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Kangaroo rats change temperature when investigating rattlesnake predators

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ABSTRACT

Predator presence causes acute stress in mammals. A prey animal's stress response increases its chance of survival during life-threatening situations through adaptive changes in behavior and physiology. Some components of the physiological stress response can lead to changes in body surface temperatures. Body temperature changes in prey could provide information about prey state to predators that sense heat, such as pit vipers. We determined whether wild rodents undergo a stress-induced change in body surface temperature upon detecting and investigating rattlesnake predators. We staged encounters between free-ranging Merriam's kangaroo rats (*Dipodomys merriami*) and tethered Mojave rattlesnakes (*Crotalus scutulatus*) at baited feeding stations, and recorded interactions with a thermal-imaging camera. Kangaroo rats showed a significant change in maximum head temperature, snout temperature, and hind leg temperature during interactions with rattlesnakes. This supports the hypothesis that presence of a predator induces body temperature changes in prey animals. If changes in prey heat signature are detectable by heat-sensitive rattlesnakes, rattlesnakes could use this information to evaluate prey vigilance or arousal before striking; however, more detailed information on the sensory ecology of the pit organ under field conditions is needed to evaluate this possibility.

1. Introduction

Prey animals have evolved behavioral and physiological responses to escape predators and cope with the risks associated with predator presence [14,29]. The physiological stress response increases survival during acute and transitory life-threatening situations [8,14,21]. Predator-induced stress in mammals is a suite of neuroendocrine processes that include physiological responses such as changes in the level of stress hormones, heat shock proteins, cardiovascular activity, breathing rate, gluconeogenesis, and activity in the gastrointestinal tract [8,21,42].

These physiological responses can result in temperature changes in prey animals. Changes in body temperature can occur due to increased cardiovascular activity induced by increased levels of the stress hormones (catecholamines and glucocorticoids; [21]). For example, exposure to predator scent directly leads to an elevated heart rate in elk (*Cervus canadensis*; [11]). In a related manner, blood is shunted away from the gastrointestinal tract and to muscles as part of a fight-or-flight response, and breathing rate increases [10,21,37,41]. Concurrently, acute stress results in elevated metabolism in most endotherms [11,21,40], leading to a temporary rise in core body temperature [9,43]. This phenomenon, termed 'stress-induced hyperthermia' has been demonstrated in a variety of taxa, including rodents, primates, and birds [1,5,9,10,43]. It manifests itself over the course of minutes and is often shown in response to handling (e.g. [24]). Stress-induced hyperthermia presumably also happens during acute predator stress, but this possibility has not yet been examined in wild animals (but see discussion of [34] below).

We hypothesized that these core body temperature changes translate to changes in body surface temperature when small mammals detect and interact with their predators. We studied this in kangaroo rats as they responded to a key predator, rattlesnakes. This question has additional relevance in this system due to the heat-sensing capabilities of rattlesnakes [20]. Rattlesnakes have evolved highly specialized infrared detectors that are used to efficiently hunt prey, even in complete darkness [7,23,27]. Through facial pit organs, rattlesnakes and other crotaline snakes can detect the infrared radiation emitted by endothermic animals [7,20]. Depending on the magnitude of the temperature change and the sensitivity of the pit organ system, temperature changes in prey animals during predator encounters may be detectable by infrared-sensitive snakes. For infrared-sensitive predators, one potential avenue of prey evaluation is prey body temperature, and snakes may use information gained through infrared radiation to evaluate prey condition or degree of vigilance. In the only example to date, tail

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flagging California ground squirrels (*Otospermophilus beecheyi*) showed an increase in tail temperatures of up to 3 °C when signaling at rattlesnakes, which in turn was associated with a behavioral reaction by snakes to this temperature change [34].

In this study, we experimentally exposed free-ranging kangaroo rats (a common prey item of many rattlesnake species) to tethered rattlesnakes at baited feeding sites and quantified kangaroo rat body surface temperature over the course of their interaction. We hypothesized that the presence of a major predator would represent a stressor sufficient to cause measureable increases in body temperature.

