



Behavioral thermal tolerances of free-ranging rattlesnakes (*Crotalus oreganus*) during the summer foraging season



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ABSTRACT

Increasing temperature due to climate change is one of the greatest challenges for wildlife worldwide. Behavioral data on free-ranging individuals is necessary to determine at what temperatures animals modify activity as this would determine their capacity to continue to move, forage, and mate under altered thermal regimes. In particular, high temperatures could limit available surface activity time and time spent on fitness-related activities. Conversely, performance, such as feeding rate, can increase with temperature potentially having positive fitness effects. Here, we examine how the hunting behaviors of free-ranging Northern Pacific Rattlesnakes (*Crotalus oreganus*) associate with air temperature and body temperature. We continuously recorded snakes in the field using videography, capturing behaviors rarely considered in past studies such as movements in and out of refuge and strikes on prey. We found that as mean daily air temperature increased, hunting activity and the likelihood of hunting at night decreased, while the number of movements and distance moved per day increased. Snakes typically retreated to refuge before body temperatures reached 31 °C. Body temperatures of snakes hunting on the surface were lower compared to temperatures of non-hunting snakes in refuge in the morning, while this relationship was inverted in the afternoon. Snake body size influenced the disparity of these temperatures. Finally, strike initiation and success occurred across a wide range of body temperatures, indicating hunting performance may not be strongly constrained by temperature. These results on the temperatures at which free-ranging rattlesnakes exhibit fitness-related behaviors could be valuable for understanding their vulnerabilities to future climates.

1. Introduction

As global temperatures continue to rise due to human-induced climate change, it has become imperative for conservation researchers to determine whether species can function and survive at higher temperatures. For ectotherms, climate change is especially important because they depend on the environment to maintain their body temperature (Cowles and Bogert, 1944). Because all physical processes are temperature-dependent, nearly every aspect of ectotherm ecology is affected by body temperature variation (Huey, 1982). Physiological, genetic, and behavioral data are all needed for risk assessments on ectotherm vulnerability to environmental change (Huey et al., 2012; Kearney et al., 2009).

In order to determine how temperature increases might influence ectotherm activity, many studies measure the critical thermal maximum (CT_{max}), the upper critical temperature for movement (Clusella-

Trullas et al., 2011; Marshall et al., 2015; Oyen et al., 2016). If ambient temperatures of future climate scenarios exceed CT_{max}, then the animal should experience a reduction in available activity time, which could result in fitness consequences or even extinction (e.g., Caldwell et al., 2015, Bruschi et al., 2016). Although informative, CT_{max} may not accurately predict activity time reduction because it is measured as the temperature causing complete immobility of the animal, typically in a laboratory setting; free-ranging animals, however, will seek more favorable microhabitats before reaching CT_{max} (Scott et al., 1982). Thus, we might better evaluate the ecological consequences of temperature by measuring actual body temperatures of free-ranging ectotherms and then determining how variations in these temperatures affect the performance of fitness-related activities (e.g., feeding rate, speed, etc.), a standard method used by researchers (Huey, 1991; Huey and Slatkin, 1976; Sinclair et al., 2016). Performance should increase with temperature until a certain point at which it drops abruptly. The

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maximum temperature animals will voluntarily accept before moving to prevent overheating is the voluntary thermal maximum (V_{max}), and this will dictate the upper limit of their activity range in the natural environment (Cowles and Bogert, 1944; Heatwole and Firth, 1982). Reductions in activity time or performance could reduce survival and reproduction. Indeed, Rohr and Palmer (2013) found that salamanders (*Ambystoma barbouri*) lose significant body mass and have higher mortality in warmer and drier conditions well within their noncritical thermal range, even when allowed to behaviorally thermoregulate.

Squamates (snakes and lizards), which make up more than half of all reptile diversity, are particularly vulnerable to climate warming (Böhm et al., 2013), and many groups have already become locally extinct (Kubisch et al., 2014; Sinervo et al., 2010). High ambient temperatures in the physical environment often prevent squamates from being active during certain parts of the day or year (Beaupre, 1995; Kearney et al., 2009; Peterson, 1987). For many terrestrial squamates, such thermal constraints on surface use may limit food acquisition by affecting available foraging time. For instance, rattlesnakes (*Crotalus lepidus*) from a thermally challenging environment have lower growth rates and smaller adult body sizes compared to snakes from a more favorable environment, presumably due to differences in time spent foraging (Beaupre, 1995). Unfavorably high thermal environments can not only limit the time spent hunting, but also result in significant energy loss due to maintenance costs (Beaupre, 1995; Kearney et al., 2009; Riechert and Tracy, 1975), further affecting fitness.

