SYMPOSIUM

Rocks and Vegetation Cover Improve Body Condition of Desert Lizards during Both Summer and Winter

Gavin Stark[*], Liang Ma[†‡], Zhi-Gao Zeng[†], Wei-guo Du[†§] and Ofir Levy [*,l]

[*]School of Zoology, Faculty of Life Sciences, Tel Aviv University, Tel Aviv 6997801, Israel; [†]Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, People's Republic of China; [‡]Princeton School of Public and International Affairs, Princeton University, Princeton, NJ 08544, USA; [§]Center for Excellence in Animal Evolution and Genetics, Chinese Academy of Sciences, Kunming 650223, People's Republic of China

From the symposium "Phenological plasticity: from molecular mechanisms to ecological and evolutionary implications" presented at the annual meeting of the Society for Integrative and Comparative Biology virtual annual meeting, January 3–February 28, 2022.

[1]E-mail: levyofir@tauex.tau.ac.il

Synopsis Microhabitats provide ecological and physiological benefits to animals, sheltering them from predation and extreme temperatures and offering an additional supply of water and food. However, most studies have assumed no energetic costs of searching for microhabitats or moving between them, or considered how the availability of microhabitats may affect the energy reserves of animals and how such effects may differ between seasons. To fill these gaps, we studied how the body condition of lizards is affected by microhabitat availability in the extreme environment of the Judean Desert. In particular, we quantified how vegetation and rock cover in the vicinity of these lizards affect their body condition during summer and winter. First, we used aerial imagery to map the vegetation/rock cover at two study sites. Next, we collected 68 adult lizards and examined how their body condition varies across seasons and availability of vegetation and rock cover. In addition, we examined how vegetation and rock cover may differ in their effective distance (i.e., the distance that best explains body condition of lizards). We found that lizards body condition was better if they were collected closer to a higher availability of vegetation or rocks. However, while close proximity (within 10 m) was the best predictor for the positive effect of rocks, a greater distance (up to 90 m) was the best predictor for the effect of the vegetation cover. Moreover, the positive effect of vegetation was 12-fold higher than the effect of rocks. Interestingly, although the lizards' body condition during winter was poorer than during summer, the positive effects of rock and vegetation cover remained constant between the seasons. This similarity of benefits across seasons suggests that shaded microhabitats have important additional ecological roles regardless of climate, and that they may provide thermoregulatory benefits in winter too. We also found a synergic effect of vegetation and rock cover on the lizards' body condition, suggesting that their roles are complementary rather than overlapping. Our research has revealed the importance of shade- and shelter-providing microhabitats in both summer and winter. We suggest that proximity to microhabitat diversity may contribute to better body condition in lizards or, alternatively, facilitates competition and attracts lizards with better body condition. Comprehending the complex interactions between animals and different microhabitats is critical for developing better conservation plans, understanding the risks of climate change, and suggesting mitigation strategies.

Introduction

Microhabitats are a key factor in the ability of animals to flourish in different environments. A high diversity of both sheltered and open microhabitats reduces competition and increases opportunities for predation (e.g., ambush predation; Davies et al. 2016) and anti-predatory behaviors (Jacob and Brown 2000; Jones et al. 2001; Mandelik et al. 2003). Moreover, microhabitats may supply shade or basking surfaces, enabling animals to maintain their preferred body temperature

under various environmental conditions (Kearney et al. 2009; Scheffers et al. 2014). However, these benefits come with energetic and missed opportunity costs, as well as increased predation risks (Huey 1974; Huey and Slatkin 1976; Basson et al. 2017). Most studies, however, have assumed that there is no energetic cost of searching for or moving between microhabitats (Buckley 2008; Kearney et al. 2009; Buckley et al. 2010; Levy et al. 2015; Levy et al. 2016a; Levy et al. 2017). Understanding how the availability of such microhabitats affects the fitness of animals is an important milestone in a world suffering from habitat loss and climate change. Empirical studies can inform us how lower availability can potentially increase the energetic costs of thermoregulation (Sears et al. 2016), food abundance, and predation; and eventually alter ecological communities (Zeng et al. 2014, 2016).

One of the key roles of microhabitats is to provide animals with the ability to maintain an optimal body temperature. In natural habitats, the main elements that provide thermal and physical shelter for animals during their activities are physical features, such as vegetation and rocks. These features also provide shelter from winds that may increase convective cooling or heating (Porter and Gates 1969; Kearney and Porter 2009; Ortega et al. 2017). However, the fate of each microhabitat in a changing environment differs. Under climate change, the availability of vegetation cover may decline as habitats become warmer and drier, especially during the summer at lower latitudes (Schulz et al. 2011; Levy et al. 2016b; Madani et al. 2018; Zhu et al. 2019; Hantson et al. 2021). In many habitats, while rocks too may offer thermal shelter to animals (Schlesinger and Shine 1994; Kearney 2002; Goldsbrough et al. 2004; Webb et al. 2004; van den Berg et al. 2015), rocky habitats are also under constant threat due to habitat degradation and loss to agriculture, industry, and urbanization. In light of such threats (e.g., Wramneby et al. 2010; Levy et al. 2016b; Fitzsimons and Michael 2017), a better understanding of the relationships between rocks/vegetation and animal populations is crucial. The loss of such microhabitats can increase the distances between shaded patches during summer, when animals need them the most for thermoregulation (Sears et al. 2016). Hence, such reduction in the availability of shade may reduce the possibilities of thermoregulation and increase the energetic costs of activity (Attum and Eason 2006). However, we still lack sufficient information on how such shifts may contribute to increasing or decreasing animals' energy reserves and affect their body condition. Moreover, the interplay between rocks and vegetation cover as thermal shelters has hardly been studied, and its understanding is crucial if we aim to develop a better comprehen-

sion of the ability of different types of thermal shelter to supply the ecological resources needed for animals' survival.

The relative role of each microhabitat is a consequence of the extent to which an animal benefits from access to it, not only from thermoregulation but also from other ecological services such as shelter from predation or access to more food (e.g., Eifler et al. 2012; Newbold and MacMahon 2014). In rocky deserts, for example, animals inhabit areas with both vegetation and rock cover, and can exploit these microhabitats as a thermoregulatory resource that enhances their performance, and increases their rates of capturing and digesting prey (Shah et al. 2004; Goldsbrough et al. 2006; Nordberg and Schwarzkopf 2019; Kearney et al. 2021; Chukwuka et al. 2021). The issue is more complex however than thermoregulation alone, as these microhabitats often play other important roles in the different ecological systems. For example, both rocks and vegetation may offer shelter not only from hot temperatures but also from predation (Mandelik et al. 2003; Segoli et al. 2016). Moreover, vegetation cover is an important food and water source for many species. Hence, although these shade-supplying microhabitats may be considered mostly important during summer as thermal shelters, the multifarious roles of rocks and vegetation are year-round.

