


Thermal ecology and baseline energetic requirements of a large-bodied ectotherm suggest resilience to climate change

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Abstract

1. Most studies on how rising temperatures will impact terrestrial ectotherms have focused on single populations or multiple sympatric species. Addressing the thermal and energetic implications of climatic variation on multiple allopatric populations of a species will help us better understand how a species may be impacted by altered climates.
2. We used eight years of thermal and behavioral data collected from four populations of Pacific rattlesnakes (*Crotalus oreganus*) living in climatically distinct habitat types (inland and coastal) to determine the field-active and laboratory-preferred body temperatures, thermoregulatory metrics, and maintenance energetic requirements of snakes from each population.
3. Physical models showed that thermal quality was best at coastal sites, but inland snakes thermoregulated more accurately despite being in more thermally constrained environments. Projected increases of 1 and 2°C in ambient temperature result in an increase in overall thermal quality at both coastal and inland sites.
4. Population differences in modeled standard metabolic rate estimates were driven by body size and not field-active body temperature, with inland snakes requiring 1.6x more food annually than coastal snakes.
5. All snakes thermoregulated with high accuracy, suggesting that small increases in ambient temperature are unlikely to impact the maintenance energetic requirements of individual snakes and that some species of large-bodied reptiles may be robust to modest thermal perturbations under conservative climate change predictions.

KEYWORDS

climate change, ectotherm, energetic requirements, metabolism, rattlesnake, thermal ecology, thermal quality

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1 | INTRODUCTION

The urgency of the biodiversity crisis is accelerating as scientists document how climate change, habitat loss, pollution, and other human-induced disturbances are causing extinction of many taxa, such as insects, amphibians (Deutsch et al., 2008), mammals (Davies et al., 2008; Thuiller et al., 2006), birds (White & Bennett, 2015; Wormworth & Mallon, 2006), and reptiles (Böhm et al., 2013; Gibbons et al., 2000; Sinervo et al., 2010; Urban, 2015). As ectotherms, reptiles depend heavily on their immediate surroundings to regulate body temperature, where even slight changes in environmental conditions can impact physiological functions (Besson & Cree, 2010; Huey, 1982; Walther et al., 2002). Researchers have begun to quantify the current and predicted effects of climate change on diverse reptile species using recently available high-resolution climate change forecasts and technology for modeling thermal landscapes (Böhm et al., 2016; Bruschi et al., 2016; Sinervo et al., 2010; Wright et al., 2016).

Small-bodied, heliothermic (sun-basking) lizards are the focus of many climate-based studies, largely because it is easy to obtain large sample sizes with limited effort and because these heat-loving species may be at high risk of further warming (Buckley et al., 2015; Clusella-Trullas et al., 2011; Pelegrin & Bucher, 2012; Sinervo et al., 2010). However, studies investigating thermal ecology in larger-bodied ectotherms have tended to only use single populations of a given species and/or focus on sympatric species (Beck, 1995; Blouin-Demers & Weatherhead, 2001; Blouin-Demers & Weatherhead, 2002; Bovo et al., 2012; Lelièvre et al., 2011; Moore, 1978), potentially because these species tend to be less common, rendering the effort and expense involved in these studies prohibitive. This, in turn, limits the scope of these studies to certain localities and prevents inferences about the possibility that climate change and environmental variation will interact in their future impacts on a given species. Furthermore, many of these studies have focused on the direct impacts of altered temperatures on the body temperature (T_b) of the population while failing to address the implications of changing T_b on the population's energetic needs (Alford & Lutterschmidt, 2012; Waldshmidt et al., 1986). To the best of our knowledge, no study to date has compared the thermal ecology and energetic requirements of a large-bodied reptile across multiple populations that inhabit distinct thermal environments.

Here, we examine the thermal ecology of a large-bodied reptile, the Pacific rattlesnake (*Crotalus oreganus*), across multiple populations while also extending our inference to quantify the energetic implications of environmental variation. The extraordinarily low metabolic rates and energetic allocation to specific physiological functions are well established in rattlesnakes (Beaupre & Duvall, 1998a, 1998b). We conducted intensive field studies collecting physiological and temperature data from four field sites on the Central Coast of California over eight years to quantify the thermal ecology (see Table S1 for explanations of terminology common in thermal ecology studies) and energy requirements of snakes on a macroecological scale. We then subjected these data to predicted

increases in ambient temperature to examine how snake annual maintenance energy requirements will be impacted in a warming world. We hypothesized that precise thermoregulation and low metabolic rates allow rattlesnakes to respond to variable thermal environments effectively, both now and in the future due to climate change. At low temperatures, the snakes expend very little energy, but as temperatures rise, their precise thermoregulation allows them to remain at body temperatures optimally suited for their physiological processes. Specifically, we predicted that the thermal quality of habitats would differ, with hot and thermally variable inland sites having poorer thermal quality than the cool and stable coastal sites. Additionally, due to the climatic differences between these habitat types, we predicted that coastal snakes would have lower field-active T_b and therefore lower annual maintenance energy expenditures than snakes at inland habitat, making them less thermally constrained both currently and in the future.

2 | MATERIALS AND METHODS

2.1 | Study species

The Pacific Rattlesnake (*Crotalus oreganus*, Holbrook 1840) ranges in western North America from southern British Columbia to Baja California, Mexico (Pook et al., 2000; Sunagar et al., 2014). The taxonomy of this species is under debate, and our four study sites fall into what is currently considered the integration zone of the northern (*C. o. oreganus*) and southern (*C. o. helleri*) subspecies (Ashton & Queiroz, 2001). However, recent evidence suggests that all these study populations genetically cluster (Holding et al., 2021); for the purpose of this study, we will refer to them as *C. oreganus*. They are habitat and dietary generalists that prey primarily on small mammals and lizards (Mackessy et al., 2003; Sparks et al., 2015; Sunagar et al., 2014). Body size varies widely among localities, but typical snout-vent lengths (SVLs) of adult male *C. oreganus* in California range from approximately 60 cm to 120 cm (Aldridge, 2002; Ashton, 2001).

2.2 | Study sites

The four study sites used for this investigation were the Chimineas Ranch in the Carrizo Plain Ecological Reserve (CR), Montaña de Oro State Park (MDO), the University of California Sedgwick Reserve (SG), and Vandenberg Air Force Base (VAFB; Figure 1a). MDO and VAFB are coastal sites characterized by rugged cliffs, canyons, and coastal scrub plant communities that experience relatively stable and mild seasonal temperatures (Figure 1b; Capehart et al., 2016; Underwood et al., 2003). CR and SG are inland sites that experience higher and more variable daily and seasonal temperatures (Figure 1b) and are dominated primarily by chaparral, oak savanna, and grassland plain habitats (Chimineas Ranch Foundation, 2019; University of California Reserve System: Natural Resources, 2019).

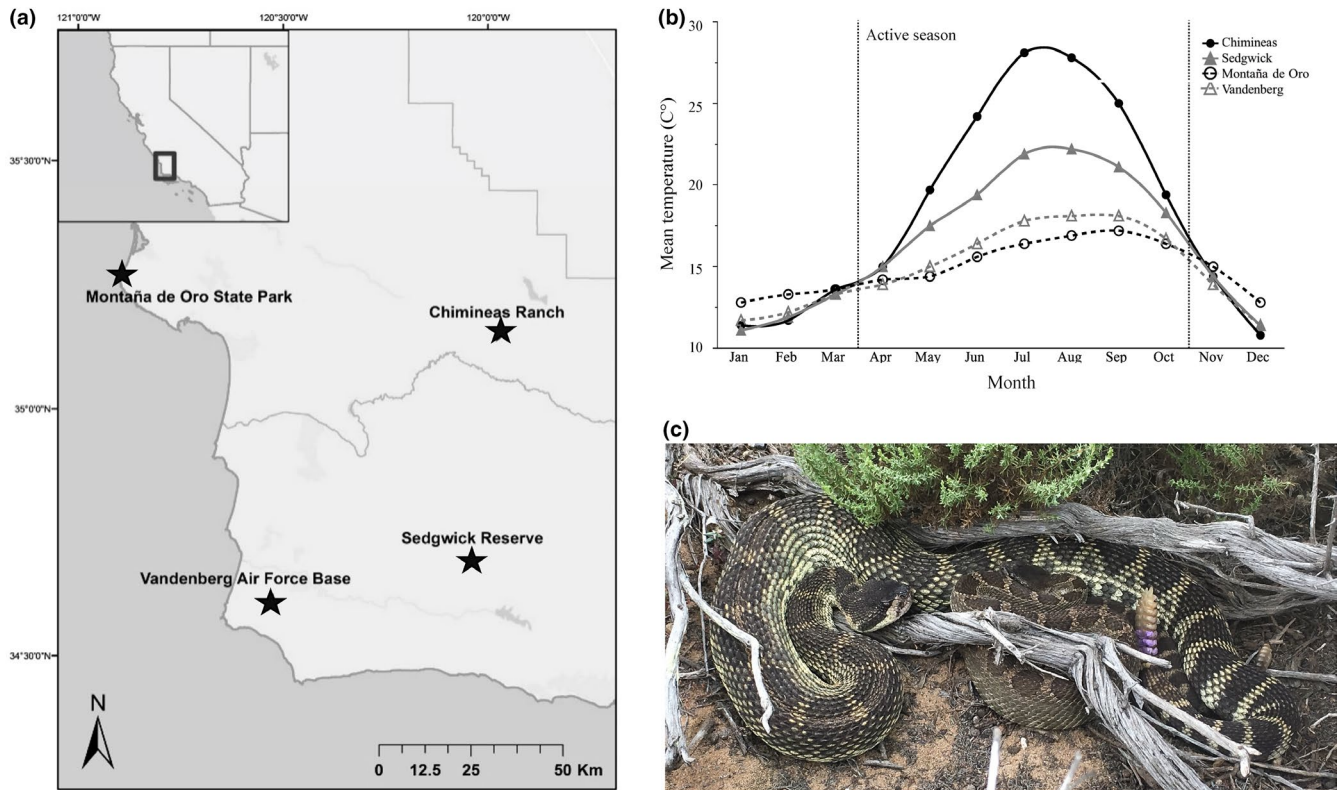


FIGURE 1 (a) Map of locations on the Central Coast of California of the four Pacific rattlesnake (*Crotalus oreganus*) populations (two coastal, two inland) used in this study. (b) Average monthly temperatures (°C) for the same corresponding sites from 2010 to 2017 (National Ocean and Atmospheric Administration & Western Regional Climate Center, 2017). (c) An adult male *Crotalus oreganus* (larger snake) resting with a smaller female mate

