intervals.

To evaluate whether the copper models provided a realistic estimate of snake temperature, we conducted calibration trials. These trials consisted of finding a snake in an ambush pose in the field (during daylight hours), and carefully approaching it so that we could place a copper model nearby in a position with similar exposure to solar radiation, orientation, etc. The model was then left in place until it achieved thermal equilibrium, after which we measured surface temperatures of both the snake and the model using a Raytek 3I-LRSL2 infrared thermometer (Raynger, Santa Cruz, CA); this instrument reads temperature over a relatively small area (23 mm diameter at the lens, expanding to 71 mm at 6 m distance). External temperatures of Shedao pit-vipers measured in this way accurately estimate internal (cloacal) temperatures of the same snakes ($n = 27$, $r = 0.95$, slope = 0.98, $P < 0.0001$, range 9–31°C, mean temperature difference <0.8°C). Simultaneously measured internal and external

temperatures of our physical models also were highly correlated ($n = 14$, $r = 0.97$, slope = 1.01; $P = 0.0001$, range 17–26°C; mean difference 0.09°C). The field calibration trials showed a close relationship between surface temperatures of snakes (whether in trees or on the ground) and the surface temperatures of nearby models ($n = 25$ trials, $r = 0.86$, slope = 0.99; $P = 0.0001$, range 13–29°C; mean difference 0.02°C).

We set out eight copper models within the study area where we scored ambush sites of snakes. Two replicate models were taped to branches of trees (*Koelreuteria paniculata*) 1 m above the ground, in places where we had previously located snakes in ambush poses. Two other models were placed on the nearby ground in full shade, and two in full sun (one on a rock, and one on grass). We had seen snakes in all of these sites. Lastly, probes were buried either 30 or 50 cm deep underground to measure temperatures in soil crevices potentially accessible to the snakes.

2.3. Snake body temperatures

To quantify temperatures of snakes in ambush positions, we recorded body-surface temperature (again, with the Raytek infrared thermometer) from snakes in terrestrial sites and arboreal perches. To characterize a snake's thermal preferendum, however, we need to create a situation where the snakes have a wide range of temperatures potentially available to them, and with no confounding between temperature and other aspects (such as exposure to predators) that might also influence habitat selection (Hertz et al., 1993). To approximate these conditions, we erected an open-topped canvas arena measuring 1 × 1 m, with walls 1 m high. Four adult pit-vipers were captured and placed within the arena mid-morning (1000 h) on a fine sunny day (16 May). The walls of the arena shaded part of the floor, so that substrate temperatures over the range 22–45°C were available throughout the period (1100–1400 h) when we measured snake temperatures at 15-min intervals with the Raytek.

2.4. Thermal background of ambush sites and temperatures of potential prey items

Arboreal and terrestrial ambush sites might differ in the thermal background against which a snake would view its potential prey items. The facial pits that give pit-vipers their common name contain specialized thermoreceptors that are used to recognize and target prey (e.g. de Cock Buning et al., 1981; de Cock Buning, 1983; Chiszar et al., 1986). Thus, the thermal background of a perch might affect the snake's ability to detect a prey item, to evaluate whether or not it is ingestible, or to launch an effective foraging strike. We used the Raytek infrared thermometer to measure thermal backgrounds

and also prey items (birds). This instrument measures infrared radiation over the range 8–14 μ . 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 about 1–15 μ (Goris and Nomoto, 1967), and more recent work on pythonid pit-organs showed peak sensitivity at 8–12 μ (Grace et al., 1999). Thus, the instrument measures radiation over the same range as the snakes (and as emitted by avian prey, = approx. 10 μ : Grace et al., 1999). To measure the thermal background of an ambush site we removed the snake, then oriented the Raytek to face in the same direction (and at the same height above ground, etc.) as the snake had been facing. The trigger was then depressed for 3 s, and we used the averaging function of the Raytek to calculate mean temperature over that period as our measure of thermal background.