Here, we determined how the availability of vegetation and rock cover differentially affects lizards throughout the two main seasons (summer and winter) in a desert habitat. In particular, we sampled lizards across gradients of vegetation and rock cover during these seasons and measured their body condition. We mapped the availability of rocks and vegetation across the lizards' studied habitat and analyzed how their body condition varied across seasons and according to the availability of these shade elements. We predicted that if the main ecological role of rock and vegetation cover is to provide thermal shelter, the high availability of shade elements would be beneficial for lizards during the summer, but would have little or no effect during winter, when temperatures are cooler and animals may not need to seek shelter from the heat. Our alternative prediction was that vegetation and rock cover would benefit the lizards during both seasons, since these microhabitats also offer other ecological benefits in addition to enabling thermoregulation. Understanding the interplay between habitat characteristics, climatic variations, and an animal's ecology and physiology could lead to a better understanding of how species interact with their environment, and what habitat features should be protected or reintroduced in order to help conserve vulnerable species under changing environmental conditions.

Methods

Study area

We conducted our study in the Judean Desert, a rain-shadow desert occupying the east-facing slope of the Judean Mountains in Israel (31°28′N, 35°10′E). The desert's eastern border is the Dead Sea, which is ∼400 m below sea level. There are two major habitats in the area that offer shelter to the local wildlife: rocky habitats, with rock accumulations that provide shelter in the interstices under and between them, and vegetation habitats, existing almost exclusively near dry river beds or streams in the area, predominated by perennial desert shrubs and annual grasses (Moncaz et al. 2012). The climate is extremely arid, with a mean annual rainfall below 100 mm in the eastern part of the desert (Baum and Artis 1966). Thermal conditions vary across seasons and between open and shaded microhabitats. During the summer, ground temperatures in the open range from 30°C in the early morning to 44°C during noon, with shade cover offering a substantial thermal shelter, with maximal ground temperatures of 37°C (Levy et al. 2016c). Winter temperatures are much cooler, with ground temperatures reaching 27°C in the open and up to 25°C under shade cover (Levy et al. 2016c). We sampled lizards at two sites in the region: Nahal Mishmar (31°22′51.1″N, 35°22′52.9″E) and Parking Tse'elim River (31°21′04.8″N, 35°21′11″E). Some areas in Nahal Mishmar are characterized by a few *Acacia raddiana* trees and denser vegetation cover (mostly bushes) than that by the Parking Tse'elim River, which is covered mostly by rocks and very sparse vegetation. At both sites, we sampled lizards in locations that vary in the availability of vegetation and rock cover. To characterize the ground temperatures during our study period, we deployed four miniature temperature loggers (iButton ds1921 thermochron, Maxim Integrated, San Jose, CA) on shaded areas (under vegetation cover, $n = 2$ at each site), and eight in the open ($n = 4$ at each site, covered by a small thin stone to avoid direct solar radiation on the logger). Temperature was measured hourly to the nearest 0.5°C during both winter (December 2019–February 2020) and summer (June 2020–September 2020).

Study animal

We focused our study on the wide-ranging *Mesalina bahaeldini* lizard (Segoli et al. 2002) from the *Messalina guttulata* species complex (Sindaco et al. 2018). This species is a small-sized lizard belonging to the family Lacertidae. The adults have a snout vent length (SVL) of males and females of 36–51 and 40–53 mm, respectively (Goldberg 2012) with a body mass of 0.6–3.2 g

when SVL > 31 mm (Orr et al. 1979). The species is widely distributed across the desert habitats in the region, including the southern Sinai Mountains, the Israeli Negev and Judean deserts, the West Bank, Jordan, and northern Saudi Arabia (Sindaco et al. 2018), with home ranges varying from 100 to 900 m^2 lizard^{-1}, with no differences between males and females or across seasons (Orr et al. 1979). *Mesalina bahaeldini* are diurnal and terrestrial, with specimens foraging for insects (mainly ants and termites) on the ground near vegetation and rock substrates, and resting below rocks and inside burrows during daytime and nighttime, respectively (Orr et al. 1979). The predators of the species include scorpions [(e.g., *Buthus* (*Leiurus*) *quinquestriatus*), centipedes (*Scolopendra* sp.)], reptiles (e.g., *Coluber rogersi*), and birds (e.g., *Lanius excubitor*) (Orr et al. 1979). The activity patterns of the species are limited by warm and cold temperatures during both summer and winter, respectively, which together with the availability of abundant rocks and sparse vegetation cover in the Judean Desert, make this ecological system an ideal model for our study.

Body condition measurements

We collected 68 adult specimens of *M. bahaeldini* by hand (SVL > 36 mm for males, and > 40 mm for females, Goldberg 2012) (permits no. 2019/42, 232, 2020/42, 436 from the Israeli Nature and Parks Authority) during summer (June–September; Nahal Mishmar: $n = 14$, Parking Tse'elim River: $n = 11$) and winter (December–February; Nahal Mishmar: $n = 21$, Parking Tse'elim River: $n = 22$) between January 2019 and December 2020. Since age and reproductive state may influence the body condition, we only collected adult males and non-gravid adult females. We were able to identify the sex of only 47 individuals (males: $n = 25$, females: $n = 22$). For each lizard, we recorded the coordinates (latitude and longitude) of the capture location using the GPS application "Map Coordinates" (∼1 m precision). We measured SVL using a digital caliper (0.01 mm precision, MT-11005x, MUNRO Scientific, London, UK) and body mass in grams using a spring scale (to the nearest 0.01 g, 20 g, PESOLA, Schindellegi, Switzerland). The lizards were then taken to Tel Aviv University for an additional experiment before being released back into their natural habitat after 72 h. To avoid pseudo-replications (Schank and Koehnle 2009), the lizards were released ∼1 km from our study sites, and the location where each lizard had been caught was not sampled again within a range of ≥100 m until the next season. We did not mark individuals before release, so our approach does not guarantee that the sampled lizards did not return to our field sites and they may

have been resampled. However, as far as we know, homing behavior of more than 280 m has never been observed in small lizards (reviewed by Ellis-Quinn and Simon 1989).