Although overheating is a concern to all ectotherms, performance can also be enhanced by temperature (e.g., feeding performance; Van Damme et al., 1991). For example, many active-foraging snakes require a minimum temperature to initiate pursuit of prey (Aubret et al., 2015; Manjarrez and Drummond, 2010). The latency to strike prey, strike velocity, and prey capture success rate are also related to body temperature in snakes (Greenwald, 1974; Vincent and Mori, 2008). The enhanced feeding frequencies and niche expansions already exhibited by some Colubrid snakes likely result from higher performance in warmer temperatures (Capula et al., 2015; DeGregorio et al., 2015; Rugiero et al., 2013). However, most of these studies have been conducted on diurnal active-foraging lizards and snakes (e.g., Colubrids) that require relatively more energy than other types of squamates. Indeed, Kearney et al. (2009) recognized a taxonomic bias in the literature, with studies mainly focusing on species that prioritize attaining relatively narrow and high body temperatures. Yet, nocturnal species are frequently found active at body temperatures that should constrain performance (Dorcas and Peterson, 1998; Huey et al., 1989), and sit-and-wait foragers hunt across a wide range of temperatures, even those considered sub-optimal (Aubret et al., 2015; Ayers and Shine, 1997; McConnachie et al., 2007; Secor and Nagy, 1994). Hence, temperature-behavior relationships should be quantified in a diversity of free-ranging ectotherms to better understand how temperature variation influences fitness-related activities such as foraging.

We used continuous fixed-videography recordings of free-ranging Northern Pacific Rattlesnakes (*Crotalus oreganus*) during their summer foraging season to understand how hunting activity time and movements are influenced by ambient air temperature, and how foraging behaviors are related to body temperature. Rattlesnakes (*Crotalus* and *Sistrurus* spp.) are important top-level predators in many North and South American ecosystems, and may exert stronger selection on prey than sympatric endothermic predators (Nowak et al., 2008). Their hunting success is linked to fitness because body size and condition are influenced by feeding frequency. Body size usually associates with female acquisition in males (Cardwell, 2008; Jellen et al., 2007), and as capital breeders, body condition influences the reproductive availability and output of females (Taylor et al., 2005). Previous work has shown that ambush-hunting snakes like rattlesnakes tolerate a wider range of temperatures than active-hunters (Brattstrom, 1965; Secor and Nagy, 1994), but if temperatures continue to increase,

they may become forced to hunt in limited microhabitats or at limited times (Rugiero et al., 2013). Such changes could lead to altered growth, reproduction, and population dynamics, as well as changes in predator-prey interactions affecting community and ecosystem structure (DeGregorio et al., 2015).

At our study site near San Jose, California, rattlesnakes are mostly diurnal and target California ground squirrels (*Otospermophilus beecheyi*) as their main prey item (Putman et al., 2016). Within the limited timeframe to hunt between the spring and fall mating seasons (Lind et al., 2010), rattlesnakes spend many hours in ambush with infrequent hunting success, partially because squirrels have evolved snake-specific antipredator defenses (reviewed in Owings and Coss, 2008). Adult squirrels detect snakes during approximately 50% of all encounters (which then deters the snake from striking; Putman et al., 2015), and, when snakes do strike, squirrels evade strike attempts 50% of the time (Putman et al., 2016). Hunting success for rattlesnakes is most likely dependent on the amount of time devoted to lying in wait in ambush; research on other populations and rattlesnake species indicates that this is likely to be generally true of ambush-hunting snakes (Barbour and Clark, 2012a; Beaupre, 1995; Clark, 2006). Therefore, if high temperatures constrain hunting activity, this would lead to reduced growth and reproductive success. Conversely, hunting performance might increase with temperature, allowing more effective capture of prey.