2. Methods

2.1. Study site and animals

Experimental trials took place outside of Rodeo, New Mexico, USA (31.888° N 109.031° W), between June 5 and August 4, 2015. Located in the Chihuahan Desert, the 200 ha study area consists of mesquite shrubland and supports large populations of Mojave rattlesnakes (*Crotalus scutulatus*) and Merriam's kangaroo rats (*Dipodomys merriami*). We captured adult kangaroo rats using Sherman live-traps baited with sunflower seeds (N = 59 individuals, 32 m/27 f, weight = 52.2 g ± 15.3 SD, hind foot length = 35.6 mm ± 3.4 SD). The study period coincides with reproductive activity in this population of Merriam's kangaroo rats (pers. obs.). We marked all individuals with a numbered metal ear tag and unique Nyanzol pelage dye markings for visual identification of individuals from a distance. Adult rattlesnakes were collected by us at night from nearby roads (N = 4) or provided to us by the Chiricahua Desert Museum (N = 2). We only used snakes large enough to prey on adult kangaroo rats (snout-vent length 525–705 mm, 122–292 g). Snakes were housed individually in plastic bins between trials and provided with water and food. All snakes were returned to their original location upon completion of the experiment. The San Diego State University Institutional Animal Care and Use Committee (APF 13-08-015C) approved all methods.

2.2. Experimental design

We used sunflower seeds to attract individual marked kangaroo rats to bait stations near their original trapping location. Capture and trials were separated by at least two days in all cases. A trial started when, upon discovering bait stations, individuals began shuttling seeds away for caching. We recorded kangaroo rats during this period for up to 10 min using a thermal imaging camera (see below) to measure baseline body temperature. We then used a temporary absence of the kangaroo rat to tether a live rattlesnake at the bait station. Snakes were tethered by using a combination of athletic tape and duct tape to attach small metal carabiners on two points along the body of the snake, which were in turn secured to metal stakes in the ground. We kept snake body temperature cooled in between trials by housing them in secured plastic bins with insulated icepacks; this facilitated handling during tethering. Although cooling snakes undoubtedly affected their behavior, snakes in this study were used only as stimuli to measure the potential effects of rattlesnake presence on kangaroo rat temperature. When returning to the bait station, the kangaroo rat discovered the snake and typically interacted with it intermittently for up to 10 min, at which point we terminated the trial. Fig. 1 shows the trapping and trial sequence. Discovery of the snake was indicated by a freeze and stare response, followed by close approaches and jumps backward away from the snake (see [13,33] for detailed characterizations of the antisnake behavior of kangaroo rats).

In order to gain insight into whether potential temperature changes were caused by the presence of a predator or simply the appearance of a novel feature at the bait station, we performed a small number of trials with an inanimate object (empty plastic jar) instead of rattlesnake predator. Due to logistical constraints in the field, the number of these trials was much smaller than the number of rattlesnake trials (60 rattlesnake trials vs. 17 control trials). Table 1 details the number of measurements, individuals, and trials in each trial type. Some individuals were tested multiple times. Trials on the same individual were separated by at least two full days. Trials took place between 21:00 h and 05:00 h, during which time fee-ranging kangaroo rats and Mojave rattlesnakes tend to be naturally active during summer months.

We recorded kangaroo rats from a distance of ~2 m throughout each trial with a FLIR T-420 thermal imaging camera (FLIR Systems, Wilsonville, OR, USA) connected to a laptop running FLIR Tools+ v5.4.1 software. The camera automatically calibrated itself intermittently against an internal thermocouple. Emissivity was assumed to be 0.95 [36,38].

2.3. Temperature variables and data extraction

We extracted still frames from infrared videos every 4 s and measured the temperature of four locations on the kangaroo rat's body using FLIR Tools+ v5.4.1 infrared imaging software. We measured the temperature of the head, snout, tail base, and hind leg (Fig. 2). For head temperature, we measured maximum temperature (eye in all cases). For hind leg measurements, an ellipse was drawn that included the maximum possible area of a kangaroo rat's hind leg, and we recorded the average temperature of the area covered by the ellipse. Because of the dynamic nature of the interaction, we were not able to record all temperatures from all still frames. Table 1 shows the total number of temperature measurements taken at each body location. We only used temperature measurements taken within 10 min of the start of each experimental period (initial bait station discovery, addition of rattlesnake or addition of plastic jar).

