2018

Energetic Consequences for a Northern, Range-Edge Lizard Population

Sean D. Powers

Matthew R. McTernan

Donald R. Powers

Roger A. Anderson

Energetic Consequences for a Northern, Range-Edge Lizard Population

Sean D. Powers[1], Matthew R. McTernan[2], Donald R. Powers[3], and Roger A. Anderson[2]

Lizards at the northern, cool edge of their geographic range in the northern hemisphere should encounter environmental conditions that differ from those living near the core of their range. To better understand how modest climate differences affect lizard energetics, we compared daily feeding and metabolism rates of individual *Sceloporus occidentalis* in two populations during mid-summer. Chuckanut Beach (CB) was a cool, maritime climate in northern Washington State, and Sondino Ranch (SR) was a warmer, drier climate in southern, inland Washington. We found no difference between populations in daily energy expenditure (DEE), as calculated from doubly labeled water estimates. The CB population, however, had significantly higher prey availability and rate of daily energy intake (DEI) as estimated from fecal pellet masses. Consequently, CB lizards had higher size-adjusted body masses than lizards from SR. Within CB, during midsummer, DEE was similar to DEI. Within the SR population, DEE trended higher than DEI during midsummer, but was not significantly different. We found no population differences in lizard activity, active body temperature, or preferred body temperature. Hence, we infer the longer activity season for the SR population may compensate for the low food availability and high daily energy cost of midsummer. Moreover, for the CB population, we infer that cooler temperatures and higher food availability allow the lizards to compensate for the shorter activity. We also suggest the CB population may benefit from the predicted warmer temperatures associated with climate change given the similar activity-period body temperatures and DEE between these lizard populations assuming food availability is sufficient.

THE fitness of individual lizards and the persistence of lizard populations may depend on whether individuals 1) have adequate time to achieve sufficient body temperatures for daily and seasonal foraging activity, and 2) have sufficient body temperatures during daily inactivity periods to digest and assimilate food for adequate production (growth, storage, and reproduction; Grant and Dunham, 1988; Dunham et al., 1989; Adolph and Porter, 1993; Levy et al., 2017). For populations located close to the core of their geographic range, it is expected that ambient temperatures will permit extended daily and seasonal activity allowing individuals adequate time to profit energetically (Grant and Dunham, 1988; Adolph and Porter, 1993; Sears and Angilletta, 2004; Kearney, 2012). In contrast, lizard populations at the extreme latitudinal or altitudinal edges of the geographic range of the species are expected to be behaviorally and physiologically constrained by ambient temperatures that are either too high or too low for activity or energy processing (Adolph and Porter, 1993; Niewiarowski, 2001; Parker and Andrews, 2007; Deutsch et al., 2008; Levy et al., 2017).

In North America, few studies have focused on how the cooler climate near the northern edge of the geographic range of a lizard species constrains individual activity and rates of production. Understanding how individuals being limited by cooler temperatures affects population persistence is important because, habitats and microhabitats permitting, these cool-climate populations may be essential for range expansion during impending climate change (Thomas et al., 1999; Parker and Andrews, 2007; Moreno-Rueda et al., 2012). Lizards from cooler climates have mechanisms to cope with cooler temperatures; however, the capacity for these mechanisms to buffer against cooler temperatures will be reduced in the northernmost parts of their range (Huey and Tewksbury, 2009; Buckley et al., 2015). Thus, it is expected that lizards living in cooler climates will have longer periods when their body temperatures are below the optimum. This inability to be sufficiently warm for extended periods will reduce the time available for food acquisition and will lower digestion rates when inactive, both of which result in low rates of production (Waldschmidt et al., 1986; Grant and Dunham, 1988, 1990; Adolph and Porter, 1993; Niewiarowski and Roosenburg, 1993; Niewiarowski, 2001).

Individual lizard growth rates depend on available activity time, food abundance and availability, and the thermal environment (Dunham, 1978; Grant and Dunham, 1990; Sinervo and Adolph, 1994; Iraeta et al., 2006). Because lizard populations in cooler climates have shorter activity seasons, individuals within these populations tend to be smaller than individuals of corresponding age in warmer climates (Grant and Dunham, 1990; Sinervo and Adolph, 1994; Sears, 2005). But as temperatures peak and photoperiods lengthen during summer in the cooler northern latitudes, daily activity can be extended, thus allowing short-term growth rates for individuals to be comparable to, or even exceed growth rates of, individuals in warm-and-drier climates (Grant and Dunham, 1988, 1990).

Current predictions by biophysical and mechanistic models for ectotherms support the notion that warmer temperatures will extend daily and seasonal activity windows, and even push population boundaries of some species northward (Deutsch et al., 2008; Huey and Tewksbury, 2009; Kearney et al., 2009; Kingsolver et al., 2013). Few data, however, are available on the energetics of lizards at the high latitude edge of their range (Buckley, 2008; Levy et al., 2017). Thus, understanding how lizards persist on the cool-climate edge of their range, and in which habitats this persistence occurs, will better inform us to how populations might respond to warming climates.

In this study, we compared daily activity patterns, daily energy expenditure (DEE), and daily energy intake (DEI) of a

---

[1] VCU Life Sciences, Virginia Commonwealth University, 1000 W Cary St., Richmond, Virginia 23284; Email: powerssd3@vcu.edu. Send reprint requests to this address.

[2] Biology Department, Western Washington University, 516 High St., Bellingham, Washington 98225; Email: (MRM) matt.mcternan1@gmail.com; and (RAA) Roger.Anderson@wwu.edu.

[3] Biology Department, George Fox University, 414 N. Meridian St., Newberg, Oregon 97132; Email: dpowers@georgefox.edu.

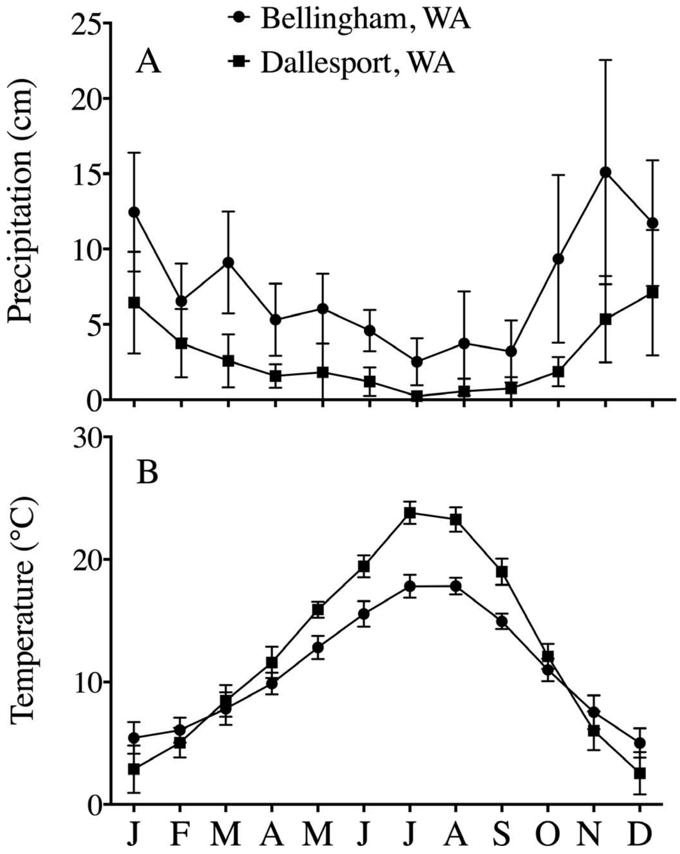

Fig. 1. Monthly profiles of mean (±SD) precipitation (A) and air temperature (B) from 1998–2008 of the regions where CB (Bellingham, WA) and SR (Dallesport, WA) are located. These data were obtained from nearby weather stations via the Western Regional Climate Center (WRCC).