Although live birds maintain high and constant internal temperatures, feathers provide effective insulation and hence, the external surface of a bird (the attribute relevant to thermoreception by a foraging pit-viper) might be considerably cooler (or warmer) than the core temperature of the same bird (Hill et al., 1980). We measured surface temperatures of live birds (buntings, warblers, robins, etc.) captured in mist-nets on Shedao. Temperatures of birds were recorded <60 s after the bird hit the net. Capture rates in mist-nets were high in the morning and evening but low at midday, so we supplemented these data with temperature readings from birds kept in captivity. These included captive-bred canaries as well as wild-caught birds; analysis revealed no thermal difference between wild and captive specimens. To measure bird temperature, the Raytek was focussed on the bird's mid-body and a 3-s average reading recorded.

3. Results

3.1. Operative temperatures

We obtained data over a 12-day period for eight copper models. Fig. 2 shows data for two days with slightly different weather conditions. Both of these days were warm and sunny; temperatures inside all models remained relatively low and invariant during cold cloudy weather. Even on sunny days, temperatures in the soil remained low (<20°C: Fig. 2). On sunny days, however, models exposed to full sun on the ground rapidly heated to >30°C. In contrast, similar models exposed to full sun on tree branches rarely attained 25°C (Fig. 2). The major weather factor driving this difference was wind, as shown by thermal traces recorded on 7 May (Fig. 2a). Temperatures of the models on branches began to rise earlier than ground temperatures, because they were exposed to the sun's rays slightly earlier. However, the

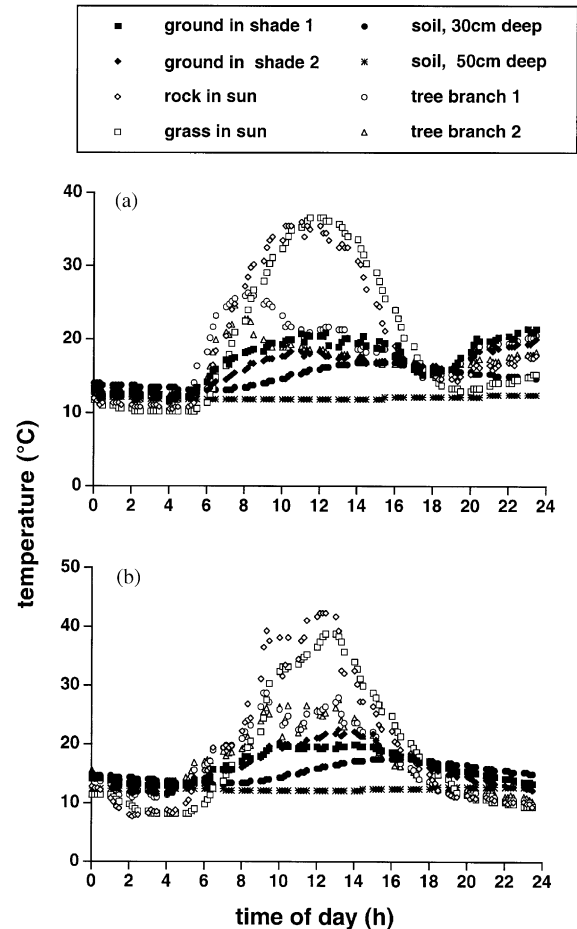


Fig. 2. Operative temperatures in physical (copper) models in a range of microhabitats on Shedao. Each graph shows data for a single day: 7 May (upper, a) and 12 May (lower, b) with slightly different weather conditions.

arboreal models rapidly cooled from 0800 h, despite the maintenance of fine sunny conditions throughout the day (as shown by the continued rise of temperatures inside ground models). The cooling of the arboreal models coincided with the arrival of strong winds at this time. In comparison, arboreal-model temperatures remained relatively high (although still cooler than ground models) on a day with only light winds (12 May: Fig. 2b). Thus, the general pattern is that models in trees were cooler than models on the ground, but that the magnitude of this difference varied with local weather conditions (especially, wind velocity).