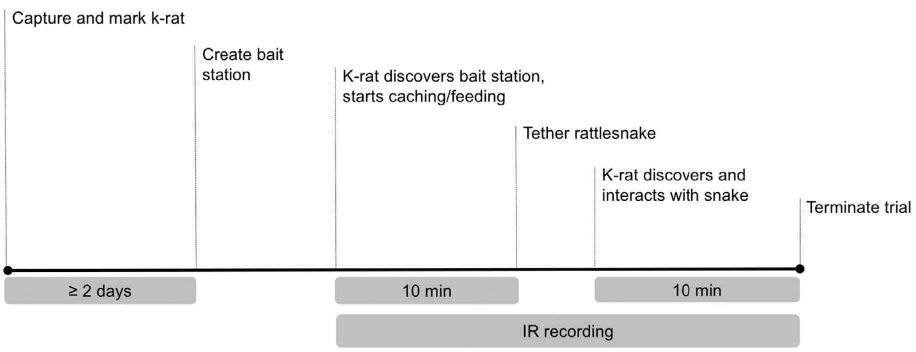

Fig. 1. Timeline of kangaroo rat trapping, attracting, and trials. The first 10 min recording period is referred to as 'baseline', the second one as 'rattlesnake' or 'control'. In control trials, we presented the kangaroo rat with a plastic jar instead of a rattlesnake during the second 10 min recording period.

Table 1
Number of experimental trials, kangaroo rats, and temperature measurements taken at each body location.

Body location	Rattlesnake trials			Control trials		
	# measurements	# individuals	# trials	# measurements	# individuals	# trials
Head	1860	53	60	381	16	17
Snout	466	51	53	97	16	17
Hind leg	1142	53	60	262	16	17
Tail base	753	51	57	228	16	17
Total		59	60		16	17

Table 2
Results of linear mixed models comparing baseline surface temperatures of kangaroo rats to temperatures after presentation of a rattlesnake and presentation of an inanimate object (control), with covariates for time since sunset and ambient temperature.

	Estimate	Std. error	t-Value	*p*-Value
Head				
Intercept	34.286	1.194	28.727	<0.001
Rattlesnake	−0.240	0.060	−4.016	<0.001
Control	0.020	0.116	0.175	0.861
Time since sunset	−0.002	0.001	−1.791	0.073
Ambient temperature	0.091	0.041	2.216	0.027
Snout				
Intercept	22.675	1.878	12.077	<0.001
Rattlesnake	−0.224	0.107	−2.106	0.036
Control	0.059	0.209	0.283	0.777
Time since sunset	−0.003	0.002	−1.480	0.140
Ambient temperature	0.172	0.065	2.663	0.008
Hind leg				
Intercept	24.690	1.987	12.424	<0.001
Rattlesnake	0.192	0.071	2.711	0.007
Control	0.230	0.129	1.779	0.075
Time since sunset	−0.007	0.002	−3.619	<0.001
Ambient temperature	0.156	0.068	2.314	0.021
Tail base				
Intercept	19.014	2.953	6.438	<0.001
Rattlesnake	−0.233	0.165	−1.412	0.158
Control	0.432	0.277	1.563	0.118
Time since sunset	−0.003	0.003	−1.037	0.300
Ambient temperature	0.413	0.101	4.091	<0.001

