

How important is temperature for strike success of ectotherms? Thermal effects on predator-prey interactions of free-ranging pit vipers (*Gloydius blomhoffii*)

Tomonori Kodama and Akira Mori

Department of Zoology, Graduate School of Science, Kyoto University, Sakyo, Kyoto, 606-8502, Japan;

Tomonori Kodama e-mail: asukamasuku@gmail.com place: Department of Zoology, Graduate School of Science, Kyoto University, Sakyo, Kyoto, 606-8502

Acknowledgements

We appreciate Alan H. Savitzky for careful and extensive review of the manuscript. We thank the staff of Takizawa Research Forest in the Field Science Center, Faculty of Agriculture, Iwate University for survey permission and assistance with data collection.

We also thank Hiroaki Yanagi, Ryobu Fukuyama, Shota Iyoda, and Yasunori Ohtake for their assistance during the research. Funding for this research was provided by JSPS Grant-in-Aid for Special Purposes grant Number JP21J23189 and Charitable Trust - Takara Harmonist Fund of 2020.

Abstract

Among various environmental factors, temperature has been considered a main determinant of outcomes of predator-prey interactions involving ectotherms. Although numerous studies have aimed to examine temperature effects on those interactions, few studies have been conducted under fully natural conditions. In this study, we examined the degree to which temperature affects the outcomes of encounters between a Japanese pit viper (Mamushi, *Gloydius blomhoffii*) and its prey under natural conditions. We continuously recorded ambushing behaviors and body temperatures of these snakes in the field using videography. We found that, over the range of temperatures at which Mamushi hunted, 1) temperature has only limited effects on whether mamushis initiate a strike at prey and whether strikes successfully hit the prey; 2) prey reactions to strikes, such as whether they dodge the strike or the latency from strike initiation to dodge, are not affected by temperature; and 3) factors such as distance to prey and prey dodging movements are greater determinants than temperature on the outcomes of encounters between free-ranging Mamushi and their prey. Our results suggest that temperature effects on the outcomes of free-ranging snake-prey interactions may be smaller than hitherto considered.

37 Keywords: Predator-prey interaction, Ectotherms, Temperature, Foraging, Snake,

38 Videography

39

40 Introduction

41 Predation and its avoidance are directly tied to survival in animals, and thus
42 evolutionary biologists have focused extensively on these behaviors. Predation is a
43 dynamic interaction that proceeds through several phases -- sometimes divided into
44 locate, decide, attack, and consume (Wootton et al. 2021) -- and ultimately results in
45 either successful capture or escape of prey. Consequently, in each phase, prey have
46 evolved diverse antipredator strategies to reduce predation risk, whereas predators have
47 evolved diverse strategies to increase the probability of predatory success. For example,
48 in the “attack” phase, various prey taxa have evolved acute sensory systems to detect
49 strikes and to initiate evasive maneuvers with high accelerations and short reaction
50 latency (Eaton 1984; Domenici et al. 2019; Freymiller et al. 2019). Conversely,
51 predators have evolved attacks involving crypsis or increased velocity and acceleration,
52 to defeat those defensive strategies (DeVries et al. 2012). These attributes by both
53 participants, which largely determine the outcomes of interactions between predators
54 and prey (Moore and Biewener 2015), are often affected by environmental conditions at
55 the time when the predator and prey encounter each other (the end of “locate” phase).
56 Thus, environmental factors are fundamental determinants of the outcomes of
57 encounters (Quinn and Cresswell 2004; Johansen and Jones 2013).

Specifically, predator-prey interactions involving ectotherms may be strongly influenced by temperature because almost all physical processes of ectotherms are temperature-dependent (Huey 1982). Accordingly, the thermal effects on strikes or evasive actions and the associated outcomes of predator-prey encounters involving ectotherms have been extensively studied across various systems and animal taxa. For example, the sprint speed of scorpions (*Parurotonus marksii*), which is considered an important factor in avoidance of predation, depends on temperature (Nisani et al 2022). The outcome of predator-prey interactions between reef fish, a planktivorous damselfish and a piscivorous dottyback, changes significantly as temperature varies: strike success increases by 41% with an increase in water temperature of only 3°C (Allan et al. 2015). Thermal effects on the feeding performance of squamates (lizards and snakes), which include most reptile species, have been also well studied. For example, Diaz (1994) showed that prey capture success and handling time by a lacertid lizard (*Psammodromus algirus*) feeding on flies significantly depended on the lizard's body temperature (T_b). In a laboratory experiment on a python (*Morelia spilota*), Ayers and Shine (1997) found that sensory performance of the python decreased at lower temperatures. Strike latency, velocity, and acceleration, as well as success rate, are affected by T_b across various taxa of snakes (Greenwald 1974; Vincent and Mori 2008;

Whitford et al. 2020). Collectively, most studies have concluded that temperature is a major factor determining the outcomes of predator-prey interactions involving ectotherms (Allan et al. 2015; Domenici et al. 2019; Greenwald 1974; Van Damme et al. 1991; Vincent and Mori 2008; Diaz 1994; Vucic-pestic et al. 2011; Wasserman et al. 2016).

Almost all previous analyses of thermal effects on the outcome of predator-prey encounters have been based on laboratory experiments (but see Putman and Clark 2017). Nonetheless a growing body of literature has shown that animal behaviors and performances differ between captive and natural conditions (Combes 2012; Moore and Biewener 2015; Whitford et al. 2020). Consequently, the extent of thermal effects on the performance of predators and prey may also differ between field and laboratory conditions. Therefore, previous laboratory studies should be complemented with observations and analyses of natural encounters between free-ranging individuals (Whitford et al. 2019b).