To estimate the body condition of each lizard, we used the "scaled mass index" of body condition, as suggested by Peig and Green (2009):

$$\hat{M}_i = M_i \times \left[\frac{SVL_0}{SVL_i} \right]^{b_{SML}},$$

where for each individual i, M_i is the body mass (g), SVL_i is the body measurement (mm), SVL_0 is the mean SVL across the measured lizards (43.03 mm), and b_{SML} is the scaling exponent (3.997). The scaling exponent was calculated by dividing the slope of the linear model between log-scaled mass and log-scaled SVL by the Pearson's r correlation coefficient between the variables. Finally, the calculated scaled mass index, $\hat{M}_i$, represents the scaled body mass when the SVL is standardized to SVL_0 (Peig and Green 2009).

Vegetation and rock cover

During summer 2020, we used a mapping drone (eBee X, SenseFly, Cheseaux-sur-Lausanne, Switzerland) equipped with a multi-spectral camera (MicaSense RedEdge-MX Multispectral Camera, Micasense Inc., Seattle, WA). Controlled by a mapping software (eMotion, SenseFly, Cheseaux-sur-Lausanne, Switzerland), the drone took images of our study sites, which were used to generate a DSM (Digital Surface Model, i.e., a 3D representation of the habitat of interest) map, an RGB orthophoto map, and a map for each spectral band (blue, green, red, red-edge, and near-IR). To map the vegetation cover, we used the Normalized Difference Vegetation Index (NDVI), a commonly used index of the greenness and vigor of vegetation in each pixel (Kriegler et al. 1969; reviewed by Huang et al. 2021), including in desert regions (Dall'Olmo and Karnieli 2002). We then created a vegetation cover map, using a fixed NDVI threshold value (NDVI > 0.14) to distinguish between bare soil and sparse vegetation. To map rock cover, we used the TERRA filtering algorithm (Pijl et al. 2020) to extract the Digital Terrain Model (DTM) from the DSM model of our study sites. Next, we extracted the height of the above-ground features, the vegetation and rock cover, by subtracting the DTM from the DSM. We then created a map of above-ground features, using a fixed height threshold value (>20 cm) to distinguish between bare ground and above-ground features that may provide thermal shelter. Finally, we extracted the rock cover by removing the vegetation pixels from the above-ground features map.

In order to validate the presence of vegetation cover and rocks on the generated maps, we compared the maps to the vegetation and rocks as seen on our RGB maps, by determining whether those that appeared on the RGB maps also appeared on the other reciprocal map, and corrected the maps accordingly. We performed this validation procedure on all capture locations of lizards within a radius of 100 m. Maps were corrected using the Serval plugin of the QGIS software.

Next, we extracted the percentage of vegetation and rock cover around the location of each lizard caught in the field at various distances from the lizards (10–100 m, at 10 m intervals). These distances enabled us to estimate the distance at which a lizard is affected by the presence of each microhabitat (i.e., effective distance).

Statistical analysis

To examine the seasonal differences in ground temperatures on shaded and open microhabitats, we fitted a linear model, with temperature as the dependent variable and season (winter/summer) and thermal shelter (open/shade) as the factorial explanatory variables. We used a generalized least squares model, with varying variances across seasons and shelters to account for heterogeneity in the temperature data, using the *gls* function of the R *nlme* package (Pinheiro et al. 2011).

To understand how vegetation and rock cover affect the body condition of our studied lizards, we fitted a linear mixed-effects model, with body condition as the response variable, season as categorical factor and the percentage of thermal shelters (vegetation and rock cover) as continuous covariates. We included the study sites (Parking Tse'elim River and Nahal Mishmar) as a random factor to account for a possible variation between sites. To account for heterogeneity in our data (less variation at high vegetation cover), we introduced an exponential variation structure into the model (Zuur et al. 2009). We used the model in a two-stage approach, in which we first searched for the effective distance (i.e., the distance of the vegetation and rock cover from the lizards that best explained their effect on body condition), and then explored how each explanatory variable affects the body condition at these effective distances. We did not include sex as a factor in our analysis since the sex of 21 individuals (31% of our dataset) was unknown, and similar testing with the remaining individuals ($n = 47$) did not show a significant effect of sex on stage 1 of the analysis (test not shown).

For the first stage, we fitted full linear models with all explanatory variables and all possible combinations of vegetation and rock cover (100 possible models overall). For each of these models, we used Akaike Information Criteria for small data sets (Burnham and Ander-

son 2002) to select the model that best explains the body condition, using the *dredge* function from the MuMIn R package (Bartoń 2020). We then identified the model that performed the best (lowest AICc), and the distances of the vegetation and rock cover that were used to fit this model. In the second stage, we selected the significant explanatory variables using Bayesian statistics, due to the observational nature of the data (Anderson et al. 2000). We first fitted the full model, with the explanatory variables, random factor, and variance structure as described above. We ran the statistical model using a Markov chain Monte Carlo (MCMC) simulation implemented in the JAGS computer program version 4.3.0 (Plummer 2017) using the r2jags R package (Su and Yajima 2021). We used non-informative priors for all model parameters. The MCMC simulation was first run for 100,000 iterations, and we calculated the mean parameters' estimation (with standard deviations and 95% confidence intervals [95% CI]) after an additional 200,000 iterations and tested the convergence of each model parameter. We then simplified the model using stepwise backwards selection. Plots of residuals versus fitted values and every explanatory variable were checked for any violations of model assumptions. All statistical analyses in this study were performed in R 4.1.2 (R Core Team, Vienna, Austria) using the RStudio 1.4.1106 (RStudio Inc., Boston, MA, USA) interface. We report mean ± SD of our collected measurements and parameter estimations.

Results

The collected lizards ($n = 68$) varied in their SVL (43.04 ± 3.01 mm, 36.3–51.8 mm), body mass (1.78 ± 0.45 g, 0.7–2.8 g), and the calculated scaled mass index, $\hat{M}_i$ (1.78 ± 0.39 g). In the open habitat, ground temperatures varied from 38.3 ± 2.5°C in the summer to 20.4 ± 1.6°C during winter (winter effect: −17.9 ± 1.5 °C , $t = -11.7$, $P < 0.001$; Fig. 1). During summer, shade temperature was lower by 5.9 ± 1.3°C than in the open (shade effect: $t = -4.4$, $P = 0.0013$), whereas there was no similar effect of shade in the winter (shade × winter interaction: 6.8 ± 2.1 °C, $t = 3.3$, $P = 0.0078$; Fig. 1).