3.2. Snake body temperatures

We obtained data for snake temperatures on three days (11, 12, 13 May). The analysis of these data needs

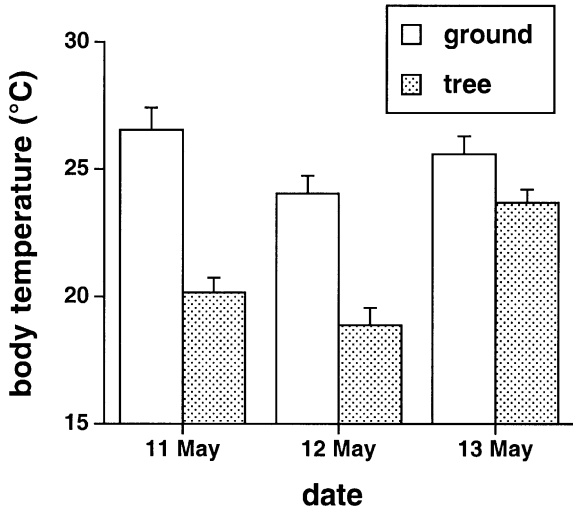


Fig. 3. Body temperatures of Shedao pit-vipers found in ambush poses in the field, as measured by dorsal skin temperature using an infrared thermometer. Histograms show mean values \pm one standard error. Sample sizes for 11, 12 and 13 May were: tree, 27, 20, 14; ground, 27, 19, 20. See text for statistical analysis of these data.

to include day as a factor because shifts in weather conditions are frequent on Shedao and may change operative temperatures (Fig. 2). On each day for which we have data, snakes in terrestrial ambush sites were significantly hotter than snakes in trees (Fig. 3). Overall, a two-factor ANOVA with date and “ground versus tree” as factors shows that snakes were hotter on the ground than in trees ($F_{1,121} = 52.19$, $P = 0.0001$). The thermal difference between tree and ground snakes was greater on some days than others (interaction term $F_{2,121} = 4.14$, $P = 0.018$), but the overall pattern was consistent (Fig. 3).

Our trials on captive snakes to measure selected temperatures provided 51 readings. The mean body temperature was 28.9°C (SD = 1.63; range 24.6–32.0°C). Most snakes were very close to this mean temperature; the range 28.5–30.5°C accounted for 78% of all readings.

3.3. Thermal background of ambush sites and temperatures of potential prey items

The surface temperatures of live birds varied over a wide range depending on local weather conditions, but were generally in the range from 15°C to 25°C (Fig. 4). Most of the ambush sites used by snakes faced towards backgrounds with temperatures cooler than this level. Many arboreal perches displayed thermal backgrounds well below 0°C (cloudless sky measured about -30°C). Arboreal perches generally had colder backgrounds than ground perches, and birds were warmer than either kind