Among various ectothermic taxa, snakes, especially ambush-foragers such as viperid species, would be suitable model organisms for field observations of predator-prey encounters. They are particularly amenable to field observations because they can be located using radiotelemetry with minimal disturbance and their foraging behavior can

be recorded continuously with fixed-videography (reviewed in Clark 2016). A growing body of literature has shown the effectiveness of vipers as research subjects for collecting quantitative data on natural encounters between free-ranging predators and prey and for examining determinants on their outcomes (Barbour and Clark 2012; Clark et al. 2012; Glaudas and Alexander 2017; Whitford et al. 2019b). In hunting, vipers remain in a typical ambush-coiled posture for a prolonged period, and once a prey animal comes within the strike range, they elicit a rapid strike toward the prey, using envenomation to immobilize it (Clark 2016). Because of the prolonged immobile ambushing period, which ranges from several days to weeks (Clark et al. 2016; Glaudas and Alexander 2017), vipers can be exposed to a wide range of Tb (Ayers and Shine 1997; Putman and Clark 2017; Secor and Nagy 1994). Despite such ideal characteristics of the interactions between ambushing snakes and their prey, to the best of our knowledge only one study (Putman and Clark 2017) has examined thermal effects on the outcomes of natural encounters between free-ranging snakes and their prey. The results of that field study challenged the traditional view of thermal effects on foraging in ectotherms, which is that low Tb should constrain foraging performance. This example emphasizes the importance of field studies of thermal effects on outcomes of predatory interactions.

The outcomes of natural encounters between a snake and its prey have been shown to be affected by various additional factors, such as distance between the snake and prey and dodging reactions and predator-deterrent signals by the prey (Clark et al. 2012; Whitford et al. 2019a, b). Thus, to examine the relative importance of temperature among the various factors influencing the outcomes of such encounters, it is essential to adopt integrative, multivariate approaches. Here, we used fixed-videography on the Mamushi (*Gloydius blomhoffii*), a medium-sized pit viper widely distributed on the main islands of Japan (Matsui and Mori 2021). This species is a typical ambush predator, similar to other vipers, and the species' active body temperature in the field varies across a wide range (12.0–31.5°C, Mori 2021). Our goal was to understand the relative importance of temperature in the outcomes of natural encounters between the Mamushi and its prey by comparing the influence of temperature with that of other variables, such as distance to prey and dodging movements by the prey.

Materials and Methods

Study site and subjects

We conducted the field survey in the Takizawa Research Forest of Iwate University, Takizawa, Iwate, Japan. The survey site is a forest area composed mainly of cedars and

130 pines. We chose this site because of high densities of mamushis and their prey. The field
131 survey was conducted between 27 April and 16 October 2021 and between April and
132 August 2022. We captured adult mamushis and surgically implanted temperature-
133 sensitive transmitters (Models SB-2T, Holohil Systems Ltd) using the established
134 method of Reinert and Cundall (1982). Transmitter weights were $< 5\%$ of snake body
135 mass. Following recovering from surgery, the snake was released at its captured location
136 (typically within 24h of surgery). We generally relocated snakes at least two times per
137 24h and recorded body temperature and their behaviors. In total, we radiotracked three
138 males and 11 females (507–601 mm in snout-vent length).

139 Field videography

140 When a snake was found in a typical ambush hunting coil (Reinert et al. 2011), we
141 positioned an infrared light and video camera (HC-VX990M or HC-W850M, Panasonic
142 Ltd.) powered by a battery to record ambush behavior and all subsequent interactions
143 with prey animals (following the method of Clark, 2006). All cameras were equipped
144 with a radio-wave receiver (IC-R10 or IC-R 20, Telecom Ltd,.) that continuously
145 received the pulse of the transmitter signal. The pulse of the temperature-sensitive
146 transmitter implanted in the snake was thereby audibly recorded by the camera, to allow
147 Tb to be calculated later (see below).

Video analysis

Prey encounters

Mamushis feed on a variety of prey animals, from centipedes, fish, amphibians, reptiles, to small birds and mammals (Mori and Moriguchi 1988; Hamanaka and Mori 2014). Therefore, in the video analysis we considered any of the above animals that were small enough to be ingested as potential prey. Prey animals were identified to the lowest taxonomic level possible. We defined a prey encounter as any time in which prey animals came within a snake's strike range, i.e., 15 cm from the snake's snout (the furthest distance at which strike initiation was observed in this study).

To estimate distance between the prey and the snake from video frames, we used the method employed in previous studies (Clark et al. 2012; Clark et al. 2016), with minor modifications. Briefly, we used Image J software to determine the distance in images from videos, using snake head length (which had been measured before the surgery of each radio-tagged snake) as a size scale in each image. Because distance estimates are subject to some imprecision due to the variation of camera angles and positions, we estimated distances to the nearest 5cm (Clark et al. 2012; Clark et al. 2016).

In each prey encounter, we recorded the pulse rate of implanted temperature-sensitive

transmitters to determine snake Tb. The transmitters increased pulse rate with increasing temperature. We created calibration curves for each transmitter before implantation, and we calculated calibration equations using polynomial regression to derive temperature from pulse rates. By doing so, we were able to determine a snake's Tb from the video data at a given time.

Snake strikes and prey reaction

If prey came within strike range in a video, we determined the occurrence of a strike. If a snake initiated a strike, we determined the strike outcome. Because strikes of snakes are occasionally too rapid to record clearly at our low frame rate (30fps), we used the following two criteria to determine strike outcome. We categorized strikes as a hit if the head of a snake clearly contacted the prey or if the snake searched for prey after the strike, i.e., when strike-induced chemosensory searching (SICS, reviewed in Teshera and Clark 2021) occurred. We categorized strikes as a miss if the video clearly shows that the head did not contact the prey or if contact was ambiguous and a snake did not show SICS. This is because we assumed that when a snake struck prey but did not show SICS, the strike either did not make contact with the prey or the snake did not envenomate the prey during that contact. These criteria have been widely used in

various studies of pitvipers using field videography (Clark et al. 2012; Clark et al. 2016; Putman et al. 2016). For each strike initiation, we also determined whether prey dodging occurred in response to the strike. We categorized prey as dodging if the prey animal's post-strike trajectory of movement deviated from its pre-strike trajectory by greater than 45° (Clark et al. 2012). We also measured the dodging latency as the time from initiation of the strike to the first visible dodging movement of the prey, by counting the number of frames, if both movements could be confirmed.