During our first stage of the statistical modeling, we found that the effective distances, as suggested by our AICc scores, were up to 10 and 90 m for rocks and vegetation cover, respectively. The worst model (ΔAICc = 25.7) produced effective distances of no greater than 10 and 20 m for vegetation and rock cover, respectively. All models that performed almost similarly to the best model (ΔAICc < 2) had an effective distance of up to 10 m for rock cover, and either 80 or 100 m for vegetation cover, suggesting that the impact of rock
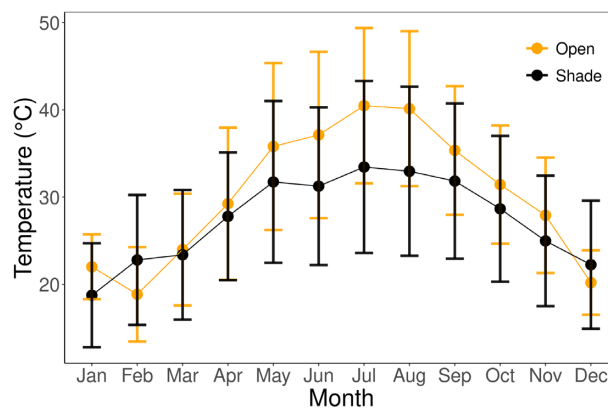

Fig. 1 The temperatures under shaded (black) and open (orange) microhabitats throughout the year in the desert. Each point and error bars represent the mean and SD of the temperatures for each month, respectively.
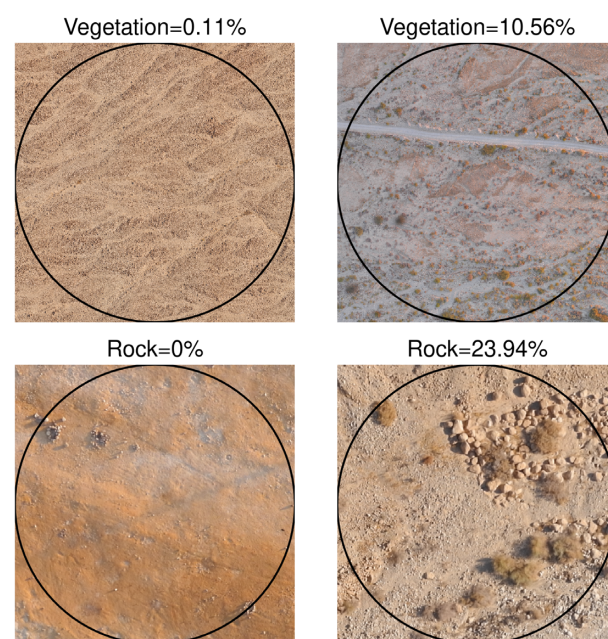

Fig. 2 Examples of the variation in landscape at the effective distances of the captured lizards. Top panels show two locations with low (left panel: <1%) and high (right panel: ~10%) availability of vegetation cover; bottom panels show two locations with low (left panel: ~0%) and high (right panel: ~24%) availability of rock cover (above 20 cm height). Circles are drawn at 90 m and 10 m radius for vegetation (top panels) and rock (bottom panels) cover, respectively.

cover is strongest at close proximity to the lizard's home range, while that of vegetation cover reaches much farther than an individual lizard's home range (>17 m radius; Orr et al. 1979). Our collected lizards varied in the availability of vegetation and rock cover at these effective distances (Fig. 2), with an average (± SD) of 1.81 ± 2.00%, and 8.63 ± 9.52% for vegetation and rock cover, respectively.
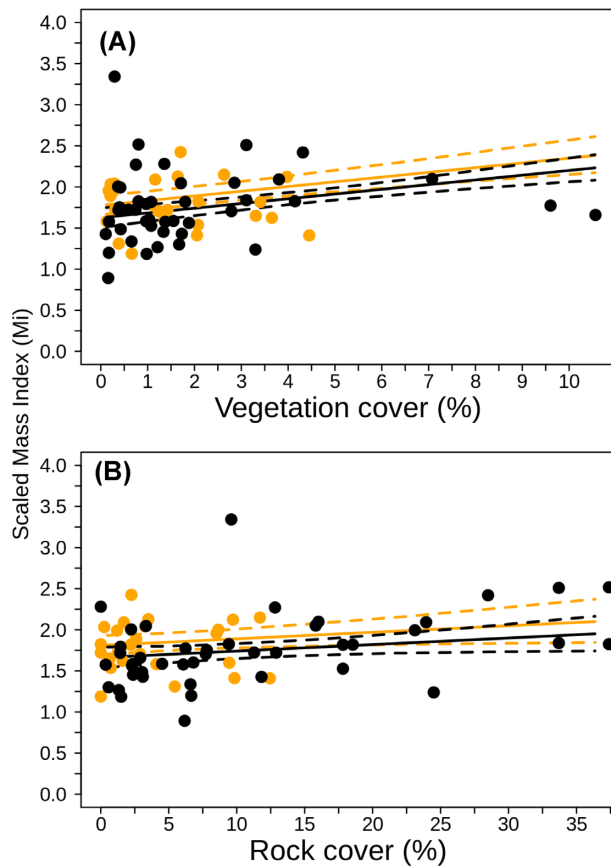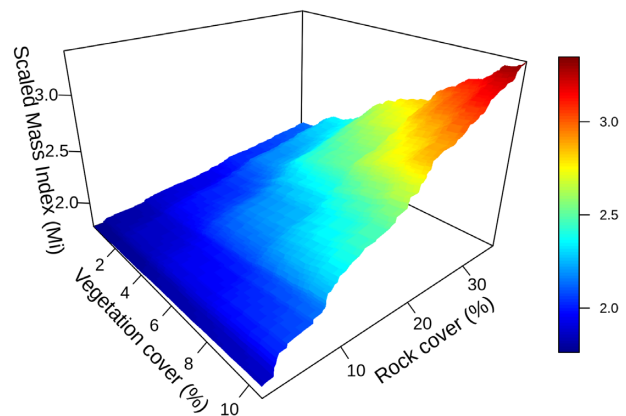
Fig. 4 Higher availability of vegetation and rock cover synergically improves lizards' body condition. The figure presents the significant interaction found in our statistical model between scaled mass index and the vegetation and rock cover. Under low vegetation cover the positive impact of rock cover is much lower than under high vegetation cover. Similarly, higher rock cover substantially strengthens the positive impact of vegetation cover. Colors represent the predicted scaled mass index of lizards.

(mean $\pm$ SD−0.236 $\pm$ 0.353 g, 95% CI [−0.444, 0.916]). Regardless of season, vegetation, and rock cover, the body condition of lizards was lower by 0.06 $\pm$ 0.01 g per 1 mm increase in SVL (95% CI [−0.079, −0.042]).