Research on temperature-behavior relationships in free-ranging snakes is not uncommon, but most studies lack detailed behavioral data because of infrequent relocation of radio-tracked individuals (e.g., Buchanan et al., 2016; Carter et al., 2015; George et al., 2015). Because we were continuously radio-tracking and video-recording our study animals, we were able to document behaviors rarely considered in the past, such as the onset of daily activity, movements in and out of refuge throughout the day, movements to new sites, and attacks on prey. With these data, we calculated the proportion of the day spent hunting on the surface, hunting in a refuge, and inactive (i.e., not hunting) in a refuge, and noted whether or not the snake stayed hunting on the surface overnight. We predicted that higher mean daily air temperatures would associate with a reduction in surface activity during the day, and increase movements in and out of refugia (presumably for thermoregulation), distance moved per day, and the likelihood of snakes remaining hunting overnight. We also predicted that snakes hunting on the surface would have higher body temperatures than snakes inactive in refugia and that hunting performance (i.e., strike initiation and success) would positively associate with body temperature.

2. Materials and methods

2.1. Study site and animals

This study was conducted from May to July 2011–2014 at the Blue Oak Ranch Reserve (BORR), Santa Clara County, California (elevation ca. 800 m). Here, habitat is characterized by steep to moderate hills covered by mixed oak woodland interspersed by grassland. We opportunistically captured adult Northern Pacific Rattlesnakes (*Crotalus oreganus*) and surgically implanted them with temperature sensitive radio transmitters (model G3, AVM Instrument Company Ltd, CA, U.S.A.) using the methods of Reinert and Cundall (1982). Transmitters weighed less than 5% of snake body mass. After surgery, we kept snakes at a field station until they resumed normal behavior and then we released them at their place of capture (snakes typically held overnight then released the following day). In total, we used 24 adult rattlesnakes in this study: 11 females and 13 males. All methods were approved by the Institutional Animal Care and Use Committee of San Diego State University (APF 13-08–015 C).

2.2. Rattlesnake behavior

From 2011–2012, we took detailed measurements of free-ranging rattlesnake behavior using fixed videography. We radio tracked snakes at least once daily and recorded their locations using a global positioning unit (Garmin Gecko, ± 6 m). If a snake was in a favorable position for video recording, we positioned a battery-powered surveillance camera over it (methods detailed in Putman et al., 2016). We continually monitored snakes with wireless video between 0700–1900 h. We only include data in which we determined snakes were in a hunting behavioral state and not digesting, shedding, or gravid. Because of rattlesnakes' simple functionally-dedicated behaviors, it is relatively easy to determine when a snake is hunting: it adopts a tightly coiled body position with a kinked neck when on the surface or an 's-shaped' body position when hunting at the entrance to a refuge (Putman et al., 2016; Reinert et al., 2011). Snakes that were loosely coiled, elongated, or moving were not considered hunting. If a snake moved out of the camera's field of view, we relocated it using radio telemetry and repositioned the camera over it. If a snake was not visible on camera for more than 1 h (i.e., it remained within a refuge), we confirmed its position using radio telemetry. Our videography methods did not appear to alter snakes' behavior because snakes rarely fled, rattled, or exhibited other overt behavior in response to our approaches.

With our video-recorded data, we calculated snakes' time hunting on the surface, time hunting in a refuge (visible in refuge with a kinked neck, such as at the mouth of a burrow or under the edge of a fallen log), and time inactive (not visible in refuge). Snakes in a refuge were considered inactive because they cannot effectively hunt in this position. We also noted whether or not snakes remained hunting on the surface overnight by determining if the snake was in the exact same position in the morning as it was when we left the field site the previous night. We are confident that snakes did not retreat to refuge during the night because our observations show that they almost never return to the exact same ambush location and position after retreating to refuge; instead, they typically either adopt a position close (within ~ 1 – 3 m) to their previous position, or begin searching widely to locate a new hunting site tens of meters from their old one. We also video-recorded snakes overnight on several occasions and those out in ambush never retreated to refuge. Finally, we noted several behavioral events: start of activity (first visible movement of snake from within a refuge for that day), emergence from a refuge (more than 50% of body moves out of refuge), retreat to a refuge (more than 50% of body moves into refuge), move to a new site, and strike at a prey item. In 2013–2014, we were no longer using fixed videography to record behavior, but we radio-tracked snakes regularly (every 1–2 h) and noted their body positions each time they were located.

