Journal of Thermal Biology 121 (2024) 103841

Contents lists available at ScienceDirect

Journal of Thermal Biology

journal homepage: www.elsevier.com/locate/jtherbio

State-dependent movement choices of desert lizards: The role of behavioural thermoregulation during summer and winter

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ARTICLE INFO

Dataset link: https://github.com/levyofi/Stark_et_al_JTB_2024

Keywords:
Desert
Climate change
Extreme environments
Thermoregulation
Refuge
Rocks
Seasonality
Vegetation

ABSTRACT

Environmental temperatures are increasing worldwide, threatening desert ectotherms already living at their thermal limits. Organisms with flexible thermoregulatory behaviours may be able to mitigate the effects of extreme temperatures by moving among microhabitats, yet little work has tracked movement patterns of desert ectotherms in the wild over diurnal scales or compared behaviour among seasons. Here, we used camera traps to track the thermoregulatory behaviour and microhabitat choices of 30 desert lizards (*Messalina bahaldini*) in custom, outdoor arenas that provided access to open, rock, and bush microhabitats. We found that in the summer, lizards preferred to move to the shaded microhabitats and remain there under warmer conditions. During winter, however, lizards' activity was not related to temperature, and lizards mostly chose to remain in the open habitat. Interestingly, in both seasons, lizards tended to remain in their current microhabitat and moved infrequently between certain combinations of microhabitats. Our study shows that thermoregulation (shade-seeking behaviour) is a major factor during summer, helping lizards to avoid extreme temperatures, but not during winter, and shows a novel effect of current microhabitat on movement, suggesting that other biotic or abiotic factors may also drive microhabitat choice. Understanding the complex factors at play in microhabitat choice is critical for developing conservation programs that effectively mitigate the negative impacts of climate change on desert animals.

1. Introduction

The ability of animals to maintain a preferred body temperature is crucial to their growth, survival and reproductive fitness in natural environments (Stevenson, 1985). Ectotherms cannot regulate their body temperature metabolically; instead, they use behaviour to optimize body temperature, e.g., through the choice of microhabitat and levels of activity, basking times and body posture — typically by shuttling between sun and shade (e.g., Angilletta, 2009; Dubois et al., 2009). By thermoregulating behaviourally, animals can also buffer highly-variable or extreme temperatures (Huey et al., 2012; Abram et al., 2017; Ortega and Pérez-Mellado, 2016), which are becoming increasingly common with global warming and habitat loss (Mantyka-pringle et al., 2012; Stott, 2016). This is particularly important in desert habitats, where many ectotherms already live at the edge of their thermal tolerance limits (Huey et al., 2012; Vale and Brito, 2015).

Yet, animals must balance the potential benefits of thermoregulatory behaviour with myriad energetic costs or risks to survival (Huey and Slatkin, 1976). For example, searching for thermally preferred locations may be energetically expensive in poor-quality environments with a low number of these locations (Basson et al., 2017; Sears and Angilletta, 2015; Milling et al., 2017; Lymburner and Blouin-Demers, 2020; Llanos-Garrido et al., 2023; Sears et al., 2016) and animals are known to move around less in environments with high predation risk or competition (e.g., Broeckhoven and le Fras Nortier Mouton, 2015; Herczeg et al., 2008; Magnuson et al., 1979; Hertz, 1992; Rusch and Angilletta, 2017). Behavioural thermoregulation may vary between seasons, influenced by shifts in animals' thermal preferences and seasonal environmental challenges (Huey and Slatkin, 1976; Angilletta, 2009). These challenges include both abiotic and biotic factors, which affect the associated costs of movement (Huey and Pianka, 1977; Ortega and Martín-Vallejo, 2019; Ortega and Pérez-Mellado, 2016). The varying and often conflicting factors involved in behavioural thermoregulation present significant challenges, making it difficult for managers to plan

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https://doi.org/10.1016/j.jtherbio.2024.103841
Received 23 October 2023; Received in revised form 1 March 2024; Accepted 6 March 2024
Available online 18 March 2024
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and implement effective conservation programs for ectotherms (Stark et al., 2022, 2023).