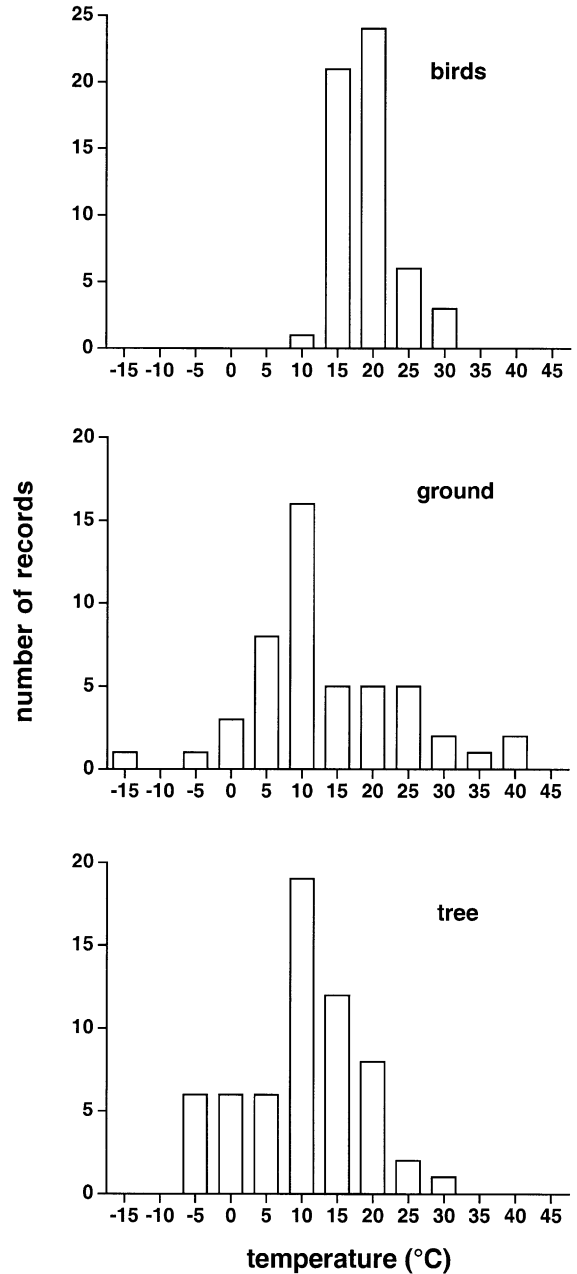


Fig. 4. Surface temperatures of live birds on Shedao compared to the thermal backgrounds available from terrestrial and arboreal foraging sites. These background temperatures were taken by pointing an infrared thermometer in the same direction as an ambushing pit-viper was oriented, and at the same height above ground. Sample sizes were: birds 55, ground 50; tree 60.

of background (mean values of 21.3°C for bird, 16.5°C for ground, and 12.5°C for tree). A one-factor ANOVA (based on ln-transformed values to normalize variances)

showed that the three distributions in Fig. 4 differed in average values ($F_{2,162} = 14.77$, $P = 0.0001$) and post-hoc (Fishers PLSD) tests confirmed that all three types differed significantly ($P < 0.05$) from each other. Nonetheless, the three distributions did overlap; in some situations, birds may not offer significant thermal contrast against the backgrounds available to foraging pit-vipers (Fig. 4).

4. Discussion

Our study on Shedao confirms that alternative ambush sites differ in thermal attributes, in ways that might affect the ability of a snake to capture prey. Specifically, snakes in trees may be more likely to “see” a prey item, but less able to capture it.

Snakes and copper models in trees were cooler than those on the ground, despite being exposed to similar levels of solar radiation (Fig. 2). Our data accord well with mathematical models and previous studies, in showing that an arboreal model’s greater exposure to wind results in it being coupled more closely to air temperature than to levels of radiation (Bakken and Gates, 1975). Terrestrial models are not only heated by their proximity to the ground, but also lie within a boundary-layer of low wind speed. In keeping with this hypothesis, the magnitude of thermal difference between tree and ground (for both snakes and models) differed among days with different wind speeds.

An alternative explanation for the lower body temperatures of arboreal snakes would involve active thermoregulation, but this idea is falsified by our data from copper models. Arboreal snakes are cool because they have no choice, rather than because they actively select low temperatures. Although our sample sizes for thermal preferences of captive snakes are small, they fit well with this scenario. Captive Shedao pit-vipers selected temperatures just below 30°C, very close to the levels reported for a diverse array of other pit-viper species (Avery, 1982; Mori et al., 2002). These data also accord with laboratory trials on the speed of defensive strikes by Shedao pit-vipers, showing that strikes were significantly faster from hotter snakes. In the laboratory, the temperature difference between arboreal and terrestrial snakes (from 20°C to 25°C: see Figs. 2 and 3) translated into a 15% increase in maximum strike speeds (from 1.49 to 1.72 m/s: Shine et al., 2002).