TABLE 1 Summary mass and sex data of Pacific rattlesnake (*Crotalus oreganus*; $N = 45$ snakes) used for preferred body temperature (T_{set}) trials, range of temperatures reached during trials, and median site T_{set}

Site	n	No. of individuals with radio-transmitters	Sex	Mass range (g)	T_{set} Range (°C)	Mean median T_{set}
CR (inland)	8	3	$M = 5$ $F = 3$	370–790	30.0–36.3	32.25
SG (inland)	11	5	$M = 10$ $F = 1$	347–912	11.7–36.6	26.47
MDO (coastal)	15	6	$M = 15$	60–860	14.8–37.6	30.55
VAFB (coastal)	11	3	$M = 11$	165–990	15.8–36.7	27.74

CR and MDO are situated to the north and are in San Luis Obispo County, CA, USA, whereas SG and VAFB are to the south in Santa Barbara County, CA, USA, (Table S2).

2.3 | Preferred body temperature (T_{set})

We constructed a laboratory thermal gradient adapted from Bovo et al. (2012), spanning a range of ecologically relevant temperatures from 8–46°C to determine preferred body temperature (T_{set}) (see Supplemental Methods; *Thermal Gradient Construction & Data Collection*). Snakes ($N = 45$) of varying size (35 cm–108.4 cm) and sex ($M = 41$, $F = 4$) were collected from all four field sites opportunistically

from September 2017 to June 2018 (Table 1). Snakes were brought back to the California Polytechnic State University (Cal Poly) campus, where basic morphometrics (mass(g) and SVL(mm)), sex, reproductive status, and presence of gut contents were recorded. Snakes were excluded from the analysis if they were found to have visible meals in their gut or detectable follicles/offspring, as these factors could dramatically alter preferred temperatures. Snakes were placed in the thermal gradient for a two-hour acclimation period (Bovo et al., 2012) followed by a 12-hr data recording period. We defined T_{set} as the interquartile range of the data (Blouin-Demers & Weatherhead, 2001; Fitzgerald et al., 2003). Data collected for this and the following components of this project were analyzed in JMP v14.0 (JMP®, SAS Institute Inc., Cary, NC, USA, 1989–2007) unless

otherwise specified. Site, sex, mass, season (Charland et al., 1990), and presence/absence of internal radio-transmitter (see below) were evaluated as predictor variables in the model examining the response variable median T_{set} (Blouin-Demers & Weatherhead, 2001; Fitzgerald et al., 2003).

2.4 | Field-active body temperatures (T_b)

Between the years of 2010–2017, we collected 85 adult, male rattlesnakes across each of the four study sites (CR = 23, SG = 28, MDO = 15, VAFB = 19; Table S3). We studied snakes at one site in each of 2010–2016 (CR: 2010, SG: 2015, MDO: 2014, VAFB: 2012, 2013), and we studied snakes simultaneously at all four sites in 2017. Subjects were transported to the laboratory at California Polytechnic State University (San Luis Obispo, California, USA) and surgically implanted with radio-transmitters (Holohil models SB-2, 5.2 g and SI-2, 11 g, 13.5 g; Holohil Systems Ltd., Carp, Ontario, CA) and Thermochron iButtons (DS1922L-F5 and DS1921G-F5 models, accuracies = $\pm 0.5^\circ\text{C}$ and $\pm 1^\circ\text{C}$ respectively, Maxim Integrated Products Inc., Rio Robles, San Jose, CA), which were set to record field-active body temperatures (T_b) every hour. Temperature loggers and radio-transmitters were implanted intracoelomically as separate units following the procedures of Claunch et al. (2017). Snakes were released within 1–2 days of surgery at the location of capture. At the end of each active season, we recaptured snakes and brought them back to the laboratory to remove iButtons and radio-transmitters. To compare the mean field-active T_b of snakes across the four sites, we used a mixed-effects model with an AR(1) covariate structure to capture the serial correlation of the within-snake observations of temperature (Millar & Anderson, 2004). Site, month, and time of day acted as fixed effects, snake ID was a random effect, and a unique time of day/date value for each data point was used for the repeated structure. Additional sin- and cos-transformed time-of-day variables were also included as fixed effects to account for the cyclic, continuous nature of time.

2.5 | Snake physical model temperatures (T_{mod})

In 2017, we deployed physical models in exposed, shaded, and burrow microhabitats throughout the four field sites to characterize the thermal landscapes potentially available to each of the rattlesnake populations (Dzialowski, 2005; Lutterschmidt & Reinert, 2012). Physical model microhabitat sites were selected based on previous observations of snake use within those areas and also with an effort to distribute them evenly throughout the area where snakes were being radiotracked. Importantly, these models represent a range of low and high temperatures available to the snakes, but do not encompass the relative amount of each microhabitat available to snakes at each field site. Physical models consisted of water-filled copper pipes, painted to approximate *C. oreganus* reflectance, with iButtons suspended inside in accordance with Bakken (1992) and Lutterschmidt and Reinert (2012) (see Supplemental Methods; *Physical Model*

Construction & Validation). Model temperature (T_{mod}) was recorded every hour for one year from June 2017 to June 2018. Five physical models were placed at each of the four study sites in various microhabitats (Blouin-Demers & Weatherhead, 2002; Lutterschmidt & Reinert, 2012): two inside typical snake refugia (e.g., ground squirrel burrows, rock burrows), two in exposed habitat (open field, gravel road), and one in a shaded habitat (under a shrub or bush). We validated models using similar-sized, adult rattlesnake carcasses. Because our models contained water (therefore had thermal inertia), they did not meet the definition of an operative temperature model (Bakken & Gates, 1975). Rather, we built our models to have thermal properties similar to those of a nonthermoregulating snake, meaning that the temperatures collected by our models reflected the full range of maximum high and low temperatures and average, adult-size animal could reach if it were to remain in the most thermally stable and most thermally variable microhabitats within each of the four study sites. For a large-bodied, nonheliothermic, nonactive shuttling ectotherm, we believe that these models were most accurate for quantifying the thermal conditions of each habitat as opposed to smaller, air-filled models (Lutterschmidt & Reinert, 2012).

To compare T_{mod} values across different sites, we used a mixed model with an AR(1) covariate structure similar to the model used for T_b (see above section on body temperature). No T_{mod} values for exposed microhabitats for SG were included because the T_{mod} exceeded iButton temperature limits, causing all exposed models at SG to fail. Additionally, T_{mod} values for the shaded CR model are unavailable for months July–December due to iButton failure. Site, month, and time of day were included as fixed effects.

2.6 | Thermal ecology variables measured

We used thermal indices developed by Hertz et al. (1993) to evaluate the extent to which a given habitat temperature (T_{mod}) permits a T_b within T_{set} to be achieved (thermal quality) and the extent to which an animal actually experiences T_b within its T_{set} (thermoregulatory accuracy). We calculated thermal quality of the environment (d_e) as the absolute value of the difference between T_{mod} and T_{set} , where high d_e values mean that the thermal quality of the environment is low and d_e values approaching zero represent more favorable thermal habitat. The metric of d_e by definition uses operative temperature (T_e , a value obtained from physical models without thermal inertia instead of the metric T_{mod}); however, we use T_{mod} here with the caveat that the models' inertia could impact their cooling and heating rates. We calculated thermoregulatory accuracy (d_b) as the absolute value of the difference between T_b and T_{set} , where high d_b values mean poor thermoregulatory accuracy (i.e., the snake's actual body temperature is much higher or lower than its T_{set}), and d_b values approaching zero represent accurate thermoregulation (Blouin-Demers & Weatherhead, 2001; Hertz et al., 1993). Calculation of thermal variables was performed in R v. 3.4.4 (R Development Core Team, 2015) using the package “dplyr” (François et al., 2018).

Individual T_{mod} values for physical models of the same site and type (for example, all CR burrow models) were averaged to calculate a mean d_e value for each time of day observation (hr) for each month. A repeated-measures ANOVA was conducted to compare overall d_e values of each study site and then rerun with results blocked by physical model (burrow, shaded, exposed) to examine differences in thermal quality among microhabitat types. Because of the need to compare multiple levels/groups (both site and microhabitats within site), the repeated-measures analyses with the AR(1) covariate structure was not used for d_e . Site, month, and time of day were included as fixed effects in this model as well as their interactions in a full factorial to account for these variables. For d_b , because we were only examining differences at the site level, we used the same statistical analysis that we used for T_b and T_{mod} values (see above sections) with site, month, and time of day included as fixed effects.