Crotalus oreganus exhibits a bimodal reproductive pattern, breeding in the spring and fall (Lind et al., 2010), while foraging occurs between these breeding seasons. Predation on adult rattlesnakes is low and typical only occurs when snakes are moving and exposing themselves to predators; in the hundreds of hours of video recordings of ambush hunting *C. oreganus*, *C. horridus*, and *C. cerastes* documented by our research group (Clark, 2006; Clark et al., 2016; Putman et al., 2016), we have witnessed no predation attempts on adult rattlesnakes. Thus, the movements of snakes we report here are unlikely to serve an antipredator function. Besides thermoregulation, all behaviors we recorded during the time of our study are most likely related to foraging.

2.3. Temperature recordings

We recorded the pulse rates of implanted temperature-sensitive transmitters to determine snake body temperatures (T_b). Transmitters increased in pulse rate with increasing temperature, and we created calibration curves for each transmitter prior to implantation using a

Percival E-36VL growth chamber. We calculated calibration equations using polynomial regression to derive temperatures from pulse rates. We recorded pulse rates of snakes monitored by fixed videography every 45 min and whenever any of the abovementioned behavioral events occurred. In 2013–2014 we recorded pulse rates of snakes each time they were located.

We also accessed ambient air temperature (T_a) data from an eKo Pro Environmental Monitoring System (model eK2120, MEMSIC Inc., MA, U.S.A.) located at our field site. T_a recordings were taken every 16 min. We acknowledge that T_a is a different metric than operative temperatures from biophysical models (which show the range of potential temperatures actually available to animals in their environment—Bakken, 1992; Huey, 1991), but we are mainly interested in examining how snake behavior is associated with gross changes in ambient temperature (i.e., the influence of daily fluctuations in weather instead of microhabitat variation). We do not use T_a to determine whether snakes are behaviorally thermoregulating (i.e., actively maintaining body temperatures different than those available in the physical environment; Peterson, 1987; Wills and Beaupre, 2000). Instead we are interested in whether snake hunting activity and movements are different on relatively warm days compared to relatively cold days. Similar methods have been used to study how mean annual temperatures influence phenology (Moreno-Rueda et al., 2009; Rugiero et al., 2013) and feeding frequency (Capula et al., 2015), how maximum daily temperatures influence refuge use (Keswick and Hofmeyr, 2014), and how mean air temperatures influence activity (George et al., 2015; Krysko, 2002) in reptiles.

2.4. Statistical analyses

2.4.1. Ambient temperature on activity and movements

We examined how T_a affected the daily hunting activity of snakes that were video-recorded for at least 7 h per day (2011–2012). For each day, we averaged all T_a measurements from 0700 to 1900 h, when we consistently recorded snake behavior, to calculate the mean daily T_a . We ran linear mixed models (LMM) using the *lme4* package in R (R v3.2.1, R Development Core Team, 2015) to determine whether mean T_a affected the proportion of time each snake spent hunting in ambush (coiled either on the surface or in refugia), spent solely on the surface (more than 50% of body out of refugia), and the sum of all movements into and out of refugia (number of emergences and retreats). Because of the need to minimize movement to retain effective crypsis for ambushing prey, we assume these movements are most likely caused by snakes' need to thermoregulate, but free-ranging snakes could also move for other reasons.

For data that did not meet linear model assumptions, we used generalized linear mixed models (GLMM) to examine temperature-activity relationships. We ran a GLMM with a Poisson distribution (log-link function) fit by the Laplace approximation to determine whether mean T_a affected total distanced moved in a day. We corrected for overdispersion in this model by modeling overdispersion as a random effect, with one random effect level for each observation (Bolker et al., 2009; Elston et al., 2001). We used another GLMM with a binomial distribution to determine whether mean T_a influenced snakes' decision to remain hunting on the surface overnight (y/n). We included snake identity and year as random effects and snake body size and sex as covariates in all models. We tested for interactions among variables when doing so increased the fit of our models (smallest AIC).

2.4.2. T_b in relation to behaviors

We calculated descriptive statistics for all temperature observations, and we examined whether T_b varied between different behaviors exhibited by snakes using LMMs. We tested whether T_b was different between occasions when snakes were hunting on the surface or inactive in a refuge (fixed factor of body position), and we also tested whether T_b differed between occasions when snakes started activity (i.e., first

visible movement of the day) and when snakes retreated to refuge (fixed factor of movement type). In each model, we included snake body size, sex, and hour of day as covariates, and snake identity and year as random effects. We again looked for interactions when doing so increased model fit (lowest AIC).