Birds are difficult prey items for snakes to capture, not only because they are fast-moving and agile, but also because they are able to travel in a medium (air) where the snakes not only cannot follow them, but also cannot detect chemical trails. Presumably for these reasons, very few snake species worldwide specialize on avian prey (Shine, 1983; Luiselli and Rugiero, 1993; Shine et al., 1996). Passerine birds on Shedao typically move

rapidly, rarely pausing at a single perching site (either in trees or on the ground) for more than 2 s (pers. obs.). Thus, a pit-viper lying in ambush may need to launch its foraging strike almost immediately. To do so, the snake must detect the bird and evaluate whether it is an appropriate prey item, a “decision” based on traits such as the size and temperature of the stimulus (Shine and Sun, 2002). These rapid evaluations are presumably facilitated by strong thermal contrast between the prey item and its background. Terrestrial ambush-sites generally provide a relatively warm background, because in most situations a terrestrial snake is facing towards the (warm) landscape rather than the (cold) sky. Thus, a snake on the ground may need to launch its strike at a bird that is only marginally warmer than the background (Fig. 4).

Intuition suggests that the very hot backgrounds of some terrestrial sites (Fig. 4) might be equally useful to the snakes in providing thermal contrast with birds. That is, the snakes’ thermoreceptors could detect the bird because it was cooler (instead of hotter) than the background. However, laboratory studies on a closely related *Gloydius* species suggest that snake thermoreceptors do not work in this way (de Cock Buning et al., 1981). They fire only in response to heat, not cold (unlike human temperature sensors). Thus, arboreal sites may offer better thermal backgrounds against which snakes can detect birds.

Nonetheless, the difference in thermal backgrounds might not significantly facilitate prey detection. First, the snake’s thermoreceptors may be so sensitive that even a trivial thermal difference between the bird and the background is sufficient for localization of prey (de Cock Buning et al., 1981; de Cock Buning, 1983). Second, our measurements of thermal background were taken at the range of angles (22° to 45° above horizontal) characteristic of arboreal perch sites (Shine and Sun, 2002). These angles are easily measured along the branches where the snakes’ heads lie. The angular orientations of the heads of snakes in terrestrial ambush sites are more difficult to measure, and some of these animals lie with the head facing almost directly upwards (see Fig. 1). Such snakes would have a very cold background against which to view approaching birds. These “head-up” postures may be widespread in pit-vipers waiting to ambush endothermic prey (e.g. see figures in Reinert et al., 1984; Brown and Greenberg, 1992). Thus, a small postural adjustment might negate the difference in thermal backgrounds between arboreal and terrestrial ambush sites.

The surface temperatures of live birds are much lower than their core temperatures (Fig. 4), because feathers provide effective insulation. Extensive studies on the relationship between ambient temperature and plumage surface temperatures in birds have revealed the same phenomenon (Hill et al., 1980), but researchers on

snakes have tended to assume that a live rodent or bird offers a thermal “target” of $>35^{\circ}\text{C}$. Indeed, some laboratory studies (Chiszar et al., 1986; Theodoratus et al., 1997) and field studies (Hayes and Duvall, 1991) have used models heated to these levels. Future work should simulate external (surface) temperatures of prey items more realistically. For example, subtle spatial variations in temperatures of different parts of the body (Hill et al., 1980) might offer reliable cues to direct a pit-viper’s strike.

We conclude that thermal factors do indeed differ between arboreal and terrestrial ambush sites, but in complex ways. Notably, a snake in a tree may be able to detect a bird’s location more easily, but be less capable of launching an effective strike to capture it. Plausibly, lower temperatures might confer benefits to a snake (reduced metabolic rates and water loss) as well as costs (lower strike speeds). We do not know whether or not these thermal issues play any significant role in ambush-site selection. Arboreal and terrestrial sites on Shedao differ in a host of other ways, such as the availability of birds of different body sizes (Sun et al., 1990; Li, 1995). Such variations may well outweigh the importance of thermal factors. Nonetheless, our data confirm that such habitat-selection decisions modify the thermal “world” experienced by an ambush predator and hence, potentially influence its selection of foraging sites.

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