2.7 | Energetics

We used snake field-active body temperatures (T_b) and morphometric data to calculate theoretical standard metabolic rates (SMR) based on the following equation established by Beaupre and Duvall (1998b, see Supplemental Methods: *Energetics*):

$$\text{SMR} = \log_{10} \text{VO}_2 = X_1 + \log_{10} \text{mass} + X_2 * \text{temperature} + X_3$$

We converted the inverse log of the SMR into annual maintenance energy requirement in Joules (19.874 J/ml O_2) and then Calories (2.3900×10^{-4} kcal/J). We then calculated the approximate annual prey requirements to meet maintenance costs of an average-sized male rattlesnake for each of the four study sites using their most common prey item, the California ground squirrel (*Otospermophilus beecheyi*; Rowe & Owings, 1990; Sparks et al., 2015). Based on previously published food assimilation experiments in the genus *Crotalus* (Beaupre & Zaidan, 2012; Secor & Nagy, 1994), we assumed an 80% energetic assimilation efficiency and that an average, adult ground squirrel weighs approximately 500 g (Evans & Holdenried, 1943) and contains roughly 690 kcal (Dorcas et al., 2004; Kaufman et al., 1975). An ANCOVA was performed to compare the daily SMR (ml $\text{O}_2 \text{ day}^{-1}$) of the four populations of snakes ($N = 85$) during their active season (April–October). Snake mass, site, and the site \times mass interaction were included in the model. Because mass was used to estimate SMR, it will inevitably be a significant predictor variable for SMR. However, we included it in the models to account for variation in snake body size among sites.

2.8 | Climate change projections

We used the California Energy Commission (2019) representative concentration pathway (RCP) climate scenario 4.5 as a “best case” scenario (emissions peak around the year 2040 then steadily decline) to estimate the changes in habitat thermal quality and therefore

energetic consequences of anthropogenic climate change on snakes. We used the “modeled projected annual mean” tool to identify the years in which the annual average temperatures increase one degree from the 2017 average for each of the four study sites (CR/SG/VAFB = 2030, MDO = 2047). We repeated this procedure for a two-degree increase as well. To make macroecological predictions, we then assumed that a 1°C increase in annual average temperature would be equivalent to the same increase in T_{mod} of all microhabitats. We calculated the proportion of current mean hourly T_{mod} for each site and microhabitat type that fell within T_{set} for 2017 as well as with 1°C and 2°C increases in mean hourly temperatures. We then calculated the percent change in these proportions between each of these three climate scenarios as well as the change in mean d_e for each site and microhabitat type. Lastly, we calculated the mean increase in annual energetic needs (kcal/year) assuming snake T_b increased along with T_{mod} by adding 1°C and 2°C to the mean hourly T_b of each snake and using the Beaupre and Duvall (1998b) equation to recalculate mean SMR for each of the four sites. We used a repeated-measures ANOVA to compare differences in current energetic needs and those projected with 1°C and 2°C increases, with site included as a factor.

3 | RESULTS

3.1 | Preferred body temperature (T_{set})

The mean of the median T_{set} of all snakes ($N = 45$) was $29.22 \pm 0.92^\circ\text{C}$ with a 50% interquartile range of $26.28 \pm 1.01^\circ\text{C} - 32.34 \pm 0.84^\circ\text{C}$

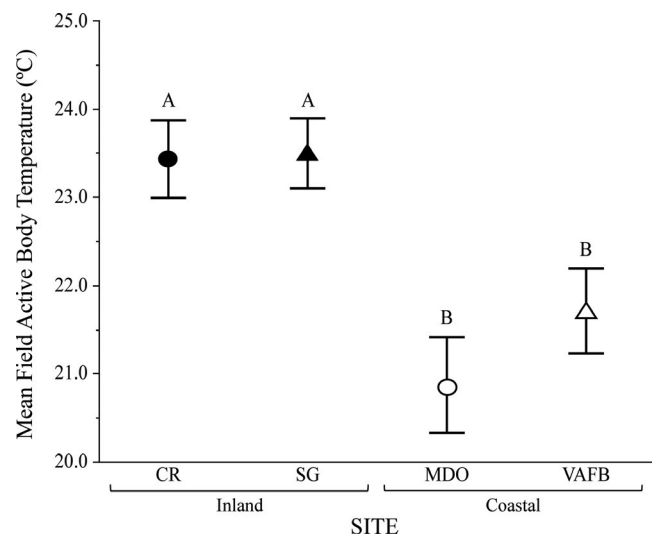


FIGURE 2 Mean hourly field-active body temperatures (T_b) for four populations of Pacific rattlesnake (*Crotalus oreganus*; $N = 85$; CR = 23, SG = 28, MDO = 15, VAFB = 19) on the Central Coast of California during the active season (April–October). Black shapes denote inland sites, white shapes denote coastal sites, circles denote northern sites, and triangles denote southern sites. Data were collected for varying lengths of time from 2010 to 2017. Different letters represent a significant difference between means, and bars represent 95% confidence intervals

(Blouin-Demers & Weatherhead, 2001). None of the factors tested (site, sex, mass, season, or presence of internal radio-transmitter) significantly affected median T_{set} ($F_{8,36} = 1.30$, $p = .27$; Figure S1).

3.2 | Field-active body temperature (T_b)

After accounting for monthly and diel variation in temperature, we found that T_b differed significantly among sites, with snakes from both CR and SG having higher mean body temperatures than snakes from both MDO and VAFB ($F_{3,83.2} = 26.16$, $p < .0001$). Tukey-Kramer post hoc tests showed no significant differences in T_b between the two coastal populations or between the two inland populations (Figure 2).

3.3 | Physical model temperatures (T_{mod})

After accounting for monthly and diel variation in temperature, we found that mean monthly T_{mod} differed significantly among sites ($F_{11} = 366.18$, $p < .0001$; Figure 3) although overall annual T_{mod} did not ($F_3 = 0.41$, $p = .75$).

3.4 | Thermal quality (d_e)

A total of 3,048 mean hourly d_e values were obtained from physical models ($n = 5$ /site) at all sites. There was a significant difference in d_e among study sites ($F_{1151,1896} = 3.62$, $p < .0001$); post hoc analysis showed no significant difference in overall mean d_e among the two coastal sites (MDO & VAFB) and SG but did show that mean CR

d_e was significantly higher (= poorer thermal quality) than all other sites. Almost all interaction terms within the full factorial model were significant (Table S4). When the same test was run with d_e values blocked by microhabitat type, there was still a significant difference in d_e among sites within each microhabitat (burrow, $F_{3,1,114} = 137.29$, $p < .0001$; shaded, $F_{3,994} = 75.13$, $p < .0001$; exposed, $F_{2,827} = 19.38$, $p < .0001$; Figure 4). Because of the failure of SG exposed physical models, no exposed d_e values were included for the overall calculations for SG, therefore resulting in a lower overall d_e value than the expected actual value and reducing the SG model sample size to $n = 3$. Due to similar ambient temperatures, we expect that SG exposed d_e values would have been similar to CR exposed values.

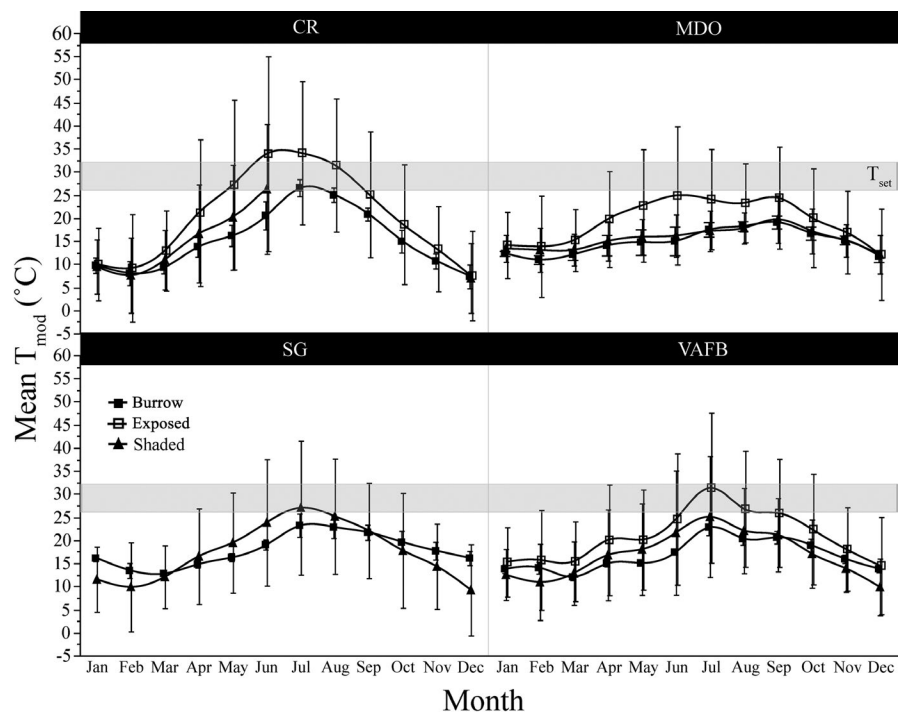
3.5 | Thermoregulatory accuracy (d_b)

Thermoregulatory accuracy (d_b) differed among study sites, with inland snakes (CR, SG) being more accurate thermoregulators than coastal snakes (MDO, VAFB; $F_{3,84.4} = 37.17$, $p < .0001$; Figure 5). Snakes at both CR and SG spent an overall larger portion of time in or near preferred body temperatures throughout the entirety of the study (Figure 5). On average, 50.89% of hourly T_b observations fell within the T_{set} for inland snakes versus only 21.63% for coastal snakes. Post hoc tests revealed no significant differences between the two inland sites or between the two coastal sites (Figure 6).