Statistical analyses

To examine whether Tb influences Mamushi strike behavior and how important Tb is for strike success compared to other factors, we used multivariate logistic regression using penalized maximum likelihood, using the *logistf* package of R ver 4.2.2 (Puhr et al. 2017). Due to the small sample size of our dataset, we limited our models to one or two predictor variables in addition to Tb and only included variables that we considered highly likely to influence strike initiation and outcome. To examine the influence on strike initiation when prey came within strike range (a binary response variable, ‘yes’ or ‘no’), we included distance and Tb as predictor variables. To examine the influence on strike outcome when a strike was initiated (a binary response variable, “hit” or

“missed”), we included prey dodge movement (a binary response variable, “dodge” or “not”), as well as distance and Tb as predictor variables. Although we recorded multiple strikes in some individuals (a total of 20 strikes from nine individual snakes were used in the statistical analysis; 1–6 strikes per snake, median=2), we treated all events as independent samples because they probably all involved independent prey items under unique field circumstances (e.g., different spatial locations and times, and high density of prey animals) (Clark 2012; Barbour and Clark 2012; Clark et al. 2016). To examine whether ambient temperature influenced the occurrence and latency of prey dodging movement, we ran a univariate logistic regression (by using the *logistf* package) and a linear regression, respectively, including snake Tb as a predictor variable for both analyses. We used snake Tb as the estimated ambient temperature because active snake Tb at night generally shows a high correlation with ambient temperatures (i.e., air or substrate temperature) and those temperatures are nearly equal (Mori et al. 2002). All values are given as mean $\pm$ SD.

Results

Snake-prey encounters

A total of 54 snake-prey encounters was recorded. Sample video recordings are

available on the website (<https://www.youtube.com/@TomonoriKodama-vd2no/videos>).

Mamushis encountered various prey species (Table 1, Table S1). Among them, 46% encounters resulted in initiation of a strike. Eight of the 25 strikes appeared to result in success, yielding a strike success rate of 32%. After successful strikes, snakes released all the mammalian prey, whereas they retained all the frog prey (mammal: 6/6, frog: 2/2). Two encounters were excluded from the statistical analysis of strike initiation because of the difficulty of estimating distance, due to the high density of bushes. Five strikes were also excluded from the statistical analysis of strike outcome, due to the difficulty of determining the occurrence of prey dodge.

Determinants of strike initiation

A total of 52 encounters, involving 10 snakes (1–11 encounters per one snake), was included in our analysis of strike initiation (Sample sizes of strike initiation and no initiation: 23 and 29, respectively, Figure 1). Distances between Mamushi and prey when snakes initiated strikes were 7.39 ± 3.3 (range: 5–15 cm), and distances when snakes did not initiate strikes were 9.83 ± 4.33 (5–15 cm). Prey encounters and strike initiation were both recorded across a wide range of snake Tb (encounter: 11.4–26.7°C, strike initiation: 13.4–25.8°C). Decreased distance between prey and predator significantly increased the probability of strike initiation (likelihood ratio: 6.49, $df = 2$,

95%CI = -0.34--0.029, $\chi^2 = 5.63$, $P = 0.018$). The probability of strike initiation was not affected by snake Tb (likelihood ratio: 6.49, $df = 2$, 95%CI = -0.044--0.30, $\chi^2 = 1.99$, $P = 0.16$).

Determinants of strike outcome

Twenty strikes from 9 snakes were included in our analysis of strike outcome (Figure 2). Prey dodge movements occurred in 1 of 6 hit strikes and in all 14 missed strikes. Distances between the Mamushi and prey animal in the case of hit strikes were 5–10 cm (mean distance: 6.67 ± 2.58 cm), and those in the case of missed strikes were 5–15 cm (7.5 ± 3.80 cm). Hit and missed strikes were recorded across a wide range of snake Tb (hit: 16.1–25.8°C; missed: 13.4–24.9°C). Prey dodging behavior significantly decreased the probability of strike success (likelihood ratio: 13.29, $df = 3$, 95%CI = -11.34--1.38, $\chi^2 = 9.99$, $P = 0.002$). Conversely, the probability of strike success was not influenced by either snake Tb (likelihood ratio: 13.29, $df = 3$, 95%CI = -0.33--1.54, $\chi^2 = 0.58$, $P = 0.45$) or distance (likelihood ratio: 13.29, $df = 3$, 95%CI = -0.50--0.50, $\chi^2 = 0.001$, $P = 0.97$).

Thermal effects on prey reaction

The probability of prey dodge movement was not affected by the estimated ambient temperature (likelihood ratio: 0.70, $df = 1$, 95%CI = -0.38--0.24, $\chi^2 = 0.15$, $P = 0.70$).

We determined prey dodging latency in 13 cases out of the 20 strikes. Prey showed dodging movement within 116.67 ± 52.70 ms (33.33 – 200). Prey dodging latency was also not affected by estimated ambient temperature ($F = 1.20$, $R^2 = 0.13$, $P = 0.31$, Figure 3).

Discussion

The main finding of this study is that in natural encounters between an ectothermic predator and its prey, temperature did not have strong effects on either strike initiation or strike outcome. For strike initiation, distance to prey was a more important determinant, and for strike outcome, the occurrence of prey dodging movements was more important. In addition, prey reaction to strikes was not affected by ambient temperature. These results challenge some key assumptions of previous studies of thermal effects on foraging behaviors of ectotherms (Allan et al. 2015; Ayers and Shine 1997; Greenwald 1974; Vincent and Mori 2008; Diaz 1994), but they lend support to the results of recent studies on rattlesnakes (Putman and Clark 2017; Whitford et al. 2020b).

Our results showed that, when encountering prey, snakes either did or did not strike across a wide range of T_b , and only the distance to prey significantly affected initiation

of the strike. These results suggest that snake Tb does not exert a strong effect on strike initiation. Ectotherms would refrain from striking prey at low Tb, if the temperature exerts strong deleterious effects on their performance by influencing variables such as prey detection and effectiveness of the strike. However, these performance variables of snakes are unlikely to be strongly affected by Tb during prey encounters involving Mamushi. First, with regard to detection of prey, sensory performance of snakes detecting prey with facial pits, especially within the strike range, may not be affected by Tb based on the following evidence. Pitvipers and most boid and pythonid snakes are generally believed to use thermal images generated by pit organs to sense, identify and target prey, in addition to using chemical and visual cues (de Cock Buning 1983). Hayes and Duval (1991) suggested that rattlesnakes do not need chemical cues during strike initiation to effectively target prey within the strike range. Thus, in detecting prey within the strike range, chemical cues may play a less important role than thermal or visual cues. The infrared imaging systems rely on thermal contrast, rather than absolute temperature (Van Dyke and Grace 2010; Chen et al. 2017). Another field study also suggested that arboreal pitvipers (*Gloydius shedaoensis*) select ambush sites that provide them with backgrounds of lower temperature, which may enable them to create thermal images of small avian prey with higher contrast (Shine and Xin 2002).