coastal population of Western Fence Lizards (*Sceloporus occidentalis*) near the northern limit of their geographic range to a more southern population living in a warmer and drier climate further inland. We hypothesized that daily activity patterns and rates of DEE and DEI would be similar between these two populations during the warmest period of the activity season. Based on our hypothesis we made three predictions. First, given the higher net primary productivity of coastal forests compared to the open woodlands in the rain shadow east of the Cascades (Del Grosso et al., 2008), we expected food availability and feeding rate to be higher for the coastal population. Second, given longer daily activity periods and warmer daily inactivity periods during mid-summer along the coast, we expected coastal lizards would have sufficient digestion and assimilation rates such that DEI would balance or even exceed DEE. Third, assuming higher food availability and sufficient opportunity for daily activity, we predicted lizards from the coastal population would have DEI rates equal to or higher than lizards from the southern inland population. To test these predictions, we measured body temperature (T_b) to determine if lizards from these populations had similar T_b when they were active. Using these data in conjunction with weather records and microhabitat temperatures, we estimated available daily activity time and activity season length for both populations. To determine rates of DEE and DEI for these lizard populations, we collected data on prey abundance, fecal production, field metabolic rates, and body condition.

MATERIALS AND METHODS

Study species and field sites.—The Western Fence Lizard (*Sceloporus occidentalis)* is a small, diurnal phrynosomatid lizard native to the western United States. Populations of *S. occidentalis* are distributed along a latitudinal gradient from southern California to northern Washington (Stebbins, 2003). Along this gradient, *S. occidentalis* occupies a diverse array of habitats including coastal margins of moist temperate forests, low elevation pine-oak woodlands, and uplands at the ecotone of fir and pine forests (Adolph, 1990; Sinervo and Adolph, 1994; Stebbins, 2003; Asbury and Adolph, 2007). These lizards are ambush predators, who largely remain stationary in visual search and pursue arthropod prey that are moving nearby (Anderson, 2007).

We collected field data at two sites from mid-July to mid-September in 2008. Sondino Ranch (SR) is an inland low elevation site (120 m) with a pine-and-oak woodland habitat located in the Columbia River Gorge, Klickitat County, Washington, 16 km east of Bingen. Sondino Ranch has a temperate climate with a mean (±SD) annual precipitation of 33.2±8.5 cm (Fig. 1A). In the winter, average ambient temperature (T_a) drops to about 3°C, and in summer, average T_a rises to about 28°C (Fig. 1B). Chuckanut Beach (CB) is a low-elevation (10 m) site at the coastal forest-edge within Chuckanut Bay in Skagit County, Washington, 12 km south of Bellingham, adjacent to a 1.5 km stretch of sandy beach. Chuckanut Beach is 334 km north of SR, at the NW extreme of the geographic range of *S. occidentalis*, and is characterized by a maritime climate that receives about 63% more precipitation annually ($\bar{x}\pm SD = 89.7\pm 11.1$ cm, Fig. 1A) than SR. From October–April average T_a at CB ranges from 5–10°C, with persistent low-clouds (Fig. 1A). In summer average T_a is about 18°C (Fig. 1B).

Prey availability.—We measured available arthropod prey using pitfall traps. Traps were 250 mL (65 mm diameter x 86.5 mm deep) plastic jars half-filled with 80–100 mL of propylene glycol (RV-Marine Antifreeze). We buried traps in pairs 0.5 m apart with their open tops flush with the ground surface in microhabitats where lizards were commonly found (open-ground, under cover of shrubs, adjacent to downed logs, rock piles, and bases of oak trees). Pitfall traps were left out for seven days at each site (CB: $n = 30$, 10–18 August; SR: $n = 24$, 20–28 August) and were checked daily. No lizards were found or observed in our pitfall traps during the sampling period. On day seven, the jars were sealed and returned to the lab for analysis of arthropod abundance and biodiversity. All arthropods were identified to taxonomic order and compared to arthropod orders found in lizard fecal pellets. The orders which overlapped with those found in fecal pellets were used to make comparisons of arthropod availability between sites. We assumed that our measurements during these seven-day periods were representative of mid-to-late summer arthropod availability when temperatures were warmest. Arthropod abundance is positively correlated with precipitation (Ballinger, 1977; Dunham, 1978), so our measurements of arthropod availability will likely be conservative given that precipitation is at its lowest during this period of the summer at both study sites.

Body size and body temperature.—Lizards were captured using a spin-casting fishing pole with a noose fashioned from dental floss tied to the end eyelet of the pole. When a lizard was encountered, the noose was carefully slipped over the head and closed just posterior to the head to capture the lizard. This noosing technique is a common method to capture lizards without causing harm or injury. Once captured, T_b was immediately measured (within 20 sec) by inserting a rapid-registering, thin-bulb mercury thermometer about 1 cm into the cloaca (Miller & Weber T-6000 Cloacal Thermometer). Captured lizards were then placed in cloth bags and held in a standard insulated plastic cooler at 25–30°C for 2–3 days allowing sufficient time to clear their gut for accurate measurement of body mass (Angilletta, 2001; R. A. Anderson, unpubl. data). After 48–72 hours, we palpated the abdomen of the lizard to confirm the gut was clear and then measured body mass (M_b; ±0.01 g) with an Ohause DP202 electronic scale and snout–vent length (SVL; ±0.5 mm) was measured with the lizard stretched against a transparent plastic ruler pressed to its ventral surface. The sex of each lizard was noted and each lizard was given 1) temporary identification with a unique sequence of three colors of transverse paint stripes on the dorsum, and 2) permanent identification with a unique set of three toe clips (never the longest toe on each rear foot), then released where it was captured.

We also measured preferred T_b of field-active lizards from both sites during the 2015 activity season. Lizards were captured and transported back to the lab (see above) and held individually in glass terraria. Each terrarium (61 cm × 6 cm × 46 cm) contained a small refuge, heating rock, water bowl, and had a heating lamp positioned approximately 10 cm above the top to provide light and heat. The heating rock, heating lamp, and refugia provided enough thermal heterogeneity for lizards to thermoregulate while in captivity. Lizards were supplied with water, and then once we verified that a lizard was post-absorptive, it was provided store-purchased crickets *ad libitum*.

Preferred T_b was measured by placing lizards on a thermal gradient. The thermal gradient is a rectangular (120 cm × 116 cm × 38 cm) box, with the roof of the gradient slanted from a height of 46 cm at the warm end down to 22 cm at the cool end. The temperature gradient is generated inside the aluminum floor of the enclosure by a heating coil embedded in the warm end and a coil of refrigerated ethelyne glycol embedded in the cool end. The substratum temperatures ranged from 50°C to 10°C. In each trial, a lizard from CB ($n = 22$) or SR ($n = 23$) had its T_b measured immediately upon removal from its terrarium before being placed on the middle of the aluminum plate, perpendicular to the length of the gradient. Lizards were left undisturbed for 20 minutes before again measuring their T_b. Before each T_b measurement, we noted its location along the gradient and we determined whether the lizard was obviously in basking or cooling posture or the lizard had an alert, albeit relaxed stance (thus meeting the assumptions for preferred temperature measurement). If the lizard was hiding or attempting to escape, then the measurement was not used in our analysis. Measurements of T_b were recorded at 0, 20, 60, 80, 100, and 120 minutes, with the initial T_b (time zero) referring to the measure taken immediately after removal from the terrarium. A minimum of three acceptable T_b measures from lizards thermoregulating in the gradient were used to calculate the mean preferred T_b for each lizard.