3.6 | Energetics

The daily SMR of snakes across all four study sites differed significantly, with inland snakes (CR, SG) having higher overall SMR than

FIGURE 3 Mean monthly Pacific rattlesnake (*Crotalus oreganus*) physical model temperatures (T_{mod}) for each of the four study sites (inland: CR, SG; coastal: MDO, VAFB) on the Central Coast of California (measured June 2017–June 2018). Mean monthly T_{mod} differed significantly among sites but overall annual T_{mod} did not. SG does not include exposed physical model values, as all exposed SG models failed, as well as the CR shaded model from months July–December. Gray bar represents the preferred body temperature range (T_{set}) of *C. oreganus*. Error bars represent $1 \pm$ standard deviation from the mean



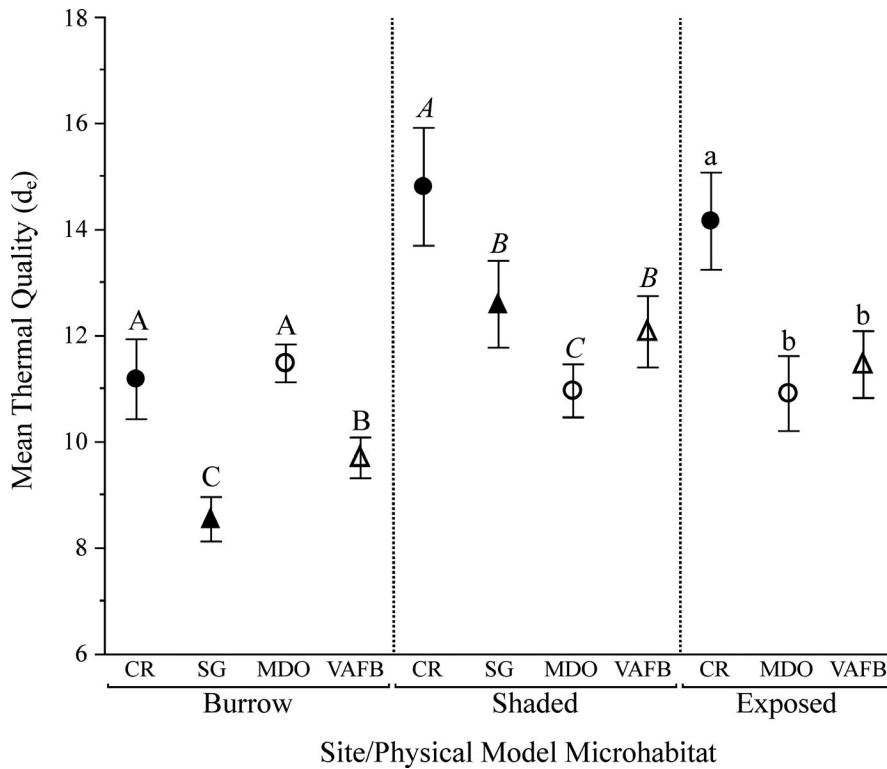


FIGURE 4 Mean thermal quality (d_e) values for each microhabitat at each of four study sites (inland: CR, SG; coastal: MDO, VAFB) from June 2017 to June 2018. Thermal quality values closer to zero are indicative of better thermal quality. Different letters indicate significant differences among physical models in the same microhabitat type (capital letters = burrows, italicized = shaded, lowercase = exposed). SG does not include exposed physical model values, as all exposed SG models failed. Values are shown with 95% confidence intervals

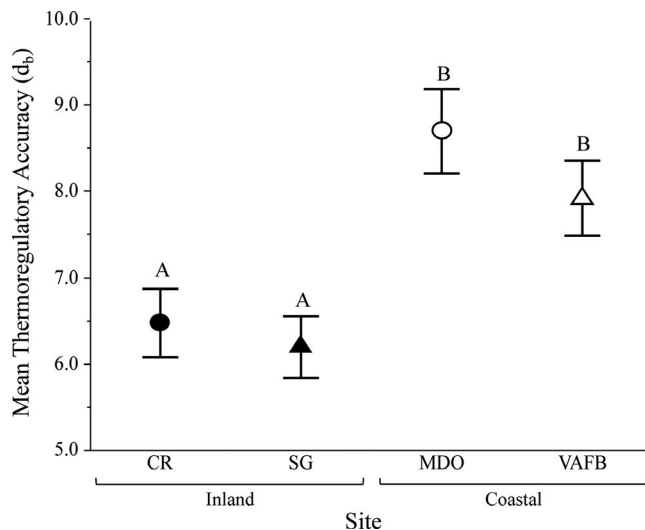


FIGURE 5 Mean thermoregulatory accuracy (d_b) for each of four populations of Pacific rattlesnake (*Crotalus oreganus*; $N = 85$; CR = 23, SG = 28, MDO = 15, VAFB = 19) on the Central Coast of California. Black shapes denote inland sites, white shapes denote coastal sites, circles denote northern sites, and triangles denote southern sites. Values closer to zero reflect higher thermoregulatory accuracy. Mean daily d_b differed significantly among sites, with inland snakes (CR, SG) thermoregulating more accurately than coastal snakes (MDO, VAFB). Different letters represent significant differences between means, and bars represent 95% confidence intervals

coastal (MDO, VAFB) snakes ($F_{7,77} = 136.68$, $p < .0001$, Figure S2). We suspect that the effect of site on SMR was not due to T_b differences among sites, but to body size differences (inland snakes are larger, Table S5). When correcting for mass (by dividing out mass

from overall SMR), we found no significant site differences among SMRs ($F_{3,81} = 1.50$, $p = .22$). However, given that the goal of this study is to examine overall differences in SMR and energetic requirements, we will only focus on whole-animal values as nonmass-corrected data will be most informative for our initial questions (Lighton & Halsey, 2011). When mean SMR values were converted to annual energetic needs, we found that individual snakes from all four populations needed to eat less than the equivalent of one adult ground squirrel year⁻¹ to satisfy maintenance energetic requirements. An average-sized, adult male inland snake would need to consume a mean of 0.80 ground squirrels per year whereas a coastal snake would need an average of 0.51 (Figure 7).

3.7 | Climate change projections

During the physical model deployment period (June 2017–June 2018), the overall proportion of hourly T_{mod} that fell below *C. oreganus* T_{set} was considerably higher (0.856) than the proportion that fell within (0.056) or above (0.085) this range. While these proportions varied among and within sites as well as microhabitat types (Table S6), this general trend held true across all categories. With a 1°C increase in T_{mod} , the overall mean proportion of hourly temperatures that fell within T_{set} increased to 0.064, with still the majority of hourly readings falling below T_{set} (0.084) and 0.091 falling above. A 2°C increase shows the same pattern, with a higher proportion of T_{mod} falling within the T_{set} range (0.075) than the previous two climate conditions, the proportion below T_{set} decreasing (0.825), and the proportion above T_{set} increasing (0.096, Figure S3). Additionally, thermal quality (d_e) of each microhabitat type and the overall thermal

FIGURE 6 Mean hourly physical model temperatures (T_{mod} , in burrows, exposed, or shaded) and Pacific rattlesnake (*Crotalus oreganus*) body temperatures (T_b) over the duration of the active season (April–October) for each of the four study sites (inland: CR, SG; coastal: MDO, VAFB) on the Central Coast of California. CR shaded means do not include data from July–December. Gray bars represent the preferred body temperature range (T_{set}) of *C. oreganus*

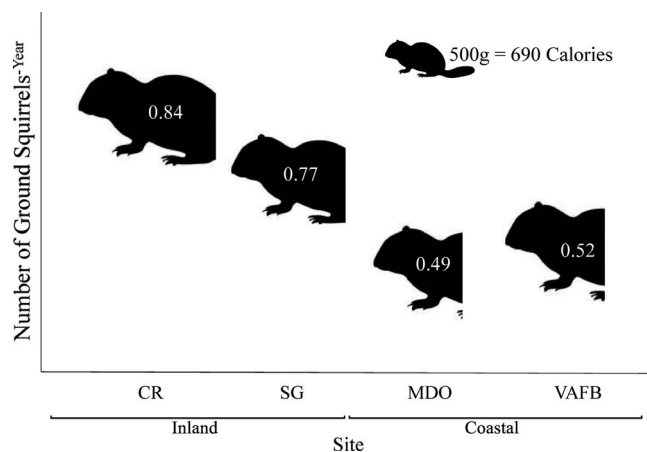
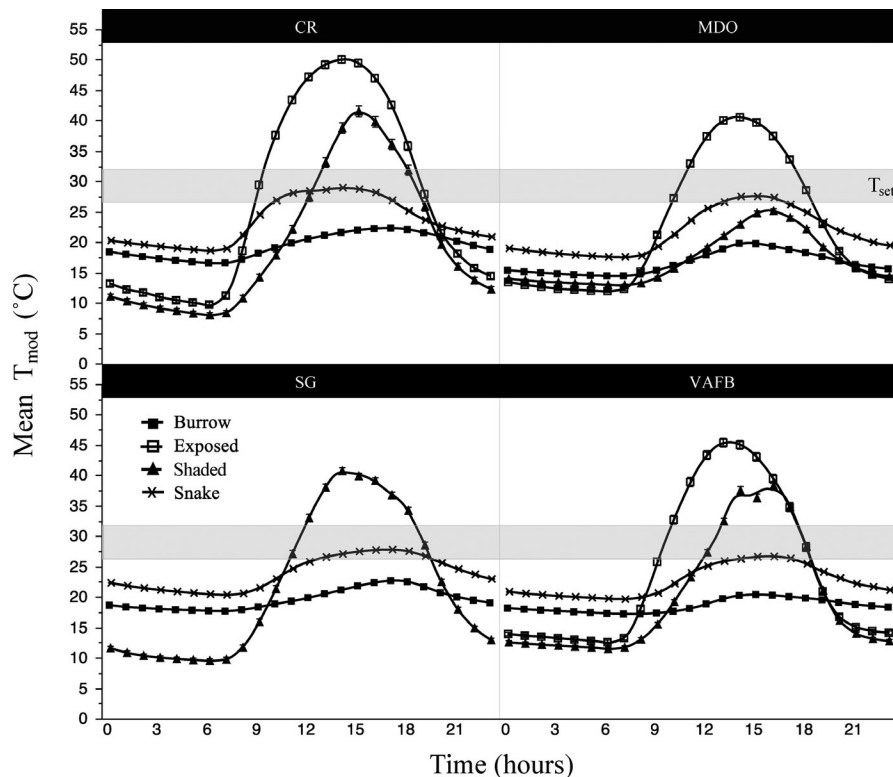