2.4. Statistical analysis

We used linear mixed models to compare baseline kangaroo rat body temperatures with temperatures after discovery of a rattlesnake or plastic jar [4]. We fitted separate models with each measured body part (head, snout, tail base, hind leg) as the response variable and experimental condition (baseline, rattlesnake, control) as fixed effects. We included random intercepts for snake ID, trial ID, and kangaroo rat ID (some kangaroo rats were the subjects of multiple trials, see above). We included trial ID as a random intercept because kangaroo rats had slightly different baseline temperatures in every trial. Circadian variation can explain differences in body temperature of about 2 °C [41], and body surface temperature tracks ambient temperature to an extent (e.g. [22,35,41]). We therefore included the covariates 'time since sunset' and 'ambient temperature'. In addition, we included a simple first-order autoregressive correlation structure (corAR1) in the residuals to account for temporal autocorrelation between sequential temperature measurements [45]. Our dataset was unbalanced (60 rattlesnake trials, 17 control trials), which can prevent correct model fitting. We fit all models in R v3.2.3 [31] using the package *nlme* [28], which is able to handle unbalanced datasets well [46]. Nevertheless, we verified that models fitted correctly by checking the confidence intervals of the variance components after fitting the models. We did not detect unusually large intervals, indicating that the models fitted correctly [46]. Means and standard errors for plotting were calculated using the *effects* package [18].

3. Results

Kangaroo rat body surface temperatures changed significantly after rattlesnake discovery at all measured body locations except for the tail base (Table 2, Fig. 3a–d). After rattlesnake presentation, head temperature decreased 0.24 °C ($\pm$0.06 SE, $p < 0.001$), snout temp decreased 0.22 °C ($\pm$ 0.11 SE, $p < 0.001$), and hind leg temperature increased 0.19 °C ($\pm$0.07 SE, $p = 0.007$); average tail base temperature did not change ($p = 0.158$). We did not test for significance of the individual ID random effect because we lacked a sufficient number of individuals that were tested multiple times. 'Ambient temperature' was a significant predictor of surface temperature at all locations. The effect of 'time since sunset' was very small in all cases, but significant in the model of hind leg temperature. Control trials with a novel but non-threatening stimulus (plastic jar) elicited no surface temperature changes (Table 2, Fig. 3). Kangaroo rats initially behaved the same way to the jar as they did to a rattlesnake, by performing a jump-back maneuver and then approaching the object. However, kangaroo rats quickly resumed feeding and/or caching seeds after this initial inspection.

4. Discussion

We found strong evidence of a change in kangaroo rat body surface temperature upon discovery of a rattlesnake. Head and snout temperatures decreased when there was a rattlesnake present, while hind leg temperature increased. Temperature changes were small (0.19–0.24 °C) but highly significant (Table 2); the magnitude of the observed changes is similar to the magnitude of body temperature changes found in chipmunks after handling stress (*Tamias striatus*; [9]). We did not observe

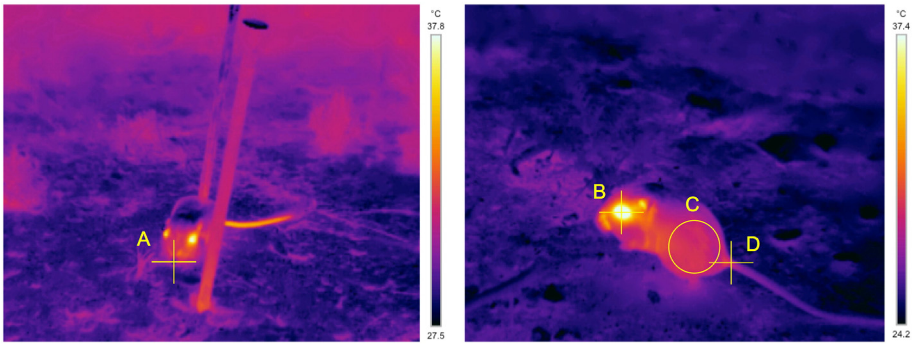

Fig. 2. Sample infrared images of kangaroo rat with measurement locations: (A) snout, (B), head maximum, (C) hind leg, and (D) tail base. The metal stakes used for tethering rattlesnakes are visible in the image on the right. Note that the temperature scales are slightly different in the two images.