To determine whether strike initiation of free-ranging rattlesnakes was associated with temperature, we ran a 2-sample *t*-test with T_b as the dependent variable and strike decision (y/n) as the independent variable for all prey encounters we recorded using fixed videography (prey within 1 m of the snake). We excluded data associated with prey that exhibited behavioral indications that they had detected the snake (as in Putman and Clark, 2015) because previous research has shown that these strongly influence snakes' decision to strike (Barbour and Clark, 2012a; Putman et al., 2015). We also only included the first prey encounter recorded for each snake at each unique ambush location. We were unable to use a mixed model that accounts for repeated observations on individual snakes for this test because of small sample sizes, and many snakes were not observed more than once. Although we recorded multiple prey encounter events for some snakes ($n = 9$ snakes, median number per snake = 2, range = 1–7), we assumed that all events were independent samples because they involved independent prey items under a unique set of circumstances such as the unique spatial and temporal location of prey (Barbour and Clark, 2012a). We were unable to statistically determine whether T_b associated with strike success because our samples sizes were too small ($N = 5–8$), but we report descriptive statistics for strike outcomes. We report mean \pm SE as part of our data summaries below.

3. Results

3.1. Effect of ambient temperature on activity and movements

Depending on the response variable (see Table 1), we had 71–125 observations of daily activity and movement behavior on 15–17 individual snakes over 2 years. Mean daily T_a influenced activity/movement behaviors in all of our models. As the average daily air

Table 1

Factors affecting various measures of daily activity and movements of Northern Pacific Rattlesnakes (*Crotalus oreganus*) during the summer foraging season. Significant outcomes are shown in bold.

Response variable	Model factors	Estimate	SE	<i>P</i>
Proportion Time Hunting ^a	(Intercept)	1.712	0.586	0.006
	Mean T_a	-0.021	0.007	0.006
	Body Size	-0.010	0.007	0.145
	Sex	0.243	0.166	0.155
Proportion Time on Surface ^a	(Intercept)	1.770	0.641	0.010
	Mean T_a	-0.018	0.007	0.022
	Body Size	-0.012	0.007	0.112
	Sex	0.265	0.183	0.157
Number of Movements ^a	(Intercept)	-2.499	3.895	0.526
	Mean T_a	0.211	0.057	0.001
	Body Size	0.002	0.042	0.967
	Sex	1.035	1.020	0.317
Distance Moved (m) ^b	(Intercept)	2.825	2.581	0.274
	Mean T_a	0.077	0.035	0.028
	Body Size	-0.029	0.029	0.325
	Sex	0.641	0.764	0.402
Hunt at Night (y/n) ^b	(Intercept)	0.286	0.364	0.431
	Mean T_a	-0.511	0.197	0.009
	Body Size	0.617	0.309	0.046
	Sex	-0.711	0.569	0.211

^a Effects tested using LMM.

^b Effects tested using GLMM.

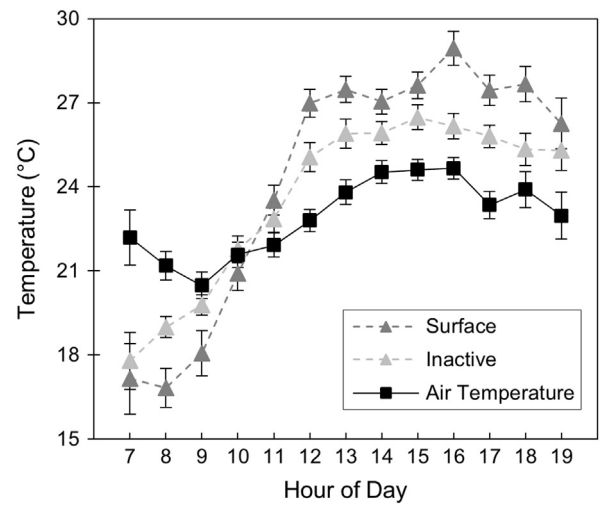


Fig. 1. Body temperatures (gray triangles) of rattlesnakes hunting on the surface and inactive in refuge in relation to hour of day. For comparison, ambient air temperature is also shown in black squares. Data were entered as continuous variables in the models and are represented as mean \pm SE here for visual clarity.

temperature increased, the proportion of time spent hunting (both on surface and in refuge) decreased ($P=0.006$), as did the proportion of time spent solely on the surface ($P=0.022$), with no effect of snake body size or sex (Table 1). Average daily air temperature also positively affected the number of movements in and out of refuge ($P=0.001$) and the total distance moved in a day ($P=0.028$), while body size and sex had no effect on these behaviors (Table 1). Finally, average daily air temperature had a negative effect on snakes hunting on the surface overnight (i.e., snakes were more likely to remain out on colder days, $P=0.009$), while snake body size had a positive effect on this behavior ($P=0.046$, Table 1).