FIGURE 7 Number of California ground squirrels (*Otospermophilus beecheyi*) an average-sized adult male Pacific rattlesnake (*Crotalus oreganus*) from each of four populations on the Central Coast of California (CR, SG, MDO, VAFB) would need to consume to meet annual maintenance energetic requirements

quality of each site are projected to improve with increases in ambient temperature (Figure 8). With the greatest increase of 2°C, CR, SG, MDO, and VAFB will, respectively, experience an overall 10, 12, 13, and 11% increase in d_e . These data suggest that rising temperatures associated with anthropogenic climate change could actually benefit *C. oreganus* as the thermal quality of their habitats increases.

Maintenance energy requirements (kcal/year) were overall significantly higher when incorporating annual increases of 1°C and 2°C in mean snake T_b ($F_{5,6} = 106.97$, $p < .00001$). However, post hoc tests revealed that whole model significance is driven

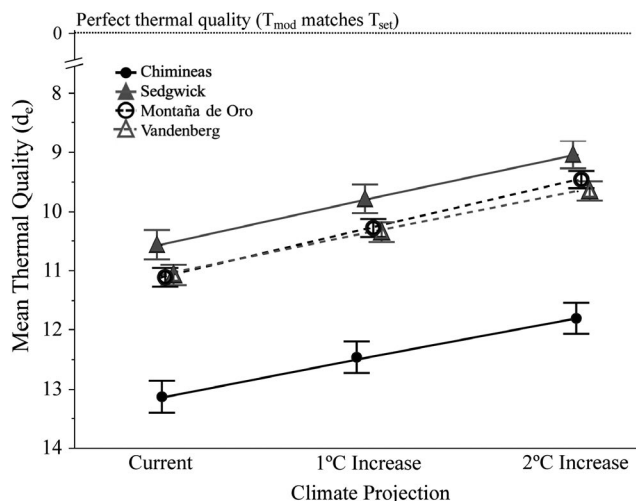


FIGURE 8 Overall thermal quality (d_e) for four study sites (CR, SG, MDO, and VAFB) on the Central Coast of California at current conditions and with a 1°C and 2°C increase in ambient temperatures. Values approaching zero represent higher thermal quality. All sites will experience an increase in d_e as ambient temperatures increase, creating potentially more favorable thermal environments for Pacific rattlesnakes (*Crotalus oreganus*) in both coastal and inland locations. Error bars represent ± 1 SEM

by the differences between current and 1°C requirements, and requirements incorporating the 2°C increase. There are no significant increases from current energetic requirements to energetic requirements with an increase in snake T_b of 1°C (8.4% increase in annual maintenance energetic requirements). With a 2°C increase from current snake T_b , mean energetic requirements increased by

another 17.6%, which was a significant increase from the current and 1°C requirements. However, when converted to mean number of squirrels per year, all populations still required roughly 1 or less large meal (Table 2).

4 | DISCUSSION

In this study, we demonstrate that populations of *C. oreganus* experience dramatically different climatic conditions but utilize thermal variation in microhabitats to thermoregulate such that differences in mean active T_b are minor and that these differences may not have major impacts on the snakes' overall energetic needs. As a moderately precise thermoregulator (Blouin-Demers & Weatherhead, 2001), *C. oreganus* will likely be able to mitigate the effects of inhabiting low-quality thermal habitat by altering thermoregulatory behaviors, and furthermore, climate change is predicted to increase the thermal quality of *C. oreganus* habitat. Thus, this rattlesnake species and others may be fairly resilient to and even positively impacted by changing climates.

The T_{set} range ($26.28 \pm 1.01^\circ\text{C}$ - $32.34 \pm 0.84^\circ\text{C}$) was similar in all four populations of *C. oreganus* and is notably wide in range, potentially because, as habitat generalists and ambush foragers, rattlesnakes are adapted to experiencing a wide range of environmental temperatures (Alford & Lutterschmidt, 2012). Other vipers also exhibit high variation in T_{set} within and among species (Table S7). This large range of temperature preferences exemplifies the tendency of larger-bodied ambush-predator ectotherms to exhibit more eurythermic behaviors that are reflective of the environments in which they are found (Bovo et al., 2012; Brattstrom, 1965; Moore, 1969). Snakes from coastal sites had significantly lower T_b than snakes from inland sites, which we expected based on different ambient temperatures. However, variation in T_b may also be related to environmental trade-offs impacting the thermoregulatory behavior, such as site differences in predation risk, as well as body size and thermal inertia (Putman & Clark, 2017), which in the case of our study is inextricably linked to source population. That is, inland snakes could experience higher T_b in part because their larger body sizes impart slower cooling rates (Stevenson, 1985). Regardless of site, both inland and coastal snakes typically exhibited field-active T_b below their T_{set} . Snakes often select ambush sites in shaded areas along small mammal trails in grass or near ground squirrel burrows (Putman et al., 2016; Theodoratus & Chiszar, 2000) and remain for an extended period

of time until a prey item passes within striking distance. Lower T_b resulting from ambush site selection may represent a thermoregulatory trade-off as snakes passively thermoconform to low-quality ambush sites (Alford & Lutterschmidt, 2012).

Our prediction that coastal sites would have overall better thermal quality than inland sites was supported (if we assume that SG would have a similar thermal quality to CR with the inclusion of values from exposed physical models), although there was no significant difference in annual overall mean T_{mod} . The lack of overall difference in mean T_{mod} is likely due to the greater variance of temperatures in inland sites throughout the year relative to coastal sites, creating similar means. However, the variation in temperature among and within these sites is best demonstrated by the significant variation in thermal quality of each microhabitat. Overall, burrows have the best thermal quality due to their more stable temperatures, and it is likely that they offer cooler temperatures and further thermal stability deeper in the burrow systems which were unattainable to us for measurement. Snakes are able to use this microhabitat as dependable thermal refugia when surface temperatures are either too hot or cold. To our surprise, shaded physical models often experienced temperatures close to those of exposed models at their respective sites. It is possible that even though these models were shaded, the extreme heat of the inland sites and frequently windy and wet conditions of the coastal sites still drove the temperatures of these models far above and below T_{set} due to conduction and convection, respectively. Because thermal quality is more variable at inland sites, this may mean that snakes need to spend more energy shuttling between thermally favorable habitat during their active summer season as well as experience restricted daily and annual activity patterns. Meanwhile, the lack of large temperature fluctuations at coastal sites means snakes can remain active for a larger portion of daylight hours and for most, if not all of the year. Although physical models allowed us to produce a coarse estimate of the thermal landscape, we are unable to account for the entire thermal configuration of each site (Sinclair et al., 2016), and a more detailed analysis within each of these sites would help elucidate some of the drivers of differences in field-active T_b observed in these populations of *C. oreganus*. Additionally, our study used environmental and body temperature data that only partially overlapped in study periods; future studies interested in making comparisons of fine-scale relationships between microhabitat temperatures and snake body temperatures should collect data across the exact same time period, even if long-term climates at study sites are relatively stable.

Site	Current no. required squirrels	No. required squirrels with 1°C increase	No. required squirrels with 2°C increase
CR (Inland)	0.84 ± 0.04	0.90 ± 0.04	1.06 ± 0.04
SG (Inland)	0.77 ± 0.04	0.86 ± 0.05	1.01 ± 0.05
MDO (Coastal)	0.49 ± 0.04	0.53 ± 0.05	0.62 ± 0.04
VAFB (Coastal)	0.52 ± 0.02	0.57 ± 0.02	0.68 ± 0.02

TABLE 2 Mean number of ground squirrels required by an average-sized, adult male Pacific rattlesnake (*Crotalus oreganus*) from four populations on the Central Coast of California required to meet annual maintenance energy requirements at current body temperature (T_b) conditions and with theoretical 1°C and 2°C increases in T_b

We were somewhat surprised to find that snakes in habitats with poorer thermal quality (inland sites) thermoregulated more accurately than snakes with access to higher quality habitats (coastal populations). While this phenomenon has been documented in multiple small lizard species (Gunderson & Leal, 2012; Sagonas et al., 2013), the number of studies reporting this in large-bodied reptiles is limited (Besson & Cree, 2010; Blouin-Demers & Weatherhead, 2001; Row & Blouin-Demers, 2006), particularly in ambush predators (Bovo et al., 2012). It is possible that the higher thermal quality of coastal sites may result in longer periods of time where ambient temperatures are closer to the T_{set} of *C. oreganus*, putting less physiological pressure on snakes to actively thermoregulate. Additionally, snakes at the poorer quality inland sites may be thermoregulating more accurately to increase physiological performance for other behaviors (e.g., mate searching, ambush, etc.) during the more limited activity hours, as Besson and Cree (2010) reported in tuatara. The results may also reflect the thermal heterogeneity of the habitats: The thermal quality of microhabitats in inland sites was more variable than those in coastal sites (Figure 4), potentially affording inland snakes a wider range of choices when thermoregulating and allowing them to find ambush sites or refugia closer to their T_{set} .