Moreover, a study showed that Pacific rattlesnakes (*Crotalus oreganus*) with lower Tb show increased sensitivity to infrared stimuli, although the mechanisms remain unclear (Bakken et al. 2018). Collectively, lower ambient and body temperatures may actually improve sensory performance within the strike range by providing snakes with clearer images of ectothermic prey against a high-contrast background.

Second, Tb may not strongly affect the outcome of snake predatory encounters, as discussed in detail below. This implies that Tb may not strongly affect strike performance (i.e., their predatory strike may have a wide optimal thermal range), and therefore the decision whether or not to strike prey may not depend on Tb.

Even if low Tb at prey encounters negatively affects snake performance, mamushis may be motivated to initiate a strike regardless of Tb. This is related to the characteristics of the ambush foraging mode. Generally, prey encounter rates of ambushing snakes under natural conditions are low (Clark 2006; Clark et al. 2016; Putman and Clark 2017; Glaudas and Alexander 2017). Thus, if mamushis do not perform strikes at sub-optimal temperatures, that would represent a significant opportunity loss. In addition, during the time snakes are ambushing prey, movement for thermoregulation may be costly, because movement may result in breaking crypsis, as well as in energetic loss. Breaking crypsis would lead to an increase in predation risk

and subsequent opportunity loss to encounter prey (Clark 2016). A recent study implied that pitvipers in an ambushing coil may be highly cryptic to predators and thus may be at low predation risk (Maag and Clark 2022). Considering the three possible reasons described above, there may be selection pressure for ambushing snakes to maintain motivation to strike at prey regardless of Tb.

Our results also showed that 1) both successful and unsuccessful strikes occurred across a wide range of Tbs, which largely overlapped each other; 2) only the occurrence of prey dodging significantly affected strike outcome; and 3) the occurrence and latency of prey dodging were not affected by estimated ambient temperature. Although our sample size is relatively small, these results suggest that snake Tb does not strongly affect strike outcomes. With regard to determinants of strike success of rattlesnakes feeding on mammalian prey under natural conditions, Whitford et al. (2019b) showed that neither strike velocity nor distance to prey significantly affect strike outcomes, whereas strike accuracy and reaction time of prey do have an effect, indicating that accuracy and lack of awareness by prey are more important determinants of successful strikes than is speed. This interpretation also seems to apply to strikes of Mamushi, in which our study shows that the occurrence of prey dodging has a highly significant effect on strike outcome. A recent study of thermal effects on predatory strike

kinematics of rattlesnakes, examining velocity, acceleration, and distance to prey, showed that only acceleration is significantly affected by Tb of the snake (Whitford et al. 2020b). That study also found that thermal effects on those variables are smaller in predatory strikes than in defensive strikes, concluding that rattlesnakes may maximize accuracy rather than speed during predatory strikes, reflecting an assumed tradeoff between speed and accuracy in animal performance. Given these previous studies and our results, body temperature does not seem to be a major determinant of strike success, although no study has directly examined thermal effects on strike accuracy. In addition, from the standpoint of prey, the present study showed that evasive responses to strikes also were not affected by temperature, which are major determinants of strike outcomes in viperid snakes (Clark et al. 2012; Clark et al. 2016; Whitford et al. 2019b; the present study). This is partly because most prey in the present study were endotherms, for which physiological processes are not highly sensitive to variation in ambient temperature. Although we recorded strikes to frogs four times (see Figure.3 and Table. S1), we did not compare temperature effects on dodging reaction between these ectothermic and endothermic prey because of the limited sample size. Future studies should examine the relationships between the effects of temperature on strike outcome and prey types in detail. Collectively, it is likely that the effects of temperature on the outcome of strikes

by mamushis might be limited because the major determinants of strike outcome for both parties do not depend on temperature.

Although temperature effects on the initiation and outcome of strikes in pitvipers are limited, the effects on other aspects of foraging may not be ignored. For example, injection of a sufficient amount of venom during the brief duration of fang contact is necessary for successful ingestion. Snake venom has at least two major functions: 1) rapid immobilization of prey and 2) facilitation of prey relocation. Venomous snakes, especially pitvipers, generally release dangerous prey (e.g., mammals or large prey) after envenomation, and the prey is relocated through scent trailing after its death (SICS; Teshera and Clark 2021). In SICS, injected venom provides chemical cues of envenomated prey to the snake, which enables the snake to trail that specific prey item. It is possible that considering the thermal dependency of muscle contractions that pressurize the venom glands, the amount of injected venom may be affected by Tb. If the quantity of venom that is injected decreases, the probability and speed of immobilizing prey would decrease, and accordingly its escape distance would increase (Hayes 1995; Hayes et al. 2002). Thus, if the amount of venom delivered depends on Tb, the success rate of both immobilizing and relocation of prey would be affected by Tb. Furthermore, considering the thermal dependence of snake locomotor performance

(Stevenson et al. 1985; Gerald et al. 2008), lower Tb may result in longer relocation of prey, leading to a lower success rate of prey ingestion due to the robbery of the carcass by other animals or due to disturbance by potential predators of the snake. Indeed, field observations on pitvipers (Clark 2016; Kodama, personal observation; Whitford et al. 2019) show that even when snakes successfully strike prey, the snakes sometimes fail to ingest their meals. Further studies on various aspects of foraging are strongly desired in order to gain a comprehensive understanding of thermal effects on snake-prey interactions.

A field study of rattlesnakes (*Crotalus oreganus*) showed that the mean Tbs did not significantly differ between when snakes strike prey and when they do not, and between when strikes hit the target and when they missed (Putman and Clark 2017). The similarity between their results and ours provides support for our conclusions that the thermal effects on outcomes of encounters between free-ranging snakes and prey are limited, at least in pitvipers. Nonetheless, studies of thermal effects on predator-prey interactions under natural conditions are still quite meager in any taxon. Future studies focusing on other taxa of ectotherms having different habitats, hunting strategies, and adaptive traits are strongly desired, to clarify whether such limited thermal effects on predator-prey interactions are ubiquitous among predatory ectotherms.