Discussion

The findings from our study provide evidence regarding the importance of access to vegetation and rocks during both summer and winter in order to maintain a good body condition in the studied lizards. In an extreme environment such as the Judean Desert, the access to these shade elements in the vicinity of the lizards substantially improved their body condition during both summer and winter in various ways, with a 12-fold stronger effect of vegetation cover than of rocks, and a synergic effect of the two. The lack of seasonal variation in these effects on the body condition supports our alternative hypotheses. In particular, the contribution of rocks and vegetation lies beyond that of thermal benefits alone, in providing other ecologically important services during both summer and winter.

The effective distance for the contribution of vegetation cover was up to 90 m. Interestingly, this distance is much greater than that of a lizard's home range (17 m radius or 900 m^2, Orr et al. 1979), suggesting that the lizards benefiting from vegetation do not only use it for shade. As a primary producer, vegetation has an important role in ecological systems, providing indirect benefits for distant animals that may never physically reach it. It is possible that the shade and food provided by vegetation determine nearby prey abundance (Johnson

Fig. 3 Higher availability of vegetation and rock cover enables lizards to acquire higher body condition. The figure presents the significant relationships found in our statistical model between scaled mass index and vegetation (**A**) and rock (**B**) covers during summer (orange) and winter (black). Solid line = mean slope; dashed line = 95% CI of slopes; points = lizards' body condition.

During the second stage of our statistical modeling, our statistical Bayesian model revealed that body condition ($\hat{M}_i$) was higher for lizards that had more vegetation and rock available within their effective distances. In particular, $\hat{M}_i$ increased by 0.008 $\pm$ 0.004 g (95% CI [0.0003, 0.016]) for every 1% increase in rock cover, and by 0.057 $\pm$ 0.011 g (95% CI [0.037, 0.078]) for every 1% increase in vegetation cover (Fig. 3). Importantly, the effect of vegetation cover was 12.3-fold higher than the effect of rock cover (95% CI [1.9, 36.9]). We also found a positive interaction between vegetation and rock cover, in which for every 1% increase in vegetation or rock cover, the positive effect of the other microhabitat increased by 0.003 $\pm$ 0.001 g per 1% increase (95% CI [0.0001, 0.006]) (Fig. 4). The body condition of lizards was lower by 0.149 $\pm$ 0.074 g during the winter (95% CI [−0.292, −0.003]), but with no interaction with vegetation cover (mean $\pm$ SD−0.098 $\pm$ 0.166, 95% CI [−0.223, 0.414]), rock cover (mean $\pm$ SD−0.230 $\pm$ 0.209 g, 95% CI [−0.179, 0.637]), or both

2000; Borkhataria et al. 2012; Guenat et al. 2017) such as insects, reducing the lizards' energetic costs of searching and increasing their foraging efficiency (Belliure et al. 1996; Attum and Eason 2006; Kearney et al. 2021). For example, in our study system, herbivorous ants (Myrmicinae) and termites (Isoptera), the main prey items for *M. bahaeldini*, may travel up to 50–100 m to reach their food (pers. obs.), exposing themselves to predation (Orr et al. 1979). *Mesalina bahaeldini,* whose home range lies within the path of these insects, will thus indirectly benefit from the proximity to vegetation.

The effective distance for rock cover was much shorter, only up to 10 m, suggesting that the ecological role of rocks functions only in close vicinity to the lizards, unlike the vegetation cover. In particular, lizards may directly benefit from rock cover as a physical shelter from the harmful effects of the high temperature in the desert summer, enabling them to effectively thermoregulate and maintain optimal temperature, reducing the costs of missed opportunities for basking (Basson et al. 2017), and enabling more efficient foraging and digestion (Melville and Schulte 2001; Amo et al. 2007; Monasterio et al. 2010). Moreover, a high availability of rocks may also shorten the lizards' escape distance when encountering predators, enabling them to exploit their home range under high predation risks (Huey 1991; Amo et al. 2007; Pietrek et al. 2009; Monasterio et al. 2010; Newbold and MacMahon 2014).

The positive synergistic effect of vegetation and rock cover on the body condition of lizards suggests that their roles are more complementary than overlapping. It is possible, for example, that the role of vegetation is more indirect than direct, as it mediates food availability, while that of rocks is more direct, offering shelter from unfavorable temperatures and predation. While such complementary interactions have rarely been studied and observed in nature, here we provide evidence that by focusing on one type of microhabitat alone, we may inadvertently underestimate the importance of others. In order to increase and improve conservation efforts or carry out sustainable habitat modifications in a particular area, we should therefore develop a better understanding of the effects of the natural microclimates in that area. Using high-resolution drone imagery, we were able here to accurately map the microhabitats at a resolution of centimeters, which is relevant for small animals such as lizards and arthropods (Pincebourde and Woods 2020). With the increasing availability of these aerial technologies, such mapping, together with on-the-ground animal surveys, can significantly improve our ability to accurately map the microhabitats in natural ecological systems and analyze the importance of different microhabitats for the animals that occupy them.

During winter, the body condition of the studied lizards was poorer, regardless of the local availability of vegetation and rocks. This decline in body condition suggests that in winter lizards either suffer from lower prey availability, as previously observed by Vonshak et al (2009) for this area, or lower opportunities for thermoregulation, since temperatures are mostly below the optimal temperature for lizards, slowing their foraging and digestion rates (Cowles 1941; Huey et al. 2021). The winter ecology of reptiles has been little studied, and here we provide evidence that even in the desert, where summer is considered the harshest climate season, the relatively cold temperatures of winter may drive ectotherms to a slower pace of energy acquisition and a negative energy balance that eventually reduce body condition regardless of access to microhabitats. Alternatively, the poorer body condition may represent a loss of energy storage for reproduction, at least for females that invest much energy in producing eggs. Nevertheless, even during winter, both vegetation and rock cover had the same effect on body condition of lizards as during summer. Thus, lizards whose home range was in close proximity to vegetation and rocks displayed a better body condition than those with less access to such cover.