Our estimates of the SMR of snakes from all four populations revealed that snakes from inland sites require on average 1.6× as much food as coastal snakes for maintenance metabolism. The equations to estimate SMR (Beaupre & Duvall, 1998a, 1998b) use mass and T_b ; while both of these were higher at inland sites, the larger body size of inland males was the major contributor to their higher SMR and therefore energy requirements. Our data show that high variation in ambient temperatures among sites translates into only minor inter-population differences in T_b due to effective thermoregulation and that these differences do not have a great impact on maintenance energy requirements. The driving factor for differences in overall metabolic rates, and therefore energetic needs, is the actual mass of the animal (Dorcas et al., 2004). Why are males larger at inland sites? There are many possibilities, including a warmer active season promoting a longer growing season (Mousseau, 1997), higher rainfall and water availability at our inland sites offsetting the negative effects of living in semi-arid habitats (Amarello et al., 2010), more competition for resources at coastal sites due to higher rattlesnake population densities and/or lower prey densities (Beaupre, 1995; Madsen & Shine, 1993), or population differences with inland snakes genetically predisposed to grow larger and/or surviving longer (Forsman, 1993). Regardless of the cause, the implications of body size and temperature variation among adult male rattlesnakes at each of these sites result in minor differences in energetic needs to fuel maintenance metabolism, with snakes from each site needing less than one adult ground squirrel per year. Importantly, our metabolic calculations are only estimates of maintenance metabolism and do not encompass energetically costly activities including digestion and movement through the environment for mate-seeking, predator avoidance, and ambush site selection (Beaupre, 1996, 2008). Furthermore, energetic needs of female rattlesnakes to produce a litter of offspring would be much higher (Beaupre, 2002; Beaupre & Duvall, 1998b). Population and sex

differences in overall energy requirements could only be ascertained by collecting field metabolic data (e.g., Beaupre, 2008).

Climate change is generally predicted to have a negative effect on most ectotherm species, especially those at lower latitudes (Sinervo et al., 2010). However, it appears that small increases in ambient temperature may prove beneficial to rattlesnakes in central California because the overall thermal quality of all microhabitats is projected to increase at all field sites. With a larger proportion of daily T_{mod} falling within the T_{set} range, snakes will be less thermally constrained, choose among a wider range of ambush sites, and be active for a longer time during the day. Specifically, snakes will be able to emerge from overwintering earlier in the year and, in turn, wait until later months before going back into hiding. This may translate into additional opportunities to find resources such as mates and food, as well as longer annual active seasons, and could feasibly result in higher reproductive output in females and therefore increased population densities of rattlesnakes. It is also possible that summer temperatures may exceed T_{set} for longer periods of time during daylight hours (particularly at the inland sites), resulting in altered behavior, such as a shift to more crepuscular/nocturnal foraging. This could lead to utilization of alternate prey sources which in turn could start a cascade of ecological effects at the community level. If the metabolic rates of these snakes rise with increasing temperatures, they would need to obtain additional energetic resources. However, as our calculations and other studies have shown, the metabolic needs of these snakes are incredibly low (Beaupre, 1995; Beaupre & Duvall, 1998b; Beck, 1995), with current baseline maintenance energetic demands being met with less than a single large meal per year. Even if mean active T_b increased 1°C or 2°C along with ambient temperature, the annual caloric requirements for maintenance would still be met with a single large prey item. That said, evidence from this study suggests that *C. oreganus* is an accurate enough thermoregulator that overall small changes in ambient temperature will likely not dramatically shift the snakes' T_b . These theoretical calculations are limited to the scope of energetic needs of the snakes from which they were calculated (i.e., resting, fasted snakes unable to thermoregulate in a metabolic chamber), so these results must also be considered in an ecological context. To fully understand the implications of climate change for rattlesnakes, we would need to take into account possible impacts on prey populations as well as changes in snake behavior as a response to changing temperatures, which may increase energetic needs beyond the scope of our models.

Overall, rattlesnakes are ideal model organisms for examining the physiological effects of climate on large-bodied ectotherms. Their life-history traits, simple behaviors, and metabolism are well studied, providing a strong foundation for examining their thermal ecology and implications of climate change on their energetic requirements. Large-scale comparative studies among multiple populations of a given species can greatly enhance our understanding of the effects of anthropogenic climate change on biodiversity. While small increases in ambient temperature may prove thermally beneficial to rattlesnakes on the Central Coast of California, alterations in climates may affect rattlesnake environments in negative ways and have cascading effects within their biotic communities. It is apparent

that in rattlesnakes, a wide-ranging T_{set} plasticity in thermoregulatory behavior, and low energetic demands may help mitigate the changes in environmental temperatures these animals will experience, even across extremely variable habitat types.

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CONFLICT OF INTEREST

None declared.

AUTHOR CONTRIBUTIONS

Hayley L. Crowell: Conceptualization (lead); data curation (lead); formal analysis (lead); investigation (equal); methodology (lead); project administration (lead); supervision (lead); visualization (lead); writing—original draft (lead). **Katherine C. King:** Data curation (equal); formal analysis (supporting); investigation (supporting); writing—original draft (supporting). **James M. Whelan:** Conceptualization (supporting); data curation (equal); formal analysis (supporting); investigation (supporting); methodology (supporting); writing—original draft (supporting). **Mallory V. Harmel:** Data curation (supporting); formal analysis (supporting); investigation (supporting); writing—original draft (supporting). **Gennese Garcia:** Data curation (supporting); investigation (supporting); writing—original draft (supporting). **Sebastian G. Gonzales:** Data curation (supporting); investigation (supporting); writing—original draft (supporting). **Paul H. Maier:** Data curation (supporting); investigation (supporting); writing—original draft (supporting). **Heather M. Neldner:** Data curation (supporting); investigation (supporting); writing—review and editing (supporting). **Thomas Nhu:** Data curation (supporting); investigation (supporting); writing—original draft (supporting). **John T. Nolan:** Data curation (supporting); investigation (supporting); writing—original draft (supporting). **Emily N. Taylor:** Conceptualization (lead); data curation (supporting); funding acquisition (lead); methodology (equal); resources (lead); supervision (supporting); validation (lead); writing—review and editing (lead).

DATA AVAILABILITY STATEMENT

All data associated with this project can be found on Dryad (<https://doi.org/10.5061/dryad.mpg4f4qzv>).

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REFERENCES

- Aldridge, R. D. (2002). The link between mating season and male reproductive anatomy in the rattlesnakes *Crotalus viridis oreganus* and *Crotalus viridis helleri*. *Journal of Herpetology*, 36(2), 295–300. [10.1670/00221511\(2002\)036\[0295:tlbmsa\]2.0.co;2](https://doi.org/10.1670/00221511(2002)036[0295:tlbmsa]2.0.co;2)
- Alford, J. G., & Lutterschmidt, W. I. (2012). Modeling energetic and theoretical costs of thermoregulatory strategy. *Journal of Biological Dynamics*, 6(1), 63–79. <https://doi.org/10.1080/17513758.2011.588342>
- Amarello, M., Nowak, E. M., Taylor, E. N., Schuett, G. W., Repp, R. A., Rosen, P. C., & Hardy, D. L. S. (2010). Potential environmental influences on variation in body size and sexual size dimorphism among Arizona populations of the western diamond-backed rattlesnake (*Crotalus atrox*). *Journal of Arid Environments*, 74, 1443–1449. <https://doi.org/10.1016/j.jaridenv.2010.05.019>
- Ashton, K. G. (2001). Body size variation among mainland populations of the Western Rattlesnake (*Crotalus viridis*). *Evolution*, 55(12), 2523–2533. <https://doi.org/10.1111/j.0014-3820.2001.tb00766.x>
- Ashton, K. G., & de Queiroz, A. (2001). Molecular systematics of the western rattlesnake, *Crotalus viridis* (Viperidae), with the comments on the utility of the D-Loop in phylogenetic studies of snakes. *Molecular Phylogenetic Evolution*, 21, 76–189. <https://doi.org/10.1006/mpev.2001.1013>
- Bakken, G. S. (1992). Measurement and application of operative and standard operative temperatures in ecology. *American Zoologist*, 32, 194–216. <https://doi.org/10.1093/icb/32.2.194>
- Bakken, G. S., & Gates, D. M. (1975). Heat-transfer analysis of animals: Some implications for field ecology, physiology, and evolution. *Perspectives of Biophysical Ecology*, 255–290. https://doi.org/10.1007/978-3-642-87810-7_16
- Beaupre, S. J. (1995). Effects of geographically variable thermal environment on bioenergetics of Mottled Rock Rattlesnakes. *Ecology*, 76(5), 1655–1665. <https://doi.org/10.2307/1938166>
- Beaupre, S. J. (1996). Field metabolic rate, water flux, and energy budgets of Mottled Rock Rattlesnakes, *Crotalus lepidus*, from two populations. *Copeia*, 2, 319–329. <https://doi.org/10.2307/1446847>
- Beaupre, S. J. (2002). *Modeling Time-Energy Allocation in Vipers: Individual responses to environmental variation and implications for populations* (pp. 463–481). Biology of the Vipers, Eagle Mountain Publishing.
- Beaupre, S. J. (2008). *Annual variation in time-energy allocation by Timber Rattlesnakes (Crotalus horridus) in relation to food acquisition* (pp. 1–11). The Biology of Rattlesnakes, Loma Linda University Press.
- Beaupre, S. J., & Duvall, D. (1998a). Integrative biology of rattlesnakes. *BioScience*, 48(7), 531–538. <https://doi.org/10.2307/1313315>
- Beaupre, S. J., & Duvall, D. (1998b). Variation in oxygen consumption of the western diamondback rattlesnake (*Crotalus atrox*): Implications for sexual size dimorphism. *Journal of Comparative Physiology B*, 168, 497–506. <https://doi.org/10.1007/s003600050170>
- Beaupre, S. J., & Zaidan, F. (2012). Digestive performance in the Timber rattlesnake (*Crotalus horridus*) with reference to temperature dependence and bioenergetic cost of growth. *Journal of Herpetology*, 46(4), 637–642. <https://doi.org/10.1670/11-108>
- Beck, D. D. (1995). Ecology and energetics of three sympatric rattlesnake species in the Sonoran Desert. *Journal of Herpetology*, 29(2), 211–223. <https://doi.org/10.2307/1564558>
- Besson, A. A., & Cree, A. (2010). A cold-adapted reptiles becomes a more effective thermoregulator in a thermally challenging