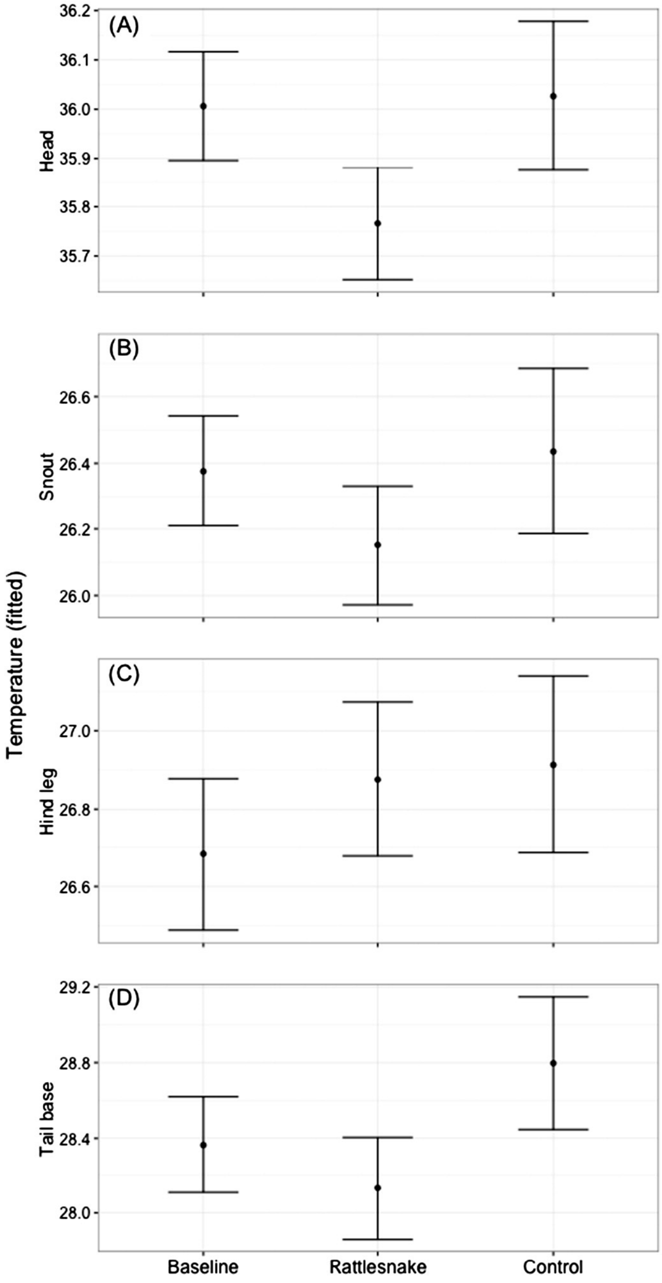

Fig. 3. Compared to baseline, kangaroo rat surface temperature changes when discovering a rattlesnake at (A) head, (B) snout, and (C) hind leg, but not (D) tail base. Temperatures did not change between baseline and control conditions. Error bars represent standard errors. Refer to Table 2 for statistical test results.

body surface temperature changes when kangaroo rats discovered a novel but harmless object, giving us confidence that observed changes were due to predator presence. We conclude that in kangaroo rats, exposure to a rattlesnake predator leads to physiological responses that manifest as changes in body surface temperature.

Contrary to our predictions, we found that head and snout temperatures decreased after exposure to a rattlesnake, whereas other studies have found that stress leads to increases in body temperature [9,24]. Stress-induced hyperthermia should increase body temperature by temporarily elevating metabolic rate [9,10,44]. However, other studies have found that body surface temperatures can decrease during stress [1,26]. The decrease in head temperature could be explained by a decrease in overall head surface temperature as a side effect of decreased snout temperature. The observed decrease in snout temperature likely resulted from evaporative cooling due to an increase in breathing rate. Elevated ventilation rates in response to acute stress have been observed in birds and fish (e.g. [10,37]) and presumably also take place in kangaroo rats. Increases in breathing rate have also been directly linked to lower rostrum temperatures in rattlesnakes (*C. durissus*; [7]). Hind leg temperature increased as a function of rattlesnake presence. This change is most likely due to blood shunting to the primary locomotory muscles as a part of the stress response [8,41]. Different mechanisms are not mutually exclusive and may even interact. For example, redistribution of blood could have amplified temperature changes at the snout in kangaroo rats [21,26]. Overall, changes in head, snout, and hind leg temperatures point to blood redistribution, blood shunting, stress-induced hyperthermia and/or elevated breathing as possible physiological mechanisms.