This lack of seasonal effect on the interaction between shade cover and seasonality indicates the complexity of the forces that together shape body condition in desert lizards. Although both the opportunity to thermoregulate and prey abundance are lower during winter, a high availability of microhabitats (rock and vegetation cover) nonetheless increases the chances of encountering prey and reaching optimal body temperature. It is possible that these microhabitats thus offer lizards the ability to avoid predators (Huey 1991; Downes and Shine 1998; Newbold et al. 2014), while increasing the availability of prey species in both seasons (Newbold and MacMahon 2014; Luna-Gómez et al. 2017; Giménez Gómez et al. 2018; Bajaru et al. 2019). Moreover, rocks may also promote basking and passive warming during the winter by enabling lizards to adjust their body angle towards the sun and maximize solar radiation intake (Martín et al. 1995). Rocks and vegetation can also offer shelter from wind, enabling lizards to minimize unfavorable conductive heat exchange (Porter and Gates 1969; Ortega et al. 2017). Alternatively, if a lizard's home range does not shift between seasons, the animal's better body condition during winter could be the result of the benefits obtained from these microhabitats during summer. Competition over such microhabitats might also lead to dominant lizards excluding subordinate ones, although no interference competition has been observed in the species (Orr et al. 1979).

The findings from our study reveal the need to further explore how the diversity of microhabitats affects the physiological state of animals, from individuals to populations and communities. Although we found a strong effect of microhabitat on body condition in our studied lizards, it is clear that the provision of thermal shelter is only one aspect of the various factors in the ecological system that may also affect body condition. Hence, we emphasize the importance of measuring additional variables, such as prey abundance near the shaded animals, since this may explain an indirect effect of shade. Moreover, to better understand the degree to which animals exploit shade, we need improved empirical tools, such as bio-tracking loggers that can capture thermoregulation via light-level sensors (Williams et al. 2020). For example, the fact that we have found a substantially smaller number of lizards during summer may have limited our analysis to lizards that are less sensitive to warm conditions and spent less time hiding inside thermal shelters. Better tracking tools will decrease such detection biases and enable more robust measurements of how changes in shade and food availability affect body condition of the same individuals over time. Finally, our study was limited to adults only, but shade availability may also affect earlier life stages and reproductive success. It is possible, for example, that animals compete over rocks and vegetation and that individuals with better body condition are able to establish their home range closer to vegetation and rocks. We suggest that measuring an animal's body condition at earlier life-stages and in different reproductive states (e.g., gravid vs non-gravid females) can help us to understand how seasonal changes and variations in climate across ontogeny and across time may affect body condition (Dunham 1978; Durst et al. 2008; Bang and Faeth 2011). These potential further studies may shed more light on the impact of microhabitats and seasonality on the energy reserves of desert species.

In conclusion, our research has demonstrated the importance of shade and of shade-providing elements, such as vegetation and rock, as ecological resources. We have shown that the seasonal changes observed in the body condition of our studied lizards are not related solely to shade availability in the desert. The high level of complexity resulting from the interactions between the various factors demonstrates the extent to which several factors may contribute to shaping the energetic budget of animals in an extreme environment. Our results suggest that we may be oversimplifying assumptions if we treat shade as mere shade and nothing more; and that we also need to account for the ecological roles of the shade-supplying elements. Under climate change, the availability of shade in many habitats will directly affect the thermoregulatory responses of various species

(Kearney et al. 2009; Sinervo et al. 2010; Kearney 2013). Consequently, there is a need to assess the significance of shade availability for animals in ensuring the stability of ecological interactions in the desert system, in order to better predict the biological impacts of climate change.

Authors contributions

All authors conceived and designed the study. G.S. collected and analyzed the data and wrote the first draft of the manuscript. O.L. contributed mentorship and materials/analysis tools. O.L., G.S., L.M., Z.G.Z., and W.G.D. commented on the first draft and participated in revising the manuscript.

Supplementary data

Supplementary data available at *ICB* online.

Conflict of interest

All authors declare that they have no conflicts of interest.

Data accessibility statement

Data used in the analyses and the associated metadata are available in Appendix S1. All codes used in the analyses will be available upon request.

References

Amo L, López P, Martín J. 2007. Refuge use: a conflict between avoiding predation and losing mass in lizards. Physiol Behav 90:334–43.

Anderson DR, Burnham KP, Thompson WL. 2000. Null hypothesis testing: problems, prevalence, and an alternative. J Wildl Manag 64:912.

Attum OA, Eason PK. 2006. Effects of vegetation loss on a sand dune lizard. J Wildl Manage 70:27–30.

Bajaru SB, Kulavmode AR, Manakadan R. 2019. Influence of microhabitat and landscape-scale factors on the richness and occupancy of small mammals in the northern Western Ghats:

a multi-species occupancy modeling approach. Mamm Biol 99:88–96.

Bang C, Faeth SH. 2011. Variation in arthropod communities in response to urbanization: seven years of arthropod monitoring in a desert city. Landsc Urban Plan 103:383–99.

Bartoń K. 2020. MuMIn: Multi-Model Inference. R package version 1.46.0. CRAN.R-project.org/package=MuMIn. Last accessed on 10 February 2022.

Basson CH, Levy O, Angilletta MJ, Clusella-Trullas S. 2017. Lizards paid a greater opportunity cost to thermoregulate in a less heterogeneous environment. Funct Ecol 31:856–65.

Baum GL, Artis D. 1966. Isolation of fungi from Judean Desert soil. Mycopathol Mycol Appl 29:350–4.

Belliure J, Carrascal LM, Diaz JA. 1996. Covariation of thermal biology and foraging mode in two mediterranean lacertid lizards. Ecology 77:1163–73.

Borkhataria RR, Collazo JA, Groom MJ. 2012. Species abundance and potential biological control services in shade vs. sun coffee in Puerto Rico. Agric Ecosyst Environ 151:1–5.

Buckley LB, Urban MC, Angilletta MJ, Crozier LG, Rissler LJ, Sears MW. 2010. Can mechanism inform species' distribution models? Ecol Lett 13:1041–54.

Buckley LB. 2008. Linking traits to energetics and population dynamics to predict lizard ranges in changing environments. Am Nat 171:E1–E19.

Burnham KP, Anderson DR. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. New York (NY): Springer. p. 488.

Chukwuka CO, Mello RSR, Cree A, Monks JM. 2021. Thermal heterogeneity of selected retreats in cool-temperate viviparous lizards suggests a potential benefit of future climate warming. J Therm Biol 97:102869.

Cowles RB. 1941. Observations on the winter activities of desert reptiles. Ecology 22:125.

Dall'Olmo G, Karnieli A. 2002. Monitoring phenological cycles of desert ecosystems using NDVI and LST data derived from NOAA-AVHRR imagery. Int J Remote Sens 23:4055–71.

Davies AB, Tambling CJ, Kerley GIH, Asner GP. 2016. Effects of vegetation structure on the location of lion kill sites in African thicket. PLoS One 11:e0149098.