- environment. *Oecologia*, 163, 571–581. <https://doi.org/10.1007/s00442-010-1571-y>
- Blouin-Demers, G., & Weatherhead, P. J. (2001). Thermal ecology of black rat snakes (*Elaphe obsoleta*) in a thermally challenging environment. *Ecology*, 82(11), 3025–3043. [https://doi.org/10.1890/0012-9658\(2001\)082\[3025:TEOBRS\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[3025:TEOBRS]2.0.CO;2)
- Blouin-Demers, G., & Weatherhead, P. (2002). Habitat-specific behavioral thermoregulation by black rat snakes (*Elaphe obsoleta obsoleta*). *Oikos*, 97(1), 59–68. <https://doi.org/10.1034/j.1600-0706.2002.970106.x>
- Böhm, M., Collen, B., Baillie, J. E. M., Bowles, P., Chanson, J., Cox, N., Hammerson, G., Hoffmann, M., Livingstone, S. R., Ram, M., Rhodin, A. G. J., Stuart, S. N., van Dijk, P. P., Young, B. E., Aftuang, L. E., Aghasyan, A., García, A., Aguilar, C., Ajtic, R., ... Zug, G. (2013). The conservation status of the world's reptiles. *Biological Conservation*, 157, 372–385. <https://doi.org/10.1016/j.biocon.2012.07.015>
- Böhm, M., Cook, D., Ma, H., Davidson, A. D., García, A., Tapley, B., Pearce-Kelly, P., & Carr, J. (2016). Hot and bothered: Using trait-based approaches to assess climate change vulnerability in reptiles. *Biological Conservation*, 204, 32–41. <https://doi.org/10.1016/j.biocon.2016.06.002>
- Bovo, R. P., Marques, O. A. V., & Andrade, D. V. (2012). When basking is not an option: Thermoregulation of a Viperid snake endemic to a small island in the South Atlantic of Brazil. *Copeia*, 2012, 408–418. <https://doi.org/10.1643/CP-11-029>
- Brattstrom, B. H. (1965). Body temperatures of reptiles. *American Midland Naturalist*, 73, 376–422. <https://doi.org/10.2307/2423461>
- Brusch, G. A. IV, Taylor, E. N., & Whitfield, S. M. (2016). Turn up the heat: Thermal tolerances of lizards at La Selva, Costa Rica. *Oecologia*, 180, 325–334. <https://doi.org/10.1007/s00442-015-3467-3>
- Buckley, L. B., Ehrenberger, J. C., & Angilletta, M. J. (2015). Thermoregulatory behavior limits local adaptation of thermal niches and confers sensitivity to climate change. *Functional Ecology*, 29, 1038–1042. <https://doi.org/10.1111/1365-2435.12406>
- California Energy Commission. (2019). *Cal-Adapt: Exploring California's climate change research*. State of California. Retrieved from <http://cal-adapt.org/>
- Capehart, G. D., Escallón, C., Vernasco, B. J., Moore, I. T., & Taylor, E. N. (2016). No drought about it: Effects of supplemental hydration on the ecology, behavior, and physiology of free-ranging rattlesnakes. *Journal of Arid Environments*, 134, 79–86. <https://doi.org/10.1016/j.jaridenv.2016.06.018>
- Charland, M. B., Gregory, P. T., & Columbia, B. (1990). The Influence of female reproductive status on thermoregulation in a viviparous snake, *Crotalus viridis*. *Copeia*, 4, 1089–1098. <https://doi.org/10.2307/1446493>
- Chimineas Ranch Foundation (2019). *Mission: Who we are & what we do*. Retrieved from <http://www.chimineasranchfoundation.org/mission.html>
- Claunch, N. M., Frazier, J. A., Escallón, C., Vernasco, B. J., Moore, I. T., & Taylor, E. N. (2017). Physiological and behavioral effects of exogenous corticosterone in a free-ranging ectotherm. *General and Comparative Endocrinology*, 248, 87–96. <https://doi.org/10.1016/j.ygcen.2017.02.008>
- Clusella-Trullas, S., Blackburn, T. M., & Chown, S. L. (2011). Climatic predictors of temperature performance curve parameters in ectotherms imply complex responses to climate change. *The American Naturalist*, 177(6), 738–751. <https://doi.org/10.1086/660021>
- Davies, T. J., Fritz, S. A., Grenyer, R., Orme, C. D. L., Bielby, J., Bininda-Emonds, O. R. P., Cardillo, M., Jones, K. E., Gittleman, J. L., Mace, G. M., & Purvis, A. (2008). Phylogenetic trees and the future of mammalian biodiversity. *Proceedings of the National Academy of Sciences*, 105(1), 11556–11563. <https://doi.org/10.1073/pnas.0801917105>
- Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C., & Martin, P. R. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *PNAS*, 105(18), 6668–6672. <https://doi.org/10.1073/pnas.0709472105>
- Dorcas, M. E., Hopkins, W. A., & Roe, J. H. (2004). Effects of body mass and temperature on standard metabolic rate in the Eastern diamond-back rattlesnake (*Crotalus adamanteus*). *Copeia*, 1, 145–151. <https://doi.org/10.1643/CP-03-074R1>
- Dzialowski, E. M. (2005). Use of operative temperature and standard operative temperature models in thermal biology. *Journal of Thermal Biology*, 30, 317–334. <https://doi.org/10.1016/j.jtherbio.2005.01.005>
- Evans, F. C., & Holdenried, R. (1943). A population study of Beechy ground squirrel in Central California. *Journal of Mammalogy*, 24(2), 231–260. <https://doi.org/10.2307/1374808>
- Fitzgerald, M., Shine, R., & Lemckert, F. (2003). A reluctant heliotherm: Thermal ecology of the arboreal snake *Hoplocephalus stephensii* (Elapidae) in dense forest. *Journal of Thermal Biology*, 28, 515–524. [https://doi.org/10.1016/S0306-4565\(03\)00052-4](https://doi.org/10.1016/S0306-4565(03)00052-4)
- Forsman, A. (1993). Survival in relation to body size and growth rate in the adder, *Vipera berus*. *Journal of Animal Ecology*, 62, 647–655. <https://doi.org/10.2307/5385>
- François, R., Henry, L., & Müller, K. (2018). *dplyr: A grammar of data manipulation*. R Package Version 0.7.7.
- Gibbons, J. W., Scott, D. E., Ryan, T. J., Buhlmann, K. A., Tuberville, T. D., Metts, B. S., & Winne, C. T. (2000). The global decline of reptiles, déjà vu amphibians. *BioScience*, 50, 653–666. [https://doi.org/10.1641/00063568\(2000\)050\[0653:TGDORD\]2.0.CO;2](https://doi.org/10.1641/00063568(2000)050[0653:TGDORD]2.0.CO;2)
- Gunderson, A., & Leal, M. (2012). Geographic variation in vulnerability to climate warming in a tropical Caribbean lizard. *Functional Ecology*, 26(4), 783–793. <https://doi.org/10.1111/j.1365-2435.2012.01987.x>
- Hertz, P. E., Huey, R. B., & Stevenson, R. D. (1993). Evaluating temperature regulation by field-active ectotherms: The fallacy of the inappropriate question. *American Naturalist*, 142, 796–818. <https://doi.org/10.1086/285573>
- Holding, M. L., Sovic, M. G., Colston, T. J., & Gibbs, H. L. (2021). The scales of coevolution: Comparative phylogeography and genetic demography of a locally adapted venomous predator and its prey. *Biological Journal of the Linnean Society*, 132(2), 297–317. <https://doi.org/10.1093/biolinnean/blaa192>
- Huey, R. B. (1982). *Temperature, physiology, and the ecology of Reptiles* (pp. 25–91). Biology of the Reptilia, Academic Press.
- Kaufman, D. W., Kaufman, G. A., & Wiener, J. G. (1975). Energy equivalents for sixteen species of xeric rodents. *Journal of Mammalogy*, 56, 946–949. <https://doi.org/10.2307/1379673>
- Lelièvre, H., Blouin-Demers, G., Pinaud, D., Lisse, H., Bonnet, X., & Lourdais, O. (2011). Contrasted thermal preferences translates into divergences in habitat use and realized performance in two sympatric snakes. *Journal of Zoology*, 284, 265–275. <https://doi.org/10.1111/j.1469-7998.2011.00802.x>
- Lighton, J. R. B., & Halsey, L. G. (2011). Flow-through respirometry applied to chamber systems: Pros and cons, hints and tips. *Comparative Biochemistry and Physiology Part A*, 158(3), 265–275. <https://doi.org/10.1016/j.cbpa.2010.11.026>
- Lutterschmidt, W. I., & Reinert, H. K. (2012). Modeling body temperature and thermal inertia of large-bodied reptiles: Support for water-filled biophysical models in radiotelemetric studies. *Journal of Thermal Biology*, 37(4), 282–285. <https://doi.org/10.1016/j.jtherbio.2011.10.011>
- Mackessy, S., Williams, K., & Ashton, K. (2003). Ontogenetic variation in venom composition and diet of *Crotalus oreganus concolor*: A case of venom paedomorphosis? *Copeia*, 4, 769–782. <https://doi.org/10.1643/HA03-037.1>
- Madsen, T., & Shine, R. (1993). Phenotypic plasticity in body sizes and sexual size dimorphism in European grass snakes. *Evolution*, 47(10), 321–325. <https://doi.org/10.2307/2410141>
- Millar, R. B., & Anderson, M. J. (2004). Remedies for pseudoreplication. *Fisheries Research*, 70, 397–407. <https://doi.org/10.1016/j.fishres.2004.08.016>