3.2. T_b in relation to behavior

We had 1707 T_b observations on 21 snakes over 4 years. Based on our data, the voluntary minimum and maximum T_b for hunting snakes were 4 °C and 39 °C, respectively. When rattlesnakes were hunting on the surface they had a higher T_b than when they were inactive in refuge, but this relationship depended on snake body size and hour of day (size*body position: -0.083 ± 0.019 , $P < 0.001$; hour of day*body position: -0.401 ± 0.069 , $P < 0.001$, Fig. 1). Larger snakes tended to have higher T_b when hunting on the surface and lower T_b when inactive compared to smaller snakes. Snakes hunting on the surface had lower T_b than snakes in refugia before 1000 h, but this pattern reversed as the hour of day progressed (Fig. 1). Sex had no effect on T_b (-1.365 ± 1.078 , $P=0.208$).

The mean T_b of snakes when they started activity for the day was 20 ± 0.58 °C (range: 8–26 °C) while the mean T_b of snakes when they sought refuge was 28 ± 0.42 °C (range: 19–39 °C). These values were statistically different from each other (8.579 ± 1.032 , $P < 0.001$, Fig. 2). We plotted the percent of occurrences snakes were found hunting on the surface as a function of their T_b (Fig. 2), producing a curve similar in shape to typical thermal performance curves—performance gradually increases to an ‘optimum’ and then abruptly drops before V_{max} (Sinclair et al., 2016). We found that when snakes were out hunting, more than 75% of their T_b recordings fell between 16–31 °C; beyond 31 °C, few snakes remained out on the surface (less than 10% of all occurrences, Fig. 2).

Strikes on prey were initiated across a wide range of temperatures (14–31 °C) and occurred throughout the day, showing no diel pattern (mean hour of day: 11 ± 0.86 h, range: 7–18 h). We found that the mean T_b of snakes was nearly significantly different between prey encounters during which strikes were initiated versus when they were

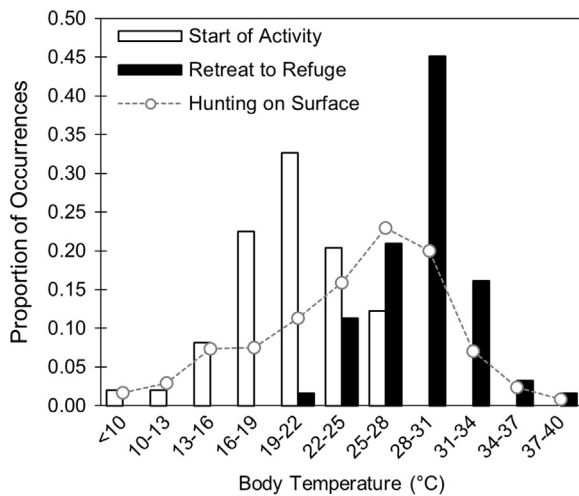


Fig. 2. Body temperature profiles of snakes when they started activity for the day (first movement within or out of nighttime refuge), retreated to refuge, and were hunting on the surface. Approximately 75% of temperature recordings when snakes were hunting on the surface fell between 16 and 31 °C, which also correspond to the peak temperatures at which snakes started activity and retreated to refuge.

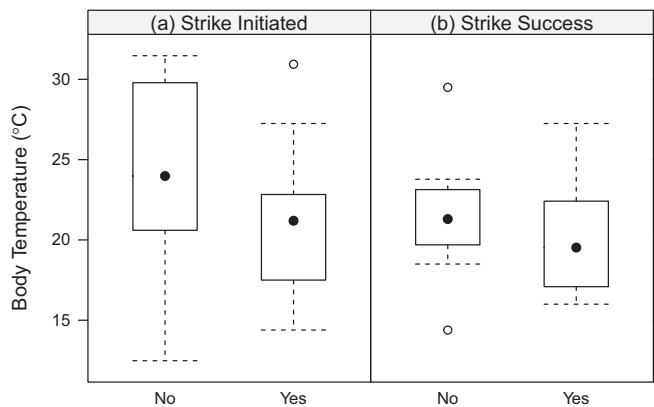


Fig. 3. Body temperatures of rattlesnakes during (a) encounters with prey when strikes were initiated ($N=14$) and not initiated ($N=16$), and (b) when initiated strikes on prey were successful ($N=8$) and unsuccessful ($N=5$). The dot in the boxplot indicates the median; the lower and upper ends indicate the 25% and 75% values, respectively. Open circles represent outlying individuals.