382

383 Data availability statement

384 The data in the present study are included in the supplementary online material (table
385 S1).

386

387 Ethical statement

388 We followed all protocols for the safe and humane handling and use of animals as
389 approved by the Regulation on Animal Experimentation at Kyoto University (Nos.
390 202118, 202216).

391

392 Conflict of interest

393 The authors declare no competing interests.

394

395 References

396 Allan, B. J., Domenici, P., Munday, P. L., & McCormick, M. I. (2015). Feeling the heat:
397 the effect of acute temperature changes on predator–prey interactions in coral reef
398 fish. *Conservation Physiology*, 3, cov011. doi: 10.1093/conphys/cov011.

399 Anderson, N. L., Hetherington, T. E., Coupe, B., Perry, G., Williams, J. B., & Lehman,

400 J. (2005). Thermoregulation in a nocturnal, tropical, arboreal snake. *Journal of*
 401 *Herpetology*, 39, 82–90. doi: 10.1670/0022-1511(2005)039[0082:TIANTA]2.0.CO;2
 402 Ayers, D. Y., & Shine, R. (1997). Thermal influences on foraging ability: body size,
 403 posture and cooling rate of an ambush predator, the python *Morelia*
 404 *spilota*. *Functional Ecology*, 11, 342–347. doi: 10.1046/j.1365-2435.1997.00093.x
 405 Barbour, M. A., & Clark, R. W. (2012). Ground squirrel tail-flag displays alter both
 406 predatory strike and ambush site selection behaviours of rattlesnakes. *Proceedings of*
 407 *the Royal Society B: Biological Sciences*, 279, 3827–3833. doi:
 408 10.1098/rspb.2012.1112
 409 Bakken, G. S., Schraft, H. A., Cattell, R. W., Tiu, D. B., & Clark, R. W. (2018). Cooler
 410 snakes respond more strongly to infrared stimuli, but we have no idea why. *Journal of*
 411 *Experimental Biology*, 221, jeb182121. doi:10.1242/jeb.182121
 412 Chen, Q., Liu, Y., Brauth, S. E., Fang, G., & Tang, Y. (2017). The thermal background
 413 determines how the infrared and visual systems interact in pit vipers. *Journal of*
 414 *Experimental Biology*, 220, 3103–3109. doi: 10.1242/jeb.155382
 415 Clark, R. W. (2006). Fixed videography to study predation behavior of an ambush
 416 foraging snake, *Crotalus horridus*. *Copeia*, 2006, 181–187. doi: 10.1643/0045-
 417 8511(2006)6[181:FVTSPB]2.0.CO;2

418 Clark, R. W. (2016). The hunting and feeding behavior of wild rattlesnakes. In Schuett,
 419 G. W., Felder, M. J., Smith, C. F., & Reiserer R. S. (Eds.), *Rattlesnakes of Arizona*, 2,
 420 (pp.58–91). Eco Publishing, Rodeo.

421 Clark, R. W., Tangco, S., & Barbour, M. A. (2012). Field video recordings reveal factors
 422 influencing predatory strike success of free-ranging rattlesnakes (*Crotalus*
 423 spp.). *Animal Behaviour*, 84, 183–190. doi: 10.1016/j.anbehav.2012.04.029

424 Clark, R. W., Dorr, S. W., Whitford, M. D., Freymiller, G. A., & Putman, B. J. (2016).
 425 Activity cycles and foraging behaviors of free-ranging sidewinder rattlesnakes
 426 (*Crotalus cerastes*): the ontogeny of hunting in a precocial vertebrate. *Zoology*, 119,
 427 196–206. doi: 10.1016/j.zool.2016.02.005

428 Combes, S. A., Rundle, D. E., Iwasaki, J. M., & Crall, J. D. (2012). Linking
 429 biomechanics and ecology through predator–prey interactions: flight performance of
 430 dragonflies and their prey. *Journal of Experimental Biology*, 215, 903–913. doi:
 431 10.1242/jeb.059394

432 de Cock Buning, T. (1983). Thermal sensitivity as a specialization for prey capture and
 433 feeding in snakes. *American Zoologist*, 23, 363–375. doi: 10.1093/icb/23.2.363

434 DeVries, M. S., Murphy, E. A. K., & Patek, S. N. (2012). Strike mechanics of an
 435 ambush predator: the spearing mantis shrimp. *Journal of Experimental Biology*, 215,

436 4374–4384. doi: 10.1242/jeb.075317

437 Díaz, J. A. (1994). Effects of body temperature on the predatory behaviour of the lizard

438 *Psammodromus algirus* hunting winged and wingless prey. *Herpetological*

439 *Journal*, 4, 145–150.

440 Domenici, P., Allan, B. J., Lefrançois, C., & McCormick, M. I. (2019). The effect of

441 climate change on the escape kinematics and performance of fishes: implications for

442 future predator–prey interactions. *Conservation Physiology*, 7, coz078. doi:

443 10.1093/conphys/coz078

444 Eaton, R. C., & Hackett, J. T. (1984). The role of the Mauthner cell in fast-starts

445 involving escape in teleost fishes. In Eaton, R. C. (Ed.), *Neural Mechanisms of*

446 *Startle Behavior* (pp. 213–266). Springer, Boston.

447 Freymiller, G. A., Whitford, M. D., Higham, T. E., & Clark, R. W. (2019). Escape

448 dynamics of free-ranging desert kangaroo rats (Rodentia: Heteromyidae) evading

449 rattlesnake strikes. *Biological Journal of the Linnean Society*, 127, 164–172. doi:

450 10.1093/biolinnean/blz027

451 Gerald, G. W., Mackey, M. J., & Claussen, D. L. (2008). Effects of temperature and

452 perch diameter on arboreal locomotion in the snake *Elaphe guttata*. *Journal of*

453 *Experimental Zoology Part A: Ecological Genetics and Physiology*, 309, 147–156.

doi: 10.1002/jez.443

Glaudas, X. & Alexander, G. J. (2017). A lure at both ends: aggressive visual mimicry signals and prey-specific luring behaviour in an ambush-foraging snake. *Behavioral Ecology and Sociobiology* 71. doi: 10.1007/s00265-016-2244-6

Glaudas, X. & Rodríguez-Robles, J. A. (2011). A two-level problem: habitat selection in relation to prey abundance in an ambush predator, the speckled rattlesnake (*Crotalus mitchellii*). *Behaviour*, 148, 1491–1524. doi: 10.1163/156853912X623739.