- Moore, R. G. (1969). *Thermoregulation in the Western rattlesnakes*, *Crotalus viridis*. Master's Thesis. Department of Biological Science, California State College at Hayward.
- Moore, R. G. (1978). Seasonal and daily activity patterns and thermoregulation in the Southwestern Speckled rattlesnake (*Crotalus mitchellii pyrrhus*) and the Colorado Desert sidewinder (*Crotalus cerastes laterorepens*). *Copeia*, 4, 439–442. <https://doi.org/10.2307/1443608>
- Mousseau, T. A. (1997). Ectotherms follow the converse to Bergmann's rule. *Evolution*, 51, 630–632. <https://doi.org/10.2307/2411138>
- Pelegri, N., & Bucher, E. H. (2012). Effects of habitat degradation on lizard assemblage in arid Chaco, central Argentina. *Journal of Arid Environments*, 79, 13–19. <https://doi.org/10.1016/j.jaridenv.2011.11.004>
- Pook, C., Wüster, W., & Thorpe, R. (2000). Historical biogeography of the Western Rattlesnake (Serpentes: Viperidae: *Crotalus viridis*), inferred from mitochondrial DNA sequence information. *Molecular Phylogenetics and Evolution*, 15, 269–282. <https://doi.org/10.1006/mpev.1999.0756>
- Putman, B. J., Barbour, M. A., & Clark, R. W. (2016). The foraging behavior of free-ranging rattlesnakes (*Crotalus oreganus*) in California ground squirrel (*Otospermophilus beecheyi*) colonies. *Herpetologica*, 72(1), 55–63. <https://doi.org/10.1655/HERPETOLOGICA-D-15-00045>
- Putman, B. J., & Clark, R. W. (2017). Behavioral thermal tolerances of free-ranging rattlesnakes (*Crotalus oreganus*) during the summer foraging season. *Journal of Thermal Biology*, 65(2017), 8–15. <https://doi.org/10.1016/j.jtherbio.2017.01.012>
- R Development Core Team (2015). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Row, J. R., & Blouin-Demers, G. (2006). Thermal quality influence effectiveness of thermoregulation, habitat use, and behavior in milk snakes. *Oecologia*, 148, 1–11. <https://doi.org/10.1007/s00442-005-0350-7>
- Rowe, M. P., & Owings, D. H. (1990). Probing, assessment, and management during interactions between ground squirrels and rattlesnakes. *Ethology*, 86, 237–249. <https://doi.org/10.1111/j.1439-0310.1990.tb00432.x>
- Sagonas, K., Valakos, E. D., & Pafilis, P. (2013). The impact of insularity on the thermoregulation of a Mediterranean lizard. *Journal of Thermal Biology*, 38(8), 480–486. <https://doi.org/10.1016/j.jtherbio.2013.08.004>
- Secor, S. M., & Nagy, K. A. (1994). Bioenergetic correlates of foraging mode for the snakes *Crotalus cerastes* and *Masticophis flagellum*. *Ecology*, 5, 1600–1614. <https://doi.org/10.2307/1939621>
- Sinclair, B. J., Marshall, K. E., Sewell, M. A., Levesque, D. L., Willett, C. S., Slotsbo, S., Dong, Y., Harley, C. D. G., Marshall, D. J., Helmuth, B. S., & Huey, R. B. (2016). Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures? *Ecology Letters*, 19, 1372–1385. <https://doi.org/10.1111/ele.12686>
- Sinervo, B., Mendez-de-la-Cruz, F., Miles, D. B., Heulin, B., Bastiaans, E., Villagran-Santa Cruz, M., Lara-Resendiz, R., Martinez-Mendez, N., Calderon-Espinosa, M. L., Meza-Lazaro, R. N., Gadsden, H., Avila, L. J., Morando, M., De la Riva, I. J., Sepulveda, P. V., Rocha, C. F. D., Ibaranguoytia, N., Puntriano, C. A., Massot, M., ... Sites, J. W. (2010). Erosion of lizard diversity by climate change and altered thermal niches. *Science*, 328, 894–899. <https://doi.org/10.1126/science.1184695>
- Sparks, A. M., Lind, C., & Taylor, E. N. (2015). Diet of the Northern Pacific Rattlesnake (*Crotalus o. oreganus*) in California. *Herpetological Review*, 46(2), 161–165.
- Stevenson, R. D. (1985). Body size and limits to the daily range of body temperature in terrestrial ectotherms. *The American Naturalist*, 125(1), 102–117. <https://doi.org/10.1086/284330>
- Sunagar, K., Undheim, E. A. B., Scheib, H., Gren, E. C. K., Cochran, C., Person, C. E., Koludarov, I., Kelln, W., Hayes, W. K., King, G. F., Antunes, A., & Fry, B. G. (2014). Intraspecific venom variation in the medically significant Southern Pacific rattlesnake (*Crotalus oreganus helleri*): Biodiscovery, clinical and evolutionary implications. *Journal of Proteomics*, 99, 68–83. <https://doi.org/10.1016/j.jprot.2014.01.013>
- Theodoratus, D. H., & Chiszar, D. (2000). Habitat selection and prey odor in the foraging behavior of Western rattlesnakes (*Crotalus viridis*). *Behaviour*, 137(1), 119–135. <https://doi.org/10.1163/156853900501908>
- Thuiller, W., Broennimann, O., Hughes, G., Alkemade, J. R. M., Midgley, G. F., & Corsi, F. (2006). Vulnerability of African mammals to anthropogenic climate change under conservative land transformation assumptions. *Global Change Biology*, 12, 424–440. <https://doi.org/10.1111/j.1365-2486.2006.01115.x>
- Underwood, E., Ustin, S., & DiPietro, D. (2003). Mapping nonnative plants using hyperspectral imagery. *Remote Sensing of Environment*, 86(2), 150–161. [https://doi.org/10.1016/S0034-4257\(03\)00096-8](https://doi.org/10.1016/S0034-4257(03)00096-8)
- University of California Reserve System: Natural Resources. (2019). *UC Reserve Santa Barbara*. Retrieved from <http://sedgwick.nrs.ucsb.edu/weather/daily-weather-2007>
- Urban, M. C. (2015). Accelerating extinction risk from climate change. *Science*, 348(6234), 571–573. <https://doi.org/10.1126/science.aaa4984>
- Waldshmidt, S. R., Jones, S. M., & Porter, W. P. (1986). The effect of body temperature and feeding regime on activity, passage time, and digestive coefficient in the lizard *Uta stansburiana*. *Physiological Zoology*, 59(3), 376–383. <https://doi.org/10.1086/physzool.59.3.30156109>
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J.-M., Hoegh-Guldberg, O., & Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, 416, 389–395. <https://doi.org/10.1038/416389a>
- Western Regional Climate Center (2017). *Cooperative Climatological Data Summaries: S. California*. Western Regional Climate Center (WRCC) and the National Ocean and Atmospheric Administration. Retrieved from <https://wrcc.dri.edu/summary/Climsmsca.html>
- White, R. L., & Bennett, P. M. (2015). Elevational distribution and extinction risk in birds. *PLoS One*, 10(4), e0121849. <https://doi.org/10.1371/journal.pone.0121849>
- Wormworth, J., & Mallon, K. (2006). *Bird Species and Climate Change. The Global Status Report. A synthesis of current scientific understanding of anthropogenic climate change impacts on global bird species now, and projected future effects. Australia*. Retrieved from https://www.wwf.or.jp/activities/data/2006climate_birdsF.pdf
- Wright, A. N., Schwartz, M. W., Hijmans, R. J., & Bradley Shaffer, H. (2016). Advances in climate models from CMIP3 to CMIP5 do not change predictions of future habitat suitability for California reptiles and amphibians. *Climatic Change*, 134(4), 579–591. <https://doi.org/10.1007/s10584-015-155>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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