not initiated ($t_{28} = 1.95$, $P=0.062$), but in the opposite direction of our prediction: snakes generally had lower body temperatures when a strike was initiated (21 ± 1.22 °C) than when it was not (24 ± 1.37 °C, Fig. 3a). Strike performance (i.e., success) did not appear to depend on snakes attaining high body temperatures because both successful and unsuccessful strikes occurred across a wide range of temperatures that largely overlapped (successful: 20 ± 1.38 °C, range: 16–27 °C; unsuccessful: 22 ± 1.76 °C, range: 14–30 °C; Fig. 3b).

4. Discussion

Increasing air temperatures could limit the hunting activity of Northern Pacific Rattlesnakes in California. No rattlesnakes were found on the surface hunting beyond a body temperature of 39 °C, and although snakes might physiologically tolerate warmer temperatures, we found in this study that the majority of time they hunt between 16 °C and 31 °C; snakes mostly retreated to refuge before body temperatures reached 31 °C (Fig. 2), well below the CT_{max} of 40 °C reported by Brattstrom (1965). Endothermic prey such as ground squirrels do not alter their activity in response to temperature as severely as these ectothermic predators (squirrels were active on the surface at our site at all times of the day throughout the summer), so

our results likely do not reflect rattlesnake responses to changing prey activity.

As average daily air temperatures increased, the proportion of time hunting on the surface decreased. Thus, similar to many ectothermic reptiles that decrease activity with increasing ambient temperature (Beaupre, 1995; Hailey and Coulson, 1996; Krysko, 2002), it seems that for hunting rattlesnakes the primary thermal challenge is not to attain high body temperatures but to stay cool (Kearney et al., 2009). If temperatures continue to rise, snakes may be limited to hunt diurnal prey in specific microhabitats that buffer them from extreme air temperatures, and the use of biophysical models will be valuable in determining the availability of such thermal refugia (Huey, 1991). Ambush site selection could become more dependent on thermal quality than on prey availability (e.g., Riechert and Tracy, 1975), and this could have fitness consequences, especially if prey learn to avoid specific ‘snake-favorable’ microhabitats. Furthermore, we found that hunting in general (both on surface and in refugia) decreased as average air temperatures increased, suggesting that even using a refuge does not entirely mitigate the effect of high air temperature. It is possible that snakes would ultimately switch activity patterns to hunt earlier or later in the season as winter temperatures become more favorable, or to hunt more at night than during the day. Such patterns have already been observed in and predicted for other snake species (Capula et al., 2015; DeGregorio et al., 2015; Moreno-Rueda et al., 2009; Rugiero et al., 2013). However, the behavioral plasticity present in populations to support such shifts may differ between species, and further research would be needed to determine if most rattlesnakes exhibit this capacity for change.

Increased temperatures should logically lead to more nighttime hunting, but our results showed the opposite: lower daily average air temperatures associated with snakes’ staying on the surface to hunt at night. It is possible that snakes may have been unable to seek shelter because of constraints associated with low temperatures; we recorded 7 days that had minimum ambient air temperatures below temperatures that snakes displayed activity in this study (11 °C) and below the minimum voluntary temperature of other rattlesnake species (12.5 °C—Brown et al., 1982). However, on these days 10 out of 14 snakes sought refuge for the night, suggesting that ambient air temperatures did not render snakes completely immobile. Although we do not know why nocturnal hunting would be negatively related to daytime temperature, it is common in other rattlesnake species for individuals to hunt both day and night (i.e., cathemeral foraging; Barbour and Clark, 2012b; Clark et al., 2016). For other species such as ratsnakes (*Pantherophis* spp), shifts to nighttime hunting due to climate change could enhance foraging success as they are able to capitalize on more prey such as nesting adult birds (DeGregorio et al., 2015). However, similar to other rattlesnake populations that specialize on diurnal prey (Beaupre, 1995), our population specializes on diurnally-active California ground squirrels (Putman et al., 2016) which are the largest consumable prey type in the environment (and presumably the most profitable). Furthermore, recent studies indicate that *C. oreganus* venom has undergone adaptation to be effective against local populations of California ground squirrels (Holding et al., 2016). Thus, although nocturnal hunting might increase time spent in ambush without the risk of overheating, it may also force snakes to switch to hunting other types of prey that are potentially less profitable, and for which they are not well adapted.