Greenwald, O. E. (1974). Thermal dependence of striking and prey capture by gopher snakes. *Copeia*, 141–148. doi: 10.2307/1443016

Hamanaka, K., Mori, A., & Moriguchi, H. (2014). Literature survey on food habit of snakes in Japan: Revisited. *Bulletin of the Herpetological Society of Japan* 2014: 167–181.

Hayes, W. K. (1995). Venom metering by juvenile prairie rattlesnakes, *Crotalus v. viridis*: effects of prey size and experience. *Animal Behaviour*, 50, 33–40. doi: 10.1006/anbe.1995.0218

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

Hayes, W. K., Herbert, S. S., Rehling, G. C., & Gennaro, J. F. (2002). Factors that

472 influence venom expenditure in viperids and other snake species during predatory
 473 and defensive contexts. In Schuett, G. W., Hogren, M. Douglas, M. E., & Green, H.
 474 W. (Eds.), *Biology of the Vipers*, (pp. 207–233). Eagle Mountain Publishing, UT.
 475 Higham, T. E., Stewart, W. J., & Wainwright, P. C. (2015). Turbulence, temperature, and
 476 turbidity: the ecomechanics of predator–prey interactions in fishes. *Integrative and*
 477 *Comparative Biology*, 55, 6–20. doi: 10.1093/icb/icv052
 478 Huey, R. B., 1982. Temperature, physiology and the ecology of reptiles. In: Gans, C.,
 479 Pough, F.H. (Eds.), *Biology of the Reptilia. Physiology C. Physiological Ecology*
 480 (pp.25–67). Academic Press, London.
 481 Johansen, J. L., & Jones, G. P. (2013). Sediment-induced turbidity impairs foraging
 482 performance and prey choice of planktivorous coral reef fishes. *Ecological*
 483 *Applications*, 23, 1504–1517. doi: 10.1890/12-0704.1. PMID: 24147419.
 484 Maag, D., & Clark, R. (2022). Safety in coils: predation rates of ambush hunting
 485 rattlesnakes are extremely low. *Amphibia-Reptilia*, 43, 1–6. doi: 10.1163/15685381-
 486 bja10101
 487 Manjarrez, J., & Drummond, H. (1996). Temperature-limited activity in the garter snake
 488 *Thamnophis melanogaster* (Colubridae). *Ethology*, 102, 146–156. doi:
 489 10.1111/j.1439-0310.1996.tb01112.x

490 Mori, A. & Moriguchi, H. (1988). Food habits of the snakes in Japan: A critical review.
 491 *Snake*, 20: 98–113.

492 Mori, A. (2021). Ecological traits of a common Japanese pit viper, the Mamushi
 493 (*Gloydus blomhoffii*), in Kyoto, with a brief geographic comparison. *Current*
 494 *herpetology*, 40, 92–102. doi: 10.5358/hsj.40.92

495 Moore, T. Y., & Biewener, A. A. (2015). Outrun or outmaneuver: predator–prey
 496 interactions as a model system for integrating biomechanical studies in a broader
 497 ecological and evolutionary context. *Integrative and Comparative Biology*, 55, 1188–
 498 1197. doi: 10.1093/icb/icv074

499 Nisani, Z., Cardenas, V., & Cox, J. (2022). Thermal ecology and the relationship
 500 between temperature and sprint speed in adult females *Paruroctonus marksii*
 501 (Scorpiones: Vaejovidae). *Journal of Arid Environments*, 197, 104675. doi:
 502 10.1016/j.jaridenv.2021.104675

503 Puhr, R., Heinze, G., Nold, M., Lusa, L., & Geroldinger, A. (2017). Firth's logistic
 504 regression with rare events: accurate effect estimates and predictions?. *Statistics in*
 505 *Medicine*, 36, 2302–2317. doi: 10.1002/sim.7273

506 Putman, B. J., Barbour, M. A., & Clark, R. W. (2016). The foraging behavior of free-
 507 ranging rattlesnakes (*Crotalus oreganus*) in California ground squirrel

508 (*Otospermophilus beecheyi*) colonies. *Herpetologica*, 72, 55–63.

509 Putman, B. J., & Clark, R. W. (2017). Behavioral thermal tolerances of free-ranging

510 rattlesnakes (*Crotalus oreganus*) during the summer foraging season. *Journal of*

511 *Thermal Biology*, 65, 8–15. doi: 10.1016/j.jtherbio.2017.01.012

512 Quinn, J. L., & Cresswell, W. (2004). Predator hunting behaviour and prey

513 vulnerability. *Journal of Animal Ecology*, 73, 143–154.

514 Reinert, H. K., & Cundall, D. (1982). An improved surgical implantation method for

515 radio-tracking snakes. *Copeia*, 1982, 702–705. doi: 10.2307/1444674

516 Reinert, H. K., MacGregor, G. A., Esch, M., Bushar, L. M., & Zappalorti, R. T. (2011).

517 Foraging ecology of timber rattlesnakes, *Crotalus horridus*. *Copeia*, 2011, 430–442.

518 doi: 41261900

519 Secor, S. M., & Nagy, K. A. (1994). Bioenergetic correlates of foraging mode for the

520 snakes *Crotalus cerastes* and *Masticophis flagellum*. *Ecology*, 75, 1600–1614. doi:

521 10.2307/1939621

522 Shine, R., & Li-Xin, S. (2002). Arboreal ambush site selection by pit-vipers *Gloydus*

523 *shedaoensis*. *Animal Behaviour*, 63, 565–576. doi: 10.1006/anbe.2001.1928

524 Stevenson, R. D., Peterson, C. R., & Tsuji, J. S. (1985). The thermal dependence of

525 locomotion, tongue flicking, digestion, and oxygen consumption in the wandering

526 garter snake. *Physiological Zoology*, 58, 46–57.