Estimating potential daily and seasonal activity.—To estimate the number of days available for lizard activity in 2008, we used (1) T_a and cloud cover data from weather stations within 2 km of each study site via the National Climatic Data Center (NCDC), (2) microhabitat temperatures (T_m; see below), (3) T_a measurements taken 2 m above the ground using a thermocouple (BAT-12 microprobe thermometer) at areas where lizards had been seen (R. A. Anderson, unpubl. data) from prior field seasons at CB, (4) T_a measurements from locations where lizards were seen or captured during our field season in 2008, and (5) weather conditions and T_a when active lizards were sighted out in the open at SR during our 2008 field season. From these data, we determined lizards could be active on days when conditions were predominately sunny (<50% cloud cover) and T_a was 15–34°C for at least four hours (Grant and Dunham, 1990; R. A. Anderson and S. D. Powers, pers. obs.).

To measure microhabitat temperatures (T_m), we used Thermocron iButtons™ (Maxim Integrated Products, DL 1922–F50) set to record at 15-minute intervals, fastened into plastic fobs, and anchored to the microhabitat substrate. Each iButton was placed with the top surface flush with the "soil" surface, and we covered it with a dusting layer of soil to shield it from direct solar radiation. At each site, we placed iButtons in microhabitats that were completely exposed to sun (near boulder and rock piles), partially shaded (base of shrubs and small trees), and completely shaded (underneath rocks and fallen logs). At CB, we also placed iButtons along west-facing rocky hillside, and at SR within grassy areas around boulder piles. We had three replicates for each microhabitat type found at each site, and all measurements were made within known lizard home ranges.

Daily energy expenditure.—We used doubly labeled water (DLW) to measure DEE (Speakman, 1997). Lizards were given an intraperitoneal injection of 50 μL of DLW (^{2}HH ^{18}O), then placed in a cloth bag inside an insulated cooler for at least 60 minutes to allow the injected isotopes to equilibrate with body water (Congdon et al., 1978; Nagy et al., 1984; Nagy and Degen, 1988; Speakman, 1997). To measure initial isotope enrichment, we collected a 50 μL blood sample from the infraorbital sinus in a 75 μL heparinized microcapillary tube, which was then flame sealed and refrigerated for later analysis. Lizards were then released at their point of capture. After 10–20 days, lizards were recaptured and a second blood sample collected as described above to measure final isotope enrichment.

Blood samples were transported to George Fox University (Newberg, OR), where they were microdistilled to obtain pure water (Nagy, 1983). Water samples were then sent to the University of New Mexico where their isotopic enrichment was measured using a Liquid Water Isotope Analyzer (24-EP, Los Gatos Research). Isotope enrichments were then used to calculate FMR (mL CO_2 $g^{-1}d^{-1}$) using equations from Nagy (1983) and Speakman (1997). Daily energy expenditure (J g^{-1} d^{-1}) was calculated by multiplying FMR by a conversion factor for an insectivorous diet (25.7 J/mL CO_2; value for insectivorous lizards; Nagy, 1983) and using a respiratory exchange ratio of 0.70 (Bennett and Nagy, 1977). DLW calculations used in this study assume that body water volume was a constant proportion of lizard mass, water and CO_2 flux rates of lizards were constant during the release interval, isotopes only labeled the lizard's body water pool (single-pool model), ^{2}H and ^{18}O only exited the lizards as CO_2 and water, ^{2}H and ^{18}O enrichment of H_2O and CO_2 exiting the lizards reflects the enrichment of the body water pool (i.e., no major fractionation errors), and there was no water or CO_2 input from the lungs or across skin of lizards

Table 1. Mean field-active and preferred T_b for CB and SR lizards. Data show no difference in field or lab measures for mean T_b between these populations.

T_b	CB ($\bar{x}$±SD°C)	SR ($\bar{x}$±SD°C)	*P* value
Field-active	34.95±1.21	35.20±1.32	0.642
Preferred	36.20±1.08	36.04±0.89	0.587

(Nagy, 1980; Nagy and Costa, 1980). For detailed analysis of these assumptions see Speakman (1997).

Between our study sites we labeled 31 lizards (CB: $n = 15$, SR: $n = 16$) during July and August. From our initial sample, we recaptured 15 lizards. One sample from SR was not used in analysis due to an injection error leaving a total of 14 lizards for comparisons (CB: $n = 4$, SR: $n = 10$). The release and recapture of CB lizards occurred between 8–26 July. At SR, six lizards were released and recaptured between 16–31 July, and the remaining five were released and recaptured between 6–20 August. It should be noted the DLW period for the SR lizards in August occurred during our pitfall trapping sampling period for SR.

Daily energy intake.—Andrews (1984) developed methods using field and lab experiments to estimate DEI from fecal production in lizards. Using these methods, we were able to estimate DEI of lizards in the field using fecal pellet mass. During our 2008 field season (mid-July to mid-September) captured lizards from both populations were placed in cloth bags and held for 48–72 hours, after which their fecal pellets were collected. This method assumes that lizards were active prior to capture date (thermal conditions 2–3 d before capture date were suitable for lizard activity) and their fecal pellets contain typically consumed prey. Lizards were held in bags in temperature-controlled cabinets (Koolatron 29-quart Voyager Cooler with thermocouple or Percival model I-35LL) to normalize daytime temperature exposure. During the day (0900–2100 hours), lizards were maintained at an approximate compromise temperature between active and resting lizards (30±2°C). At night (2100–0900 hours), temperature was not regulated and ranged from 15–20°C. Collected fecal pellets were dried at 65°C until they reached constant mass (~48 hours). Dried fecal pellets were dissected and non-organic items removed (e.g., small rocks and pebbles). The remaining organic material was then weighed to the nearest 0.0001 g. Daily energy intake was estimated from the mass of the organic matter using the equations in Andrews (1984). We collected fecal pellets from a total of 43 lizards (CB: $n = 23$, SR: $n = 20$). It should be noted the timing of fecal pellet collection overlapped with pitfall trapping and DLW. At CB, 13 of these lizards captured coincided with pitfall trapping and 10 lizards captured coincided with DLW sampling. At SR, the capture of 11 lizards coincided with pitfall trapping and 12 lizards captured coincided with DLW.

Statistical analyses.—For between-site comparisons we used Student's t-tests, or Mann-Whitney U-tests if the data did not meet the assumption of normality or equal variance. Before making energetic comparisons, we $\log_{10}$ transformed our data to determine the scaling relationship of DEE with lizard M_b using linear regression. Using these data, we allometrically adjusted values for DEE and DEI for M_b effects on rates of metabolism. Differences in body condition between populations was assessed by using body size data from adult lizards. We analyzed these data using linear regression with M_b as a function of SVL. These data were $\log_{10}$ transformed prior to analysis and differences in body condition between sites were tested using ANCOVA with log(SVL) as a covariate. All statistical analyses were done using R (R Core Team, 2017).