Downes S, Shine R. 1998. Heat, safety or solitude? Using habitat selection experiments to identify a lizard's priorities. Anim Behav 55:1387–96.

Dunham AE. 1978. Food availability as a proximate factor influencing individual growth rates in the iguanid lizard *Sceloporus merriami*. Ecology 59:770–8.

Durst SL, Theimer TC, Paxton EH, Sogge MK. 2008. Temporal variation in the arthropod community of desert riparian habitats with varying amounts of saltcedar (*Tamarix ramosissima*). J Arid Environ 72:1644–53.

Eifler DA, Eifler MA, Brown TK. 2012. Habitat selection by foraging Texas horned lizards. Southwest Nat 57:39–43.

Ellis-Quinn BA, Simon CA. 1989. Homing behavior of the lizard *Sceloporus jarrovi*. J Herpetol 23:146.

Fitzsimons JA, Michael DR. 2017. Rocky outcrops: a hard road in the conservation of critical habitats. Biol Conserv 211:36–44.

Giménez Gómez VC, Lomáscolo SB, Zurita GA, Ocampo F. 2018. Daily activity patterns and thermal tolerance of three sympatric dung beetle species (Scarabaeidae:Scarabaeinae: Eu-

craniini) from the Monte Desert, Argentina. Neotrop Entomol 47:821–7.

Goldberg SR. 2012. Reproduction in the desert lacerta, *Mesalina guttulata*, from Israel. Zool Middle East 56:27–30.

Goldsbrough CL, Hochuli DF, Shine R. 2004. Fitness benefits of retreat-site selection: spiders, rocks, and thermal cues. Ecology 85:1635–41.

Goldsbrough CL, Shine R, Hochuli DF. 2006. Factors affecting retreat-site selection by coppertail skinks (*Ctenotus taeniolatus*) from sandstone outcrops in eastern Australia. Austral Ecol 31:326–36.

Guenat S, Kaartinen R, Jonsson M. 2017. Shade trees decrease pest abundances on brassica crops in Kenya. Agroforest Syst 93:1–12.

Hantson S, Huxman TE, Kimball S, Randerson JT, Goulden ML. 2021. Warming as a driver of vegetation loss in the Sonoran desert of California. J Geophys Res Biogeosci 126:e2020JG005942.

Huang S, Tang L, Hupy JP, Wang Y, Shao G. 2021. A commentary review on the use of normalized difference vegetation index (NDVI) in the era of popular remote sensing. J For Res 32:1–6.

Huey RB, Ma L, Levy O, Kearney MR. 2021. Three questions about the eco-physiology of overwintering underground. Ecol Lett 24:170–85.

Huey RB, Slatkin M. 1976. Cost and benefits of lizard thermoregulation. Q Rev Biol 51:363–84.

Huey RB. 1974. Behavioral thermoregulation in lizards: importance of associated costs. Science 184:1001–3.

Huey RB. 1991. Physiological consequences of habitat selection. Am Nat 137:S91–S115.

Jacob J, Brown JS. 2000. Microhabitat use, giving-up densities and temporal activity as short- and long-term anti-predator behaviors in common voles. Oikos 91:131–8.

Johnson MD. 2000. Effects of shade-tree species and crop structure on the winter arthropod and bird communities in a Jamaican shade coffee plantation 1. Biotropica 32:133–45.

Jones M, Mandelik Y, Dayan T. 2001. Coexistence of temporally partitioned spiny mice: roles of habitat structure and foraging behavior. Ecology 82:2164–76.

Kearney M. 2002. Hot rocks and much-too-hot rocks: seasonal patterns of retreat-site selection by a nocturnal ectotherm. J Therm Biol 27:205–18.

Kearney M. 2013. Activity restriction and the mechanistic basis for extinctions under climate warming. Ecol Lett 16:1470–9.

Kearney M, Porter W. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecol Lett 12:334–50.

Kearney M, Shine R, Porter WP. 2009. The potential for behavioral thermoregulation to buffer "cold-blooded" animals against climate warming. Proc Natl Acad Sci 106:3835–40.

Kearney MR, Porter WP, Huey RB. 2021. Modeling the joint effects of body size and microclimate on heat budgets and foraging opportunities of ectotherms. Methods Ecol Evol 12:458–67.

Kriegler FJ, Malila WA, Nalepka RF, Richardson W. 1969. Preprocessing transformations and their effects on multispectral recognition. Michigan (CA): Environmental Research Institute of Michigan. p. 97.

Levy O, Borchert JD, Rusch TW, Buckley LB, Angilletta MJ. 2017. Diminishing returns limit energetic costs of climate change. Ecology 98:1217–28.

Levy O, Buckley LB, Keitt TH, Angilletta MJ. 2016. Ontogeny constrains phenology: opportunities for activity and reproduction interact to dictate potential phenologies in a changing climate. Ecol Lett 19:620–8.

Levy O, Buckley LB, Keitt TH, Angilletta MJ. 2016. A dynamically downscaled projection of past and future microclimates. Ecology 97:1888.

Levy O, Buckley LB, Keitt TH, Smith CD, Boateng KO, Kumar DS, Angilletta MJ. 2015. Resolving the life cycle alters expected impacts of climate change. Proc Biol Sci 282: 20150837.

Levy O, Dayan T, Porter WP, Kronfeld-Schor N. 2016. Foraging activity pattern is shaped by water loss rates in a diurnal desert rodent. Am Nat 188:205–18.

Luna-Gómez MI, García A, Santos-Barrera G. 2017. Spatial and temporal distribution and microhabitat use of aquatic breeding amphibians (Anura) in a seasonally dry tropical forest in Chamela, Rev biol trop 65:1082.

Madani N, Kimball JS, Ballantyne AP, Affleck DLR, van Bodegom PM, Reich PB, Kattge J, Sala A, Nazeri M, Jones MO, et al. 2018. Future global productivity will be affected by plant trait response to climate. Sci Rep 8:2870.

Mandelik Y, Jones M, Dayan T. 2003. Structurally complex habitat and sensory adaptations mediate the behavioural responses of a desert rodent to an indirect cue for increased predation risk. Evol Ecol Res 5:501–15.

Martín J, López P, Carrascal LM, Salvador A. 1995. Adjustment of basking postures in the high-altitude Iberian rock lizard (*Lacerta monticola*). Can J Zool 73:1065–8.

Melville J, Schulte II JA. 2001. Correlates of active body temperatures and microhabitat occupation in nine species of central Australian agamid lizards. Austral Ecol 26: 660–9.

Monasterio C, Salvador A, Díaz JA. 2010. Altitude and rock cover explain the distribution and abundance of a mediterranean alpine lizard. J Herpetol 44:158–63.