We also found that snakes made more movements in and out of refugia and moved greater distances during the day on warmer days compared to colder days. Other studies have also found that free-ranging snakes are more active on warmer days (George et al., 2015; Huang et al., 2013). However, because rattlesnakes are ambush hunters that must hide themselves from unaware prey, increased thermoregulation could reduce prey encounter rates as snakes break crypsis and draw attention to themselves. Additionally, increased time spent moving could lead to higher predation risk as snakes are also

exposing themselves to potential predators as they break crypsis to move. Massasauga rattlesnakes (*Sistrurus catenatus*) refrain from moving to different habitats to thermoregulate (i.e., they tolerate less than optimal body temperatures) likely because increasing conspicuousness is more costly than maintaining a lower body temperature (Harvey and Weatherhead, 2010).

In the mornings, generally before 1000 h, the T_b of hunting snakes was lower than inactive snakes, but as the day progressed, the T_b of hunting snakes switched to being higher than the T_b of inactive snakes (Fig. 1). This supports previous research which shows that rattlesnakes often tolerate a wide range of temperatures while hunting compared to active-foraging snakes, and that snakes in refuge maintain a more stable temperature than snakes on the surface (Davis et al., 2008; Harvey and Weatherhead, 2010; Secor and Nagy, 1994). Larger rattlesnakes also maintained a higher T_b when on surface and a lower T_b when in refuge compared to smaller snakes. This suggests that snakes of differing body sizes have different thermal inertias. In general, larger snakes should retain heat for longer than smaller snakes due to reduced surface-to-volume scaling, and they should differ from ambient temperatures more than smaller snakes (Stevenson, 1985). This phenomenon has been demonstrated in other ectothermic reptiles (Garrick, 2008). Larger snakes were also more likely to remain hunting overnight, likely because they have lower rates of cooling than smaller snakes. Ayers and Shine (1997) found that large pythons (*Morelia s. spilota*) cool at slower rates than small pythons, thus extending their ability to hunt nocturnally active prey.

Many studies assume low temperatures limit snakes' ability to strike and capture prey (Harvey and Weatherhead, 2010; Shine et al., 2002b), but only a few have demonstrated that strike initiation and performance associate with temperature (Greenwald, 1974; Shine et al., 2002a; Vincent and Mori, 2008). Other studies have found that snakes are feeding more as climate warms, suggesting higher performance due to higher temperatures (Capula et al., 2015; George et al., 2015). However, although our sample size is limited, body temperature did not strongly influence the strike behaviors of rattlesnakes. Snakes did not require a minimum threshold temperature to initiate a strike and strike success did not appear to occur only at higher temperatures. Performing well at low temperatures might be a general pattern among ambush-hunting squamates (Aubret et al., 2015; McConnachie et al., 2007) because prey encounter rates are typically low (e.g., there would be many opportunity costs if they cannot attack when cold) and the cost of thermoregulation is high (e.g., breaking crypsis) (Huey and Slatkin, 1976). Success is likely more dependent on prey's awareness of the snake and expression of antisnake behaviors than the performance of the snake, which we have shown in our past research (Barbour and Clark, 2012a; Clark et al., 2012; Putman et al., 2015).

In conclusion, our study provides quantitative data on the temperatures at which rattlesnakes exhibit thermoregulatory and fitness-related behaviors during the summer foraging season. Increased air temperatures limit snakes' time hunting on the surface and increase both thermoregulation and daily movement distances. Such responses that enhance snake conspicuousness could reduce encounters with preferred prey items and increase predation risk. In addition, hunting performance (i.e., strikes) was not associated with higher temperatures. Predictive models based on operative temperatures would be worthwhile in determining whether these temperature-behavior relationships will lead to negative impacts on rattlesnake populations in the face of climate change.

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