RESULTS

Prey availability.—Between our two study sites, we collected arthropods from 20 different orders. All 20 were found at CB and 16 were found at SR. After dissecting fecal pellets from both populations, we found six orders (Araneae, Blattaria, Coleoptera, Diptera, Hemiptera, and Hymenoptera) in common with those found in pitfall traps. We restricted our analysis to these six orders since they were dietary components for both populations. In spite of higher variability across pitfall trap pairs, mean arthropod count was significantly higher at CB ($\bar{x}$±SD = 140.4±127.0) than SR ($\bar{x}$±SD = 22.8±32.0; $t_{1,25} = 5.125$, $P < 0.001$).

Body size and body temperature.—Between study sites we captured 109 adult lizards (SVL ≥ 40 mm; CB, $n = 45$; SR, $n = 65$). In adult lizards, SVL was not significantly different between sites ($W = 1223$, $P = 0.056$), although SR lizards trend towards being slightly larger. Lizards caught at CB exhibited a greater range in SVL than lizards at SR (CB: $\bar{x}$±SD = 64.0±11.1 mm, range = 34.0–77.0 mm; SR: $\bar{x}$±SD = 69.1±5.8 mm, range = 53.0–81.5 mm). Linear regressions of M_b as a function of SVL were significant for both populations (Fig. 2; CB: $R^2 = 0.96$, $F_{1,45} = 1188.1$, $P < 0.001$; SR: $R^2 = 0.86$, $F_{1,64} = 396.9$, $P < 0.001$), and ANCOVA showed body condition of adult lizards at CB was significantly higher (LS means±SE: CB = 0.395±0.015, SR = 0.423±0.015; ANCOVA: $F_{1,110} = 11.8$, $P < 0.001$). At CB, we only sighted and captured one juvenile in mid-September during the last week of the mark-recapture study. At SR, we captured nine juveniles, and juveniles were regularly sighted throughout the mark-recapture study. Body temperatures of active lizards at CB ($n = 29$) and SR ($n = 27$) were not significantly different (Table 1; $t_{1,54} = 0.735$, $P = 0.642$). Pooled, active T_b ($\bar{x}$±SD) for both sites was 35.07±1.26°C ($n = 56$). In the lab, preferred T_b of CB ($n = 22$) and SR lizards ($n = 23$) were also not significantly different ($t_{1,43} = 0.548$, $P = 0.587$). Pooled, lab-preferred T_b ($\bar{x}$±SD) for both populations was 36.12±0.99°C ($n = 43$).

Estimated daily and seasonal activity.—During the 2008 activity season, there were 82 fewer days at CB where daytime was predominately sunny (<50% cloud cover) and T_a was within 15–34°C for more than four hours (Fig. 3). Therefore, we estimate that the CB activity season was approximately three months shorter relative to SR. The beginning of the activity period also differs at each site. Because the CB population along the Chuckanut Bay coast was at a south-west-facing beach immediately adjacent to a densely forested, high coastal hill (typical of coastal populations of *S. occidentalis*, R. A. Anderson, unpubl. data), lizard microhabitats were not exposed to sunlight until late morning, no sooner than ~1000 hours. In contrast, at SR lizard microhabitats received sun exposure earlier in the morning, thus causing rapid warming in the pine-oak woodlands and allowing lizard activity to begin as early as ~0800 hours (S. D. Powers and R. A. Anderson, pers. obs.; Fig. 4).

During the summer, surface temperatures (T_m) in open and exposed microhabitats at SR exceed active mean T_b by as much

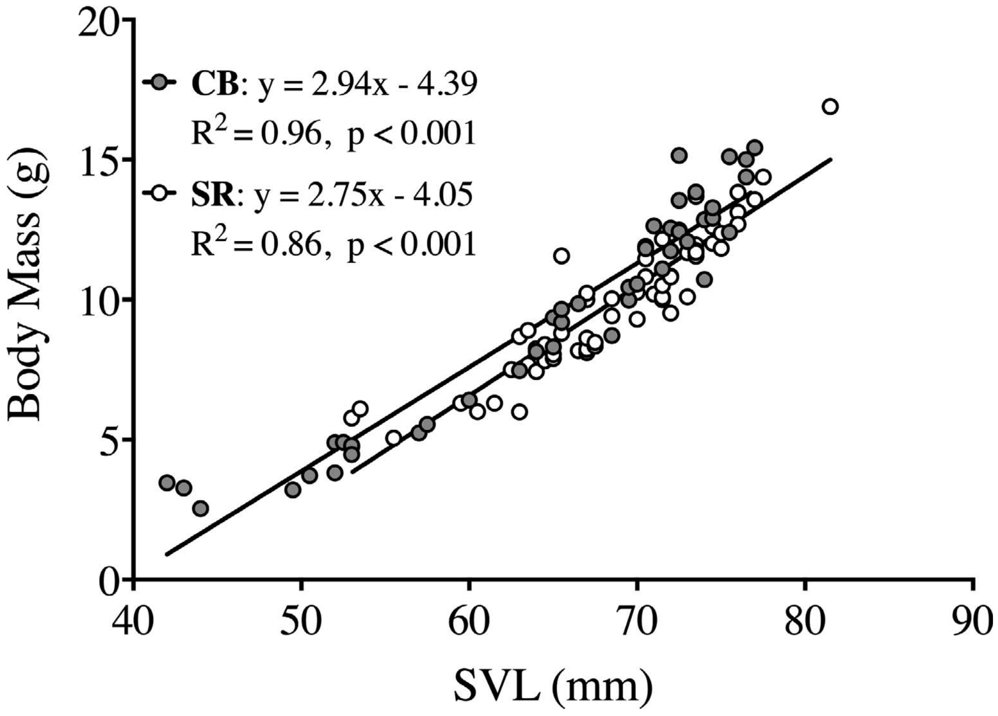

Fig. 2. Linear regressions of mass and SVL for both populations. Mass and SVL were correlated, and analyses of log-transformed data revealed CB lizards were significantly heavier per unit SVL ($F_{1,110}$ = 11.80, $P <$ 0.01).

as 15°C during mid-afternoon, while T_m in unexposed microclimates range from 18–30°C during the same period. At CB, however, mean T_m generally does not exceed mean T_b. Air temperatures in the open at sunlit rocky hillsides did exceed active mean T_b, but only by ~2°C for a short period (~1330–1530 hours). However, T_m in other unexposed microhabitats ranged from 15–25°C. We estimate that during the warmest part of the summer, at CB lizard activity began at ~1000 hours and ended at ~1800 hours. In contrast, at SR lizard activity began at ~0830 hours and ended at about the same time (~1800 hours). Warm T_m (>34°C) at SR, however, forced lizards to become inactive or retreat to more shaded and less exposed microhabitats during midafternoon (~1300–1600 hours), resulting in a bimodal activity pattern. These data also corresponded with sightings of active lizards when we were out in the field. But on days when weather conditions permitted activity at either CB or SR, the amount of time during a single day when activity could occur was not different for lizards between sites ($t_{1,14} = 0.98$, $P = 0.360$; Fig. 5).