Moncaz A, Faiman R, Kirstein O, Warburg A. 2012. Breeding sites of *Phlebotomus sergenti*, the sand fly vector of cutaneous leishmaniasis in the Judean Desert. PLoS Negl Trop Dis 6:e1725.

Newbold A, Martin BP, Cullinane C, Bots M. 2014. Detection of apoptotic cells using immunohistochemistry. Cold Spring Harb Protoc 2014:1196–201.

Newbold TAS, MacMahon JA. 2014. Determinants of habitat selection by desert horned lizards (*Phrynosoma platyrhinos*): the importance of abiotic factors associated with vegetation structure. J Herpetol 48:306–16.

Nordberg EJ, Schwarzkopf L. 2019. Heat seekers: a tropical nocturnal lizard uses behavioral thermoregulation to exploit rare microclimates at night. J Therm Biol 82: 107–14.

Orr Y, Shachak M, Steinberger Y. 1979. Ecology of the small spotted lizard (*Eremias guttulata guttulata*) in the Negev desert (Israel). J Arid Environ 2:151–61.

Ortega Z, Mencía A, Pérez-Mellado V. 2017. Wind constraints on the thermoregulation of high mountain lizards. Int J Biometeorol 61:565–73.

Peig J, Green AJ. 2009. New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. Oikos 118:1883–91.

Pietrek AG, Walker RS, Novaro AJ. 2009. Susceptibility of lizards to predation under two levels of vegetative cover. J Arid Environ 73:574–7.

Pijl A, Bailly J-S, Feurer D, El Maaoui MA, Boussema MR, Tarolli P. 2020. TERRA: terrain extraction from elevation Rasters through repetitive anisotropic filtering. Int J Appl Earth Obs Geoinf 84:101977.

Pincebourde S, Woods HA. 2020. There is plenty of room at the bottom: microclimates drive insect vulnerability to climate change. Curr Opin Insect Sci 41:63–70.

Pinheiro J, Bates D, DebRoy S, Sarkar D, the R Development Core Team. 2011. nlme: linear and nonlinear mixed effects models. R Package Version 3:1–155.

Plummer M. 2017. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. mcmc-jags.sourceforge.io. Last accessed 13th February 2022.

Porter WP, Gates DM. 1969. Thermodynamic equilibria of animals with environment. Ecol Monogr 39:227–44.

Schank JC, Koehnle TJ. 2009. Pseudoreplication is a pseudoproblem. J Comp Psychol 123:421–33.

Scheffers BR, Edwards DP, Diesmos A, Williams SE, Evans TA. 2014. Microhabitats reduce animal's exposure to climate extremes. Global Change Biol 20:495–503.

Schlesinger CA, Shine R. 1994. Choosing a rock: perspectives of a bush-rock collector and a saxicolous lizard. Biol Conserv 67:49–56.

Schulz N, Aceituno P, Richter M. 2011. Phytogeographic divisions, climate change and plant dieback along the coastal desert of northern Chile. Erdkunde 65:169–87.

Sears MW, Angilletta MJ, Schuler MS, Borchert J, Dilliplane KF, Stegman M, Rusch TW, Mitchell WA. 2016. Configuration of the thermal landscape determines thermoregulatory performance of ectotherms. Proc Natl Acad Sci 113:10595–600.

Segoli M, Cohen T, Werner YL. 2002. A new lizard of the genus Mesalina from Mt. Sinai, Egypt (Reptilia: Squamata: Sauria: Lacertidae). Faunist Abh Dresden 23:157–76.

Segoli M, Groner E, Ayal Y. 2016. The importance of plant cover and predation in shaping a desert community. J Arid Environ 135:33–8.

Shah B, Shine R, Hudson S, Kearney M. 2004. Experimental analysis of retreat-site selection by thick-tailed geckos *Nephrurus milii*. Austral Ecol 29:547–52.

Sindaco R, SimÓ-Riudalbas M, Sacchi R, Carranza S. 2018. Systematics of the *Mesalina guttulata* species complex (Squamata: Lacertidae) from Arabia with the description of two new species. Zootaxa 4429:513–47.

Sinervo B, Méndez-de-la-Cruz F, Miles DB, Heulin B, Bastiaans E, Villagrán-Santa Cruz M, Lara-Resendiz R, Martínez-Méndez N, Calderón-Espinosa ML, Meza-Lázaro RN, et al. 2010. Erosion of lizard diversity by climate change and altered thermal niches.Science 328:894–9.

Su Y-S, Yajima M. 2021. R2jags: Using R to Run "JAGS." R package version 0.7-1CRAN.R-project.org/package=R2jags. Last accessed on 13 February 2022.

van den Berg FT, Thompson MB, Hochuli DF. 2015. When hot rocks get hotter: behavior and acclimatization mitigate exposure to extreme temperatures in a spider. Ecosphere 6:1–17.

Vonshak M, Dayan T, Kronfeld-Schor N. 2009. Arthropods as a prey resource: patterns of diel, seasonal, and spatial availability. J Arid Environ 73:458–62.

Webb JK, Pringle RM, Shine R. 2004. How do nocturnal snakes select diurnal retreat sites? Copeia 2004: 919–25.

Williams HJ, Taylor LA, Benhamou S, Bijleveld AI, Clay TA, de Grissac S, Demšar U, English HM, Franconi N, Gómez-Laich A, et al. 2020. Optimizing the use of biologgers for movement ecology research. J Anim Ecol 89: 186–206.

Wramneby A, Smith B, Samuelsson P. 2010. Hot spots of vegetation-climate feedbacks under future greenhouse forcing in Europe. J Geophys Res 115:D21119.

Zeng Z-G, Bi J-H, Li S-R, Chen S-Y, Pike DA, Gao Y, Du W-G. 2014. Effects of habitat alteration on lizard community and food web structure in a desert steppe ecosystem. Biol Conserv 179:86–92.

Zeng Z-G, Bi J-H, Li S-R, Wang Y, Robbins TR, Chen S-Y, Du W-G. 2016. Habitat alteration influences a desert steppe lizard community: implications of species-specific preferences and performance. Herpetol Monogr 30:34–48.

Zhu Y, Zhang J, Zhang Y, Qin S, Shao Y, Gao Y. 2019. Responses of vegetation to climatic variations in the desert region of northern China. Catena 175:27–36.

Zuur AF, Ieno EN, Walker N, Saveliev AA, Smith GM. 2009. Mixed effects models and extensions in ecology with R. New York (NY): Springer. p. 574.