527 Takeuchi, H. (2021). Viperidae. In: Herpetological Society of Japan (ed.), *Amphibians*
528 *and Reptiles of Japan* (pp. 195–202). Sunrise Publishing, Hikone.

529 Teshera, M. S., & Clark, R. W. (2021). Strike-induced chemosensory searching in
530 reptiles: a review. *Herpetological Monographs*, 35, 28–52. doi: 10.1655/0733-1347-
531 35.1.28

532 Van Damme, R., Bauwens, D., & Verheyen, R. F. (1991). The thermal dependence of
533 feeding behaviour, food consumption and gut-passage time in the lizard *Lacerta*
534 *vivipara* Jacquin. *Functional Ecology*, 5, 507–517. doi: 10.2307/2389633.

535 Van Dyke, J. U., & Grace, M. S. (2010). The role of thermal contrast in infrared-based
536 defensive targeting by the copperhead, *Agkistrodon contortrix*. *Animal Behaviour*, 79,
537 993–999. doi: 10.1016/j.anbehav.2010.01.012

538 Vincent, S. E., & Mori, A. (2008). Determinants of feeding performance in free-ranging
539 pit-vipers (Viperidae: *Ovophis okinavensis*): key roles for head size and body
540 temperature. *Biological Journal of the Linnean Society*, 93, 53–62. doi:
541 10.1111/j.1095-8312.2007.00928.x

542 Vucic-Pestic, O., Ehnes, R. B., Rall, B. C., & Brose, U. (2011). Warming up the system:
543 higher predator feeding rates but lower energetic efficiencies. *Global Change*

544 *Biology*, 17, 1301–1310. doi: 10.1111/j.1365-2486.2010.02329.x

545 Wasserman, R. J., Alexander, M. E., Weyl, O. L., Barrios-O'Neill, D., Froneman, P. W.,

546 & Dalu, T. (2016). Emergent effects of structural complexity and temperature on

547 predator–prey interactions. *Ecosphere*, 7, e01239. doi: 10.1002/ecs2.1239

548 Whitford, M. D., Freymiller, G. A., & Clark, R. W. (2019a). Managing predators: The

549 influence of kangaroo rat antipredator displays on sidewinder rattlesnake hunting

550 behavior. *Ethology*, 125, 450–456. doi: 10.1111/eth.12869

551 Whitford, M. D., Freymiller, G. A., Higham, T. E., & Clark, R. W. (2019b).

552 Determinants of predation success: how to survive an attack from a

553 rattlesnake. *Functional Ecology*, 33, 1099–1109. doi: 10.1111/1365-2435.13318

554 Whitford, M. D., Freymiller, G. A., Higham, T. E., & Clark, R. W. (2020). The effects of

555 temperature on the kinematics of rattlesnake predatory strikes in both captive and

556 field environments. *Integrative Organismal Biology*, 2, obaa025. doi:

557 10.1093/iob/obaa025

558 Wootton, K. L., Curtsdotter, A., Roslin, T., Bommarco, R., & Jonsson, T. (2021).

559 Towards a modular theory of trophic interactions. *Functional Ecology*, 37, 26–43.

560 doi: 10.1111/1365-2435.13954

561

Table 1. The total numbers of prey encounters and their outcomes recorded with video. Some of them were excluded from the statistical analysis because of low quality of video images. Numbers in parentheses indicate sample sizes used for statistical analyses.

Prey type	Prey species	Encounter	Strike initiation	Strike success
Mammal	<i>Apodemus speciosus</i>	32 (31)	16 (15)	5 (4)
	<i>Apodemus argenteus</i>	2 (2)	0	0
	<i>Microtus montebelli</i>	1 (1)	1 (1)	0
	<i>Urotrichus talpoides</i>	2 (2)	0	0
	Unknown	8 (7)	2 (0)	1 (0)
Frog	<i>Rana tagoi</i>	4 (4)	2 (1)	1 (1)
	<i>Dryophytes japonicus</i>	2 (2)	2 (1)	1 (1)
	Unknown	2 (2)	2 (2)	0
Bird	Unknown	1 (1)	0	0
Total		54 (52)	25 (20)	8 (6)

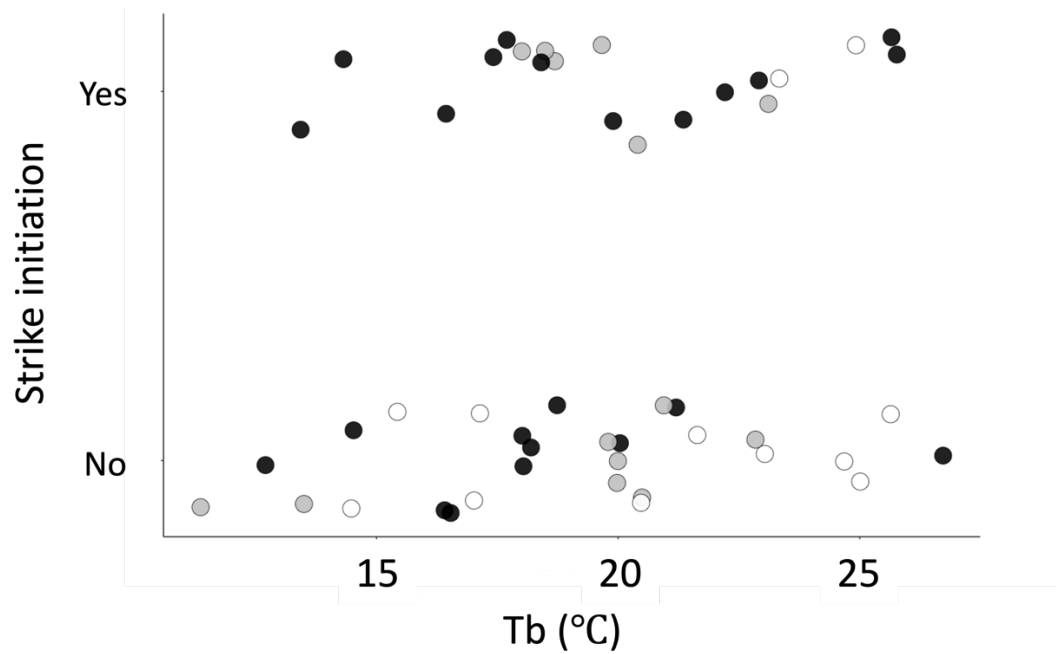


Figure 1. Response of Mamushi (strike, Yes; no strike, No) to prey coming within the strike range (15cm), at various body temperatures (Tb). The color of the points indicates distance to prey: black, 5cm; gray, 10cm; white, 15cm. We jittered the location of data points around Yes and No to avoid overlapping values; the values are binary, and all data points are either Yes or No.