Daily energy expenditure and daily energy intake.—Our DEE (J $g^{-1}d^{-1}$) values were similar to values reported by Bennett and Nagy (1977) for *S. occidentalis* during periods of extended activity. Scaling DEE with M_b did not differ between

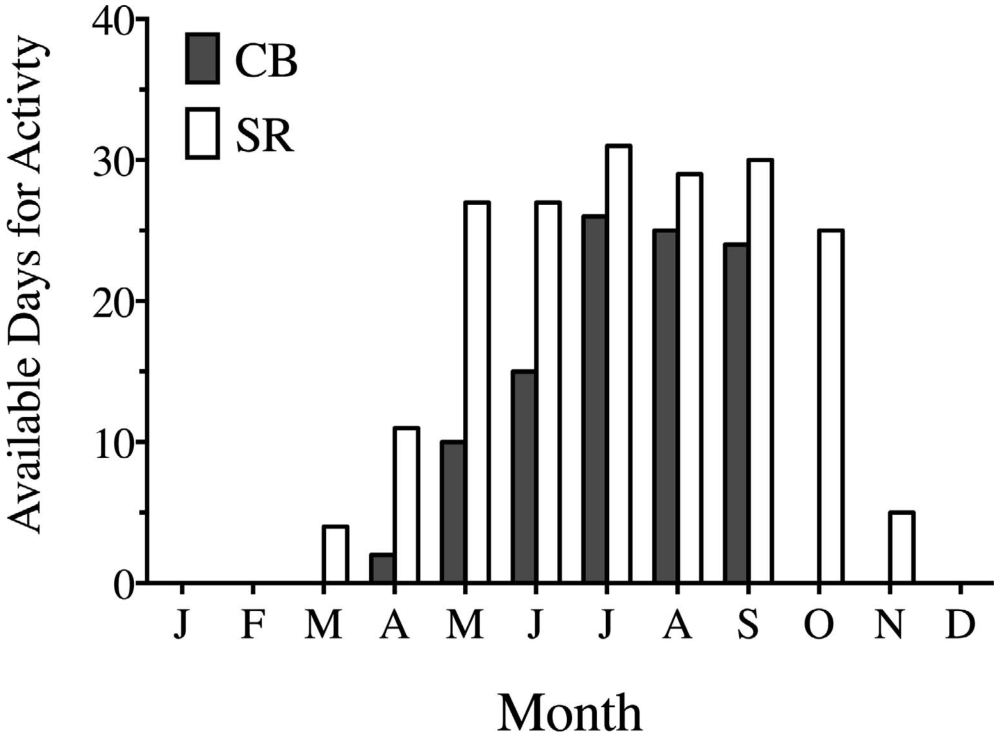

Fig. 3. Estimation of the number of predominantly sunny days with ≥4 hours of available activity per month for CB and SR. On average, CB (17.0±9.7 d m^{-1}) lizards have fewer days of activity relative to SR lizards (21.0±11.1 d m^{-1}). We estimate that CB lizards had 102 days of activity in 2008, while SR lizards had 189 d of activity.

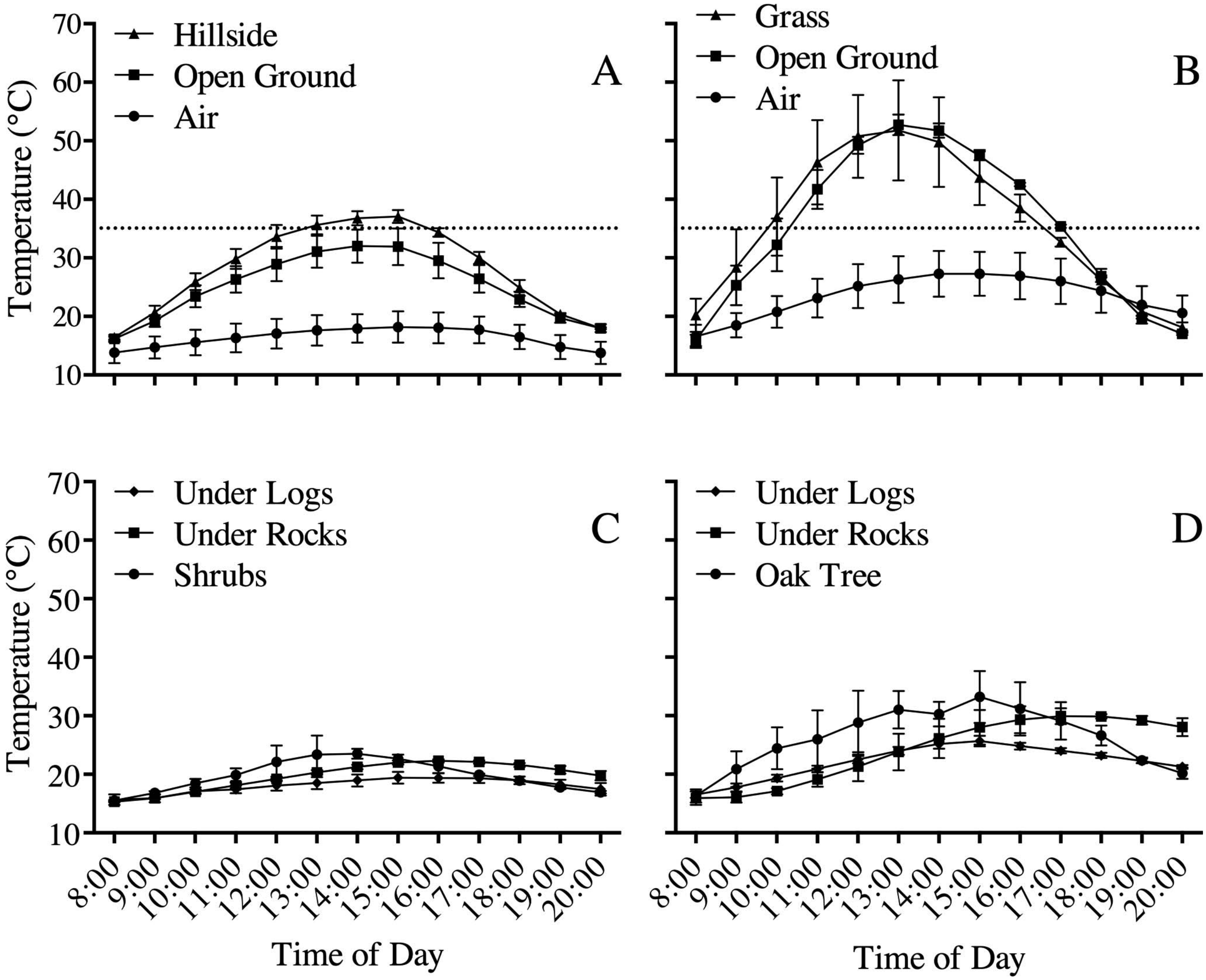

Fig. 4. Hourly temperature profiles ($\bar{x}$±SD) of lizard microhabitats during the 2008 study period. The top two figures represent exposed microhabitats found at CB (A) and SR (B). The dotted lines represent the mean field-active body temperatures of lizards at each population. The bottom two figures represent unexposed microhabitats found at CB (C) and SR (D).

populations (slope: $F_{1,10} = 0.538$, $P = 0.480$; intercepts: $F_{1,10} = 2.916$, $P = 0.116$), so data were pooled for further analysis. The allometric slope of the pooled data was 0.85 with log(M_b) accounting for 77% of the variation in log(DEE; Fig. 6). Using this scaling exponent to correct for M_b differences in our samples, DEE at CB ($\bar{x}$±SD = 193.31±18.65 J $g^{-0.85}d^{-1}$) was not significantly different from SR ($\bar{x}$±SD = 174.46±19.48 J $g^{-0.85}d^{-1}$; W = 32.0, $P = 0.106$; Fig. 7), whereas DEI rates for CB lizards ($\bar{x}$±SD = 211.08±64.85 J $g^{-0.85}d^{-1}$) were significantly higher than for SR lizards ($\bar{x}$±SD = 141.23±43.36 J $g^{-0.85}d^{-1}$, $t_{1,40} = 4.136$, $P < 0.001$; Fig. 7). When comparing DEI to DEE within sites we found that mean DEI for CB was similar to mean DEE (W = 36.0, $P = 0.607$). At SR, while we cannot show clear statistical difference between DEE and DEI (W = 142.0, $P = 0.067$), mean DEI rates clearly trend lower than mean DEI.