Unlike head, snout, and hind leg temperatures, tail base temperature was not affected by rattlesnake presentation. This was surprising since we expected temperature changes to be most easily measurable at the mostly furless and uninsulated tail. Ambient temperature had by far the largest effect in the tail base model. We therefore suspect that tail temperature in kangaroo rats is closely linked to ambient temperature, perhaps as part of a thermoregulatory mechanism as found in other rodents [32]. Ambient temperature was a significant predictor of body surface temperature in all models. This was not surprising since the surface temperature of even an imperfectly insulated animal should vary with ambient temperature to an extent (e.g. [22,35,41]). The estimate of the effect of 'time since sunset' was small in all cases, and it was a significant predictor only of hind leg temperature.

Since temperature changes in kangaroo rats were small, it is unclear if rattlesnakes could use this information to evaluate prey before striking. Rattlesnakes can detect infrared radiation from prey animals [20] and electrophysiological studies have shown that the pit membrane is sensitive to temperature changes as small as 0.003 °C [6,15]. A behavioral study on western diamondback rattlesnakes (*C. atrox*; [17]) suggested pit organs are even more sensitive than the threshold reported by Bullock and Diecke [6]. Rattlesnakes can also detect thermal contrast (difference in temperature between an object and its surroundings; [39]); temperature decreases in some body parts should therefore lead to an altered thermal outline of the prey animal against the background. Although it is unlikely that a prey temperature difference of 0.2 °C at a typical striking distance of about 30 cm would translate to a 0.003 °C temperature change on the pit organ membrane [2], our estimates of the magnitude of body temperature changes in kangaroo rats are coarse. We used values taken from periodic scan samples of body temperature for statistical analyses. It is possible that this methodology masks fluctuations in small mammal body temperature that occur for brief periods, so that the full degree of thermal heterogeneity is not captured by our methodology. Additionally, our current understanding of snake infrared detection is primarily based on models rather than measured empirically; more experiments in ecologically relevant settings are needed to evaluate the sensory parameters of this system and its role in predatory behavior.

If snakes can detect the small temperature changes observed in this study, they may use this information to evaluate potential prey. Predators strategically evaluate the condition or degree of vigilance of potential prey during predator-prey interactions [3]. Accurate prey evaluation is critical to hunting success, and predators profit from making accurate hunting decisions informed by prey cues [25]. Rattlesnake strike success rate in the wild is typically < 50%, with most missed strikes being attributable to rapid evasive maneuvers by prey [12]. Furthermore, kangaroo rats and ground squirrels that have recently interacted with rattlesnakes and are in a state of heightened vigilance exhibit quicker reaction times and evasive startle movements in response to surprise attacks [19,30]. Therefore, accurate evaluation of prey vigilance is especially important for sit-and-wait predators like rattlesnakes. The temperature changes we observed in kangaroo rats are likely indicative of physiological arousal and predator awareness. Importantly, temperature changes would be relevant to rattlesnakes regardless of whether the cause of arousal was a predator or another stimulus in the environment. Stress mediated changes in body surface temperature like the ones reported here may cause an endothermic animal to essentially 'leak' information to snake predators. Snakes might take advantage of this leaked information by adjusting predatory behavior accordingly, for example by deciding to only strike from shorter distances at animals that appear to be aroused. To date there is only one study that has included data relevant to this possibility: tail flagging ground squirrels exhibit tail temperatures up to 3 °C higher when interacting with rattlesnakes in captivity, who in turn show a behavioral response by retreating from the squirrel [34]. Although this temperature change is larger than the changes elicited in this study, it highlights the possibility of a much broader phenomenon involving interactions between pit vipers and their endothermic prey. Temperature-mediated pursuit deterrence signals, or perhaps even thermal camouflage, remain avenues of research open to exploration. Further studies will address whether snakes respond to the temperature changes we observed in kangaroo rats.

Competing interests

No competing interests declared.

Author contributions

Conceptualization: HAS, RWC; Methodology: HAS, RWC; Data analysis: HAS; Writing – original draft preparation: HAS; Writing – review and editing: HAS, RWC; Funding acquisition: RWC, HAS

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