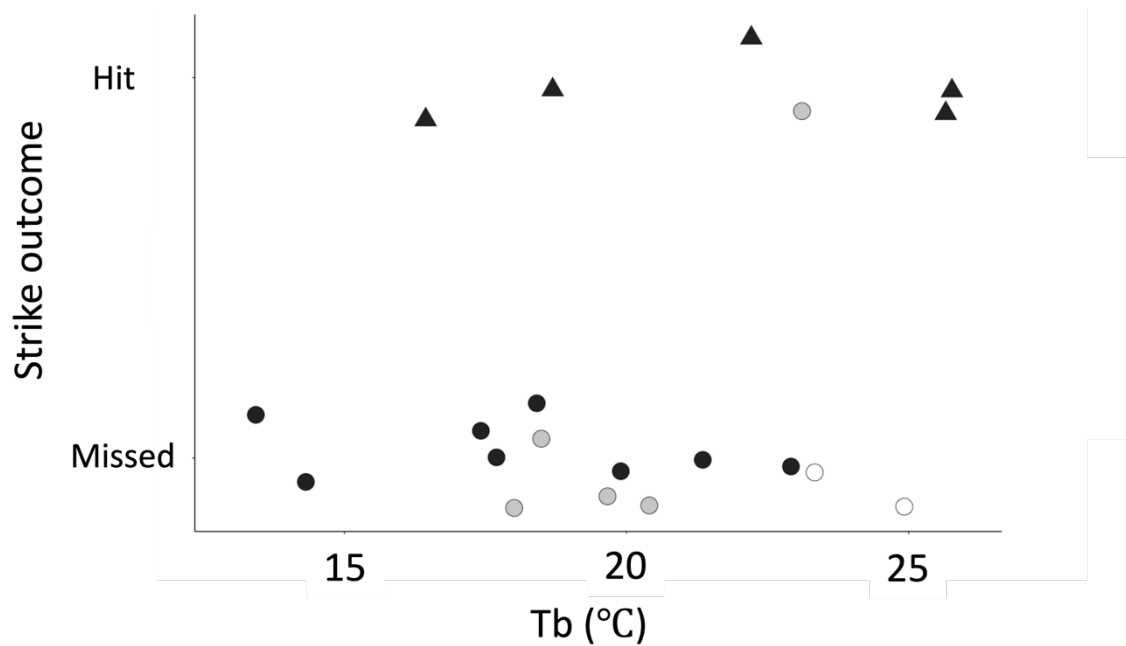


Figure 2. Strike outcomes (Hit or Missed) of each strike at prey, at various body temperatures (Tb). The color of the points indicates distance to prey; black, 5cm; gray, 10cm; white, 15cm. Circles and triangles indicate that prey dodged or did not dodge, respectively. We jittered the location of data points around Hit and Missed to avoid overlapping values; the values are binary, and all data points were either Hit or Missed.

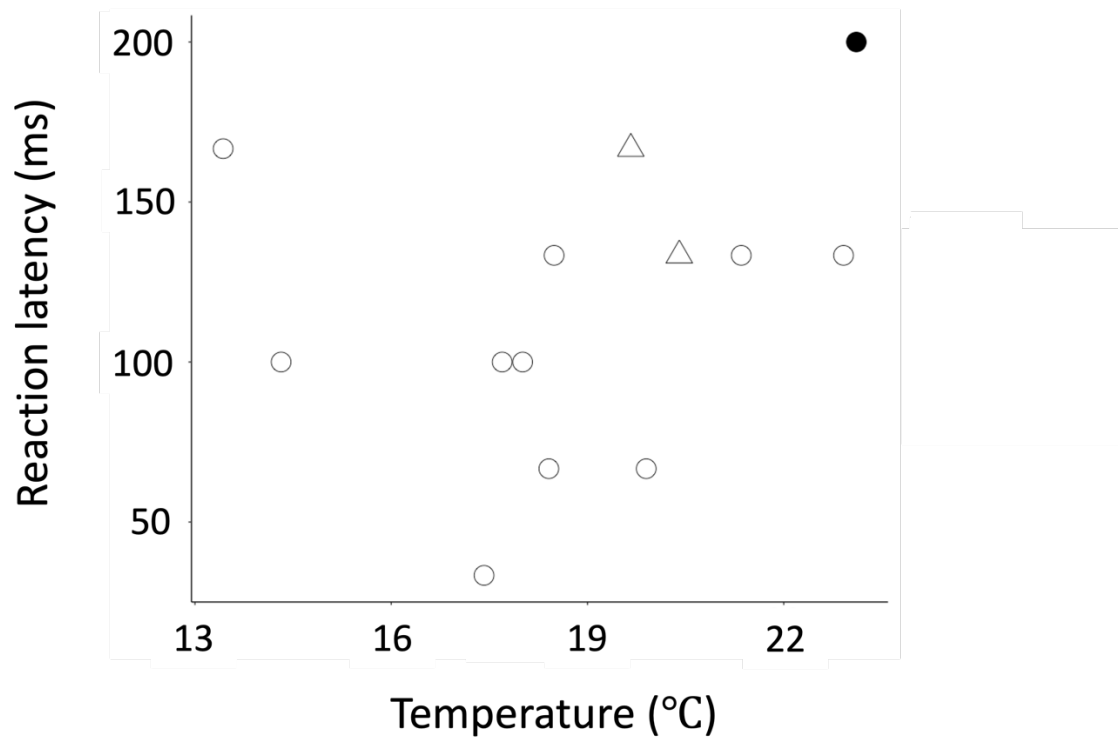


Figure 3. Scatter plots of prey reaction latency in response to snake strikes, in relation to estimated ambient temperature. Circles indicate reactions of mammals; triangles indicate reactions of frogs. Open and closed symbols indicate missed strikes or hits, respectively.