DISCUSSION

Overall, the data we collected support our hypothesis that daily activity patterns and rates of DEE and DEI would be similar between CB (cooler and wetter climate) and SR (warmer and drier climate) during the warmest period of the activity season. Our first prediction that food availability was higher at CB was supported by our arthropod sampling which showed that mean arthropod availability was significantly higher at CB. Our second prediction of increased summer activity at CB and that these lizards would be in energy balance was supported by our T_m data which showed lizard microhabitats were generally cooler relative to SR habitats. Furthermore, we found no difference in DEE rates or DEI rates for CB lizards. Lastly, our third prediction that DEI rates at CB would be similar to or exceed DEI rates at SR was also supported.

The scaling of our DEE data is consistent with Nagy's (2005) review of the allometric relationship between DEE and body size in terrestrial vertebrates (including reptiles). The allometric slope for our lizards fell within the 95% CI of the allometric slope for reptiles (0.83–0.95; Nagy et al., 1999) and was higher than the slope for basal or standard metabolic rates (0.67 or 0.75; Nagy, 2005). This higher slope suggests the energetic benefit of a larger body size is reduced by the

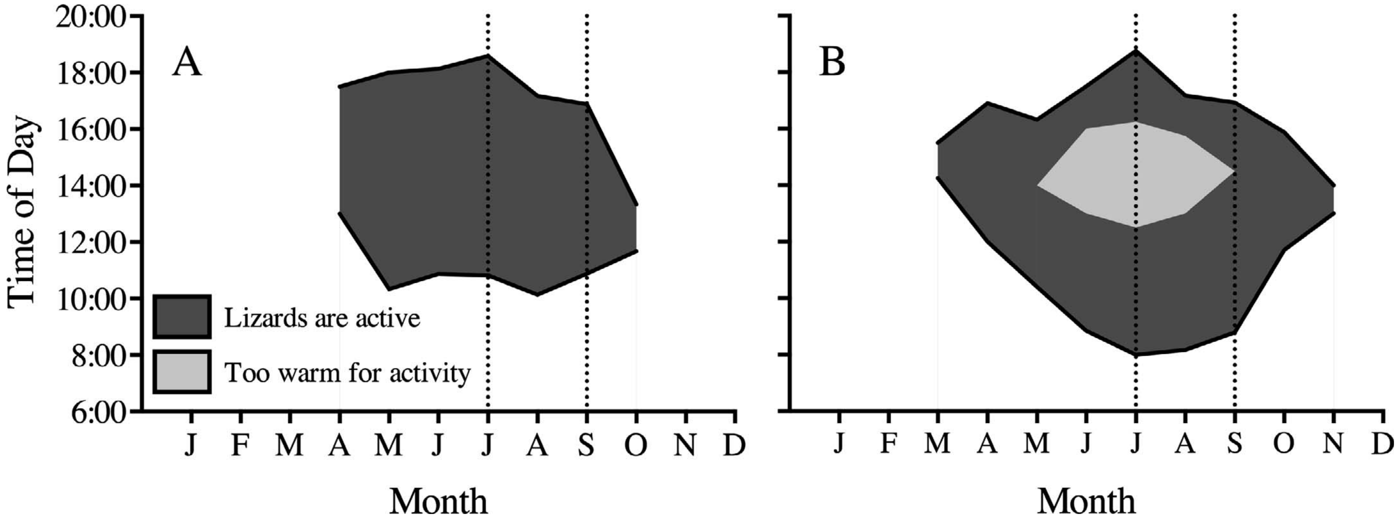

Fig. 5. Estimations of available activity time for CB (A) and SR (B) during the 2008 activity season. Estimations were based on weather station data, microhabitat temperature data, and field observations. The vertical dotted lines enclose the estimated activity for lizards during the study period. These data show available activity time was similar between study sites (CB = 5.70±2.32 h d^{-1}, SR = 4.92±2.4 h d^{-1}).

inclusion of activity relative to standard or resting metabolic rates (Glazier, 2005; Kaufmann et al., 2013). When compared to other lizards, the allometric slope of our populations of *S. occidentalis* (0.85) was at the low end of the 95% CI (0.86–0.97) for all lizards (Nagy et al., 1999). This was likely due to the fact that ambush predators, like *S. occidentalis*, typically have lower DEE rates because they move very little relative to active foragers which spend the majority of their activity period in movement (Anderson and Karasov, 1981; Andrews, 1984; Nagy, 2005).

Daily energy intake was highly variable in both populations, likely reflecting opportunistic foraging in this species (Anderson and Karasov, 1981; Anderson, 2007). Based on our comparisons of DEI with DEE within each population, it is reasonable to infer lizards from the CB population were in energy balance on days when they were active. In contrast to the CB population, it may be inferred that SR lizards had some difficulty maintaining energy balance on days when they were active. The patterns of DEI can largely be explained by the differences in food availability between sites. The higher food availability at CB is likely due to higher plant productivity associated with higher rainfall (Dunham, 1978; Grant and Dunham, 1990; Niewiarowski and Roosenburg, 1993; Iraeta et al., 2006; Kearney, 2012) and presumably accounts for the higher DEI rates and body condition measured in this study (Ballinger, 1977). Lizard productivity is determined both by food abundance and daily activity (Anderson and Karasov, 1988; Congdon, 1989; Grant and Dunham, 1990; Sinervo, 1990; Adolph and Porter, 1993; Niewiarowski and Roosenburg, 1993); thus, it can be inferred that the combination of high food abundance and continuous activity periods during the summer allowed CB lizards to have sufficient productivity to sustain the population.

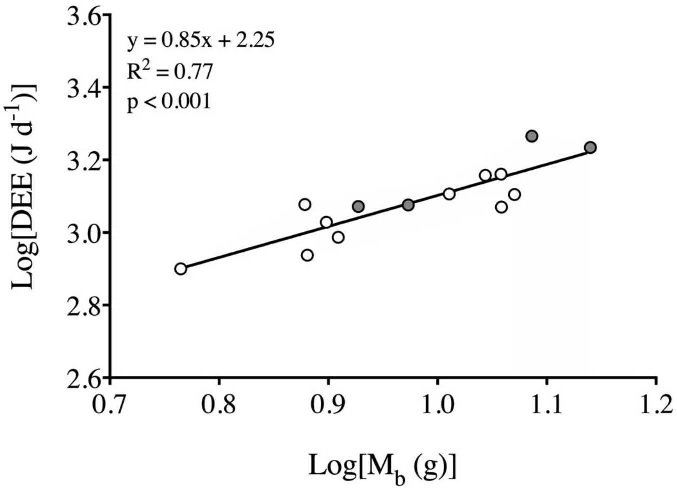

Fig. 6. Allometric relationship of log(DEE) as a function of log(M_b). This relationship was significant ($F_{1,12} = 40.03$, $P < 0.001$) with log(M_b) accounting for 77% of the variation in log(DEE). Open circles represent lizards from SR and filled circles represent lizards from CB.

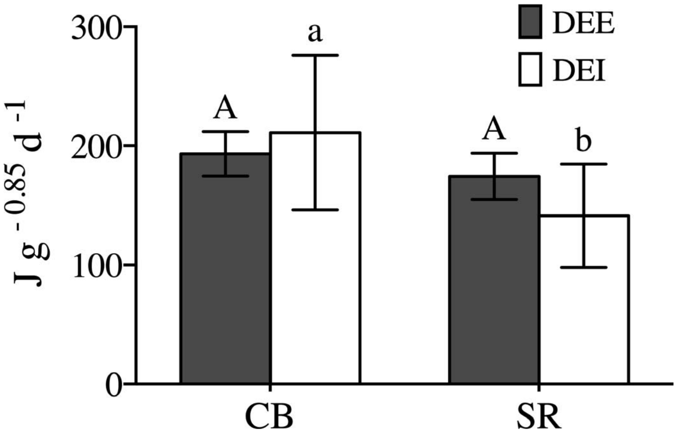

Fig. 7. Comparisons of DEE rates and DEI rates between populations ($\bar{x}$±SD). Daily energy expenditure rates for CB lizards ($n = 4$, 193.31±18.65 J $g^{-0.85}d^{-1}$) were similar to DEE rates measured for SR lizards ($n = 10$, 174.46±19.48 J $g^{-0.85}d^{-1}$; W = 32.0, $P = 0.106$). Mean DEI rates for CB lizards ($n = 20$, 211.08±64.85 J $g^{-0.85}d^{-1}$) were significantly higher than SR lizards ($n = 22$, 141.23±43.36 J $g^{-0.85}d^{-1}$; $t_{1,40} = 4.136$, $P < 0.001$). Within populations, DEE rates and DEI rates were not different at CB (W = 36.0, $P = 0.607$). At SR, the difference in DEI rates and DEE rates were not significantly different (W = 142.0, $P = 0.067$), but DEI rates trended lower than DEE rates. Capital letters represent statistical comparisons of DEE rates between sites, and lowercase letters represent statistical comparisons of DEI rates between sites. Significant differences are indicated by different letters.

Typically, populations found in warmer climates, such as SR, have longer activity periods and more opportunities to capture prey (Karasov and Anderson, 1984; Grant and Dunham, 1990; Adolph and Porter, 1993; Niewiarowski and Roosenburg, 1993). However, if food availability is lower, longer activity periods will result in lower harvesting and energy assimilation rates (Congdon, 1989; Adolph and Porter, 1993).

While activity started ~2 hours earlier at SR than at CB, lizards at SR were forced to take a ~3 hr hiatus midafternoon when T_m of exposed microhabitats exceeded active T_b (Fig. 5). Even though DEE and total daily activity time apparently are equal for SR and CB in mid-summer (Fig. 5), because (1) CB lizards are able to forage continuously throughout the day and (2) food availability is greater at CB, the mean hourly energy consumption of CB lizards (Fig. 7) should be higher, thus allowing them to meet or exceed daily energy demands. DEI rates at SR, while not significantly different from DEE, trended lower than their rates of DEE (Fig. 7); thus, during the mid-summer measurement period, SR lizards may have had to rely more on fat stores, which resulted in their lower M_b per unit SVL relative to CB lizards. Because summer appears to be an energetic challenge at SR, a longer activity season that includes days without periods of extreme high T_m is likely required to meet annual productivity costs (Congdon, 1989; Grant and Dunham, 1990; Adolph and Porter, 1993). When we visited SR in spring 2008, we observed abundant young, green foliage and many flying insects (R. A. Anderson and S. D. Powers, pers. obs.), so it is likely that spring productivity (i.e., growth and storage) is high for SR lizards**.**

Although CB lizards benefit from consistently mild T_m and high food availability during summer, the short activity season does have a cost in reduced time for lizard productivity. Lizard growth depends on the cumulative number of activity days (i.e., ability to forage) and food availability (Grant and Dunham, 1990; Adolph and Porter, 1993). We would expect a shorter activity season at CB to result in a lower SVL for young lizards in their first year after hibernation. The distribution of lizard SVL at CB included relatively small individuals compared to the size distribution at SR, corroborating our inference of a truncated activity season for hatchlings at CB.

While the scope of our study was limited, we suggest the data we have provided can help inform our predictions of the impacts of warming temperatures. It is apparent this CB population at the cooler, northwestern edge of the geographic range of *S. occidentalis* is able to persist by taking full advantage of high food availability during their relatively short summer activity period. Given the lack of differences in active or preferred T_b between these populations, it appears these lizards have the physiological and behavioral capacity to persist in this region (Deutsch et al., 2008; Kearney et al., 2009; Huey et al., 2012; Kingsolver et al., 2013). While the SR population may be increasingly challenged by the warmer temperatures and drier weather predicted for summers in the coming decades (Ruokolainen and Räisänen, 2009), from our data, we infer that the CB population may benefit from warmer and drier climate. Higher temperatures would increase activity periods, thereby allowing more time to acquire and process resources—assuming sufficient food availability (Adolph and Porter, 1993; Angilletta, 2001; Deutsch et al., 2008). A warming climate further north may also allow CB lizards to extend their coastal range to higher latitudes which would make it likely that populations like CB would be responsible for range expansion of *S. occidentalis* (Parker and Andrews, 2007; Buckley, 2010; Moreno-Rueda et al., 2012; Ceia-Hasse et al., 2014; Levy et al., 2017).

ACKNOWLEDGMENTS

We thank B. Wolf and his lab for processing all of our DLW samples and F. Slavens for allowing us to use his property during data collection. This project was funded by the WWU Fund for the Enhancement of Graduate Research and the WWU Biology Graduate Committee Fund. This study was conducted under the Washington Department of Fish and Wildlife scientific collection permit #08-267 and was approved by the WWU Institutional Animal Care and Use Committee.

LITERATURE CITED

Adolph, S. C. 1990. Influence of behavioral thermoregulation on microhabitat use by two *Sceloporus* lizards. Ecology 71:315–327.

Adolph, S. C., and W. P. Porter. 1993. Temperature, activity, and lizard life histories. The American Naturalist 142:273–295.

Anderson, R. A. 2007. Food acquisition modes and habitat use in lizards: questions from an integrative perspective, p. 450–490. *In:* Lizard Ecology: The Evolutionary Consequences of Foraging Mode. S. M. Reilly, L. D. McBrayer, and D. B. Miles (eds.). Cambridge University Press, Cambridge, U.K.

Anderson, R. A., and W. H. Karasov. 1981. Contrasts in energy intake and expenditure in sit-and-wait and widely foraging lizards. Oecologia 49:67–72.

Anderson, R. A., and W. H. Karasov. 1988. Energetics of the lizard *Cnemidophorus tigris* and life history consequences of food-aquistion mode. Ecological Monographs 58:79–100.

Andrews, R. M. 1984. Energetics of sit-and-wait and widely-searching lizard predators. Vertebrate Ecology and Systematics 10:137–144.

Angilletta, M. 2001. Thermal and physiological constraints on energy asimilation in a widespread lizard (*Sceloporus undulatus*). Ecology 82:3044–3056.

Asbury, D. A., and S. C. Adolph. 2007. Behavioural plasticity in an ecological generalist: microhabitat use by western fence lizards. Evolutionary Ecology Research 9:801–815.

Ballinger, R. E. 1977. Reproductive strategies: food availability as a source of proximal variation in a lizard. Ecology 58: 628–635.

Bennett, A. F., and K. A. Nagy. 1977. Energy-expenditure in free-ranging lizards. Ecology 58:697–700.

Buckley, L. B. 2008. Linking traits to energetics and population dynamics to predict lizard ranges in changing environments. The American Naturalist 171:E1–E19.

Buckley, L. B. 2010. The range implications of lizard traits in changing environments. Global Ecology and Biogeography 19:452–464.

Buckley, L. B., J. C. Ehrenberger, M. J. Angilletta, and R. Wilson. 2015. Thermoregulatory behaviour limits local adaptation of thermal niches and confers sensitivity to climate change. Functional Ecology 29:1038–1047.

Ceia-Hasse, A., B. Sinervo, L. Vicente, and H. M. Pereira. 2014. Integrating ecophysiological models into species distribution projections of European reptile range shifts in response to climate change. Ecography 37:679–688.

Congdon, J. D. 1989. Proximate and evolutionary constraints on energy relations of reptiles. Physiological Zoology 62:356–373.

Congdon, J. D., W. W. King, and K. A. Nagy. 1978. Validation of HTO-18 method for determination of CO_2 production of lizards (genus *Sceloporus*). Copeia 1978:360–362.

Del Grosso, S., W. Parton, T. Stohlgren, D. L. Zheng, D. Bachelet, S. Prince, K. Hibbard, and R. Olson. 2008. Global potential net primary production predicted from vegetation class, precipitation, and temperature. Ecology 89:2117–2126.

Deutsch, C. A., J. J. Tewksbury, R. B. Huey, K. S. Sheldon, C. K. Ghalambor, D. C. Haak, and P. R. Martin. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. Proceedings of the National Academy of Sciences of the United States of America 105:6668–6672.

Dunham, A. E. 1978. Food availability as a proximate factor influencing individual growth rates in the iguanid lizard *Sceloporus merriami*. Ecology 59:770–778.

Dunham, A. E., B. W. Grant, and K. L. Overall. 1989. Interfaces between biophysical and physiological ecology and the population ecology of terrestrial vertebrate ectotherms. Physiological Zoology 62:335–355.

Glazier, D. S. 2005. Beyond the '3/4-power law': variation in the intra-and interspecific scaling of metabolic rate in animals. Biological Reviews 80:611–662.

Grant, B. W., and A. E. Dunham. 1988. Thermally imposed time constraints on the activity of the desert lizard *Sceloporus merriami*. Ecology 69:167–176.

Grant, B. W., and A. E. Dunham. 1990. Elevational covariation in environmental constraints and life histories of the desert lizard *Sceloporus merriami*. Ecology 71:1765–1776.

Huey, R. B., M. R. Kearney, A. Krockenberger, J. A. M. Holtum, M. Jess, and S. E. Williams. 2012. Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. Philosophical Transactions of the Royal Society B: Biological Sciences 367:1665–1679.

Huey, R. B., and J. J. Tewksbury. 2009. Can behavior douse the fire of climate warming? Proceedings of the National Academy of Sciences of the United States of America 106: 3647–3648.

Iraeta, P., C. Monasterio, A. Salvador, and J. A. Diaz. 2006. Mediterranean hatchling lizards grow faster at higher altitude: a reciprocal transplant experiment. Functional Ecology 20:865–872.

Karasov, W. H., and R. A. Anderson. 1984. Interhabitat differences in energy acquisition and expenditure in a lizard. Ecology 65:235–247.

Kaufmann, C., C. Reim, and W. U. Blanckenhorn. 2013. Size-dependent insect flight energetics at different sugar supplies. Biological Journal of the Linnean Society 108: 565–578.

Kearney, M. 2012. Metabolic theory, life history and the distribution of a terrestrial ectotherm. Functional Ecology 26:167–179.

Kearney, M., R. Shine, and W. P. Porter. 2009. The potential for behavioral thermoregulation to buffer "cold-blooded" animals against climate warming. Proceedings of the National Academy of Sciences of the United States of America 106:3835–3840.

Kingsolver, J. G., S. E. Diamond, and L. B. Buckley. 2013. Heat stress and the fitness consequences of climate change for terrestrial ectotherms. Functional Ecology 27:1415–1423.

Levy, O., J. D. Borchert, T. W. Rusch, L. B. Buckley, and M. J. Angilletta. 2017. Diminishing returns limit energetic costs of climate change. Ecology 98:1217–1228.

Moreno-Rueda, G., J. M. Pleguezuelos, M. Pizarro, and A. Montori. 2012. Northward shifts of the distributions of spanish reptiles in association with climate change. Conservation Biology 26:278–283.

Nagy, K. A. 1980. CO_2 production in animals: analysis of potential errors in the doubly labeled water method. American Journal of Physiology 238:R466–R473.

Nagy, K. A. 1983. The Doubly Labeled Water Method: A Guide to Its Use. University of California, Los Angeles, Los Angeles.

Nagy, K. A. 2005. Field metabolic rate and body size. Journal of Experimental Biology 208:1621–1625.

Nagy, K. A., and D. P. Costa. 1980. Water flux in animals: analysis of potential errors in the tritiated-water method. American Journal of Physiology 238:R454–R465.

Nagy, K. A., and A. A. Degen. 1988. Do desert geckos conserve energy and water by being nocturnal? Physiological Zoology 61:495–499.

Nagy, K. A., I. A. Girard, and T. K. Brown. 1999. Energetics of free-ranging mammals, reptiles, and birds. Annual Review of Nutrition 19:247–277.

Nagy, K. A., R. B. Huey, and A. F. Bennett. 1984. Field energetics and foraging mode of Kalahari lacertid lizards. Ecology 65:588–596.

Niewiarowski, P. H. 2001. Energy budgets, growth rates, and thermal constraints: toward an integrative approach to the study of life-history variation. The American Naturalist 157:421–433.

Niewiarowski, P. H., and W. Roosenburg. 1993. Reciprocal transplant reveals sources of variation in growth rates of the lizard *Sceloporus undulatus*. Ecology 74:1992–2002.

Parker, S. L., and R. M. Andrews. 2007. Incubation temperature and phenotypic traits of *Sceloporus undulatus:* implications for the northern limits of distribution. Oecologia 151:218–231.

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Ruokolainen, L., and J. Räisänen. 2009. How soon will climate records of the 20th century be broken according to climate model simulations? Tellus A 61:476–490.

Sears, M. W. 2005. Geographic variation in the life history of the sagebrush lizard: the role of thermal constraints on activity. Oecologia 143:25–36.

Sears, M. W., and M. J. Angilletta. 2004. Body size clines in *Sceloporus* lizards: proximate mechanisms and demographic constraints. Integrative and Comparative Biology 44: 433–442.

Sinervo, B. 1990. Evolution of thermal physiology and growth rate between populations of the western fence lizard (*Sceloporus occidentalis*). Oecologia 83:228–237.

Sinervo, B., and S. C. Adolph. 1994. Growth plasticity and thermal opportunity in *Sceloporus* lizards. Ecology 75:776–790.

Speakman, J. R. 1997. Doubly Labelled Water: Theory and Practice. Chapman & Hall, London.

Stebbins, R. C. 2003. A Field Guide to Western Reptiles and Amphibians. Houghton Mifflin Company, New York.

Thomas, J. A., R. J. Rose, R. T. Clarke, C. D. Thomas, and N. R. Webb. 1999. Intraspecific variation in habitat availability among ectothermic animals near their climatic limits and their centres of range. Functional Ecology 13:55–64.

Waldschmidt, S. R., S. M. Jones, and W. P. Porter. 1986. The effect of body temperature and feeding regime on activity, passage time, and digestive coefficient in the lizard *Uta stansburiana*. Physiological Zoology 59:376–383.