Though vital to thermoregulation, the movement behaviour of ectotherms remains poorly studied due to the challenges of tracking and monitoring these behaviours in natural environments (e.g., Broeckhoven and le Fras Nortier Mouton, 2015; Sears et al., 2016; Smith and Ballinger, 2001a; Kearney et al., 2018). Traditional methods of direct observation, though useful, are limited because observers can alter the observed animals' behaviour (Kerr et al., 2004; Griffin and Haythorpe, 2011). In some habitats, such as deserts, harsh environmental conditions make it even more difficult to obtain direct observations, further limiting the scope of data available on species' movements. In recent years, camera trapping technology has enabled animal behaviours, including movement, to be monitored more efficiently and reliably across a wide range of taxa (Bridges and Noss, 2011; Stanton-Jones et al., 2018). Camera traps are non-invasive, automated, and allow continuous tracking of behavioural patterns, thus providing more comprehensive data than traditional methods (Broeckhoven and le Fras Nortier Mouton, 2015). Despite this, the use of camera traps in studies on ectotherms, specifically reptiles, has been limited to only a few species (e.g., monitor and girdled lizards; Ariefiandy et al., 2013; Broeckhoven and le Fras Nortier Mouton, 2015; Stanton-Jones et al., 2018) and has not focused on thermoregulatory behaviour (Broeckhoven and le Fras Nortier Mouton, 2015; Stanton-Jones et al., 2018; Ariefiandy et al., 2013). Here, we used camera traps to continuously track the microhabitat choices of a desert lizard, *Messalina bahaldini*, under semi-natural conditions during summer and winter. In extremely heterogeneous habitats, such as deserts, ectotherms devote considerable time and energy towards maintaining an optimal body temperature (Rangel-Patiño et al., 2020). These costs are likely to be exacerbated with climate change, forcing ectotherms to avoid overheating by increasing usage of thermal refuges for extended periods (Rangel-Patiño et al., 2020). Previous work has demonstrated that desert lizards depend on diverse microhabitats (e.g., bushes, rocks, and burrows) as a significant resource, but those studies primarily used estimates from statistical or biophysical models rather than field data and did not track lizard movements within and between seasons (Li et al., 2017; Parlin et al., 2020; Stark et al., 2022, 2023) (but see; Kearney et al., 2018).

To do this, we used custom field enclosures to evaluate how the thermoregulatory behaviour of lizards depends on the season, the thermal conditions of microhabitats (e.g., bush, rock, open) available to them, and the required movement from the lizard to a given microhabitat. An earlier study found that for desert lizards in close proximity to rocks and bushes had better body condition during both summer and winter, probably since these habitats have major abiotic and biotic roles (Stark et al., 2022). However, a biophysical model suggested that the lizards should use these habitats as shade cover for thermoregulation during summer (Stark et al., 2023). Based on these results, we hypothesized that lizards in the current study would spend time under bushes and rocks in both summer and winter, but that timing would only be related with temperature during summer. We expected that in winter, lizards would prefer the open microhabitat, especially during relatively warm daytime hours, but that in summer they would increase activity in shaded microhabitats during the day when temperatures were hot. We also hypothesized that lizards would minimize movement costs by preferring to stay at their current microhabitat (i.e., avoid moving to a different microhabitat) unless behavioural thermoregulation was needed to avoid unfavourable conditions.

2. Materials and methods

2.1. 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 approximately 400 m below sea level. The area consists of two major habitats that offer shelter to the local wildlife: rocky areas characterized by rock accumulations that provide shelter in the interstices under and between them, and vegetation that exist mainly near dry river beds or streams, but also within rocky areas, and are dominated 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 at noon. Shade cover offers substantial thermal shelter, with maximal ground temperatures reaching only 37 °C (Levy et al., 2016). Winter temperatures are much cooler and more uniform across habitats, with ground temperatures reaching 27 °C in the open and 25 °C under shade cover (Levy et al., 2016). We sampled lizards from 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., 6″E). Some areas in Nahal Mishmar are characterized by a few *Acacia raddiana* trees and denser vegetation cover (mostly bushes), in contrast with the Parking Tse'elim River, which is covered mostly by rocks and very sparse vegetation. At both sites, we sampled lizards from locations that varied in vegetation and rock cover.

2.2. 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) of the Lacertidae family. The species is widely distributed across 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, and no sexual dimorphism between males and females (Orr et al., 1979). *Mesalina bahaeldini* are small, with an adult SVL ranging from 36–51 mm for males and 40–53 mm for females, respectively (Goldberg, 2012). The species is diurnal and terrestrial, forage for insects (mainly ants and termites) on the ground near vegetation and rock substrates, and rest below rocks and inside burrows during the day and night, respectively (Orr et al., 1979). Their main predators include: scorpions (e.g., *Buthus (Leiurus) quinquestriatus*), centipedes (*Scolopendra* sp.), other reptiles (e.g., *Coluber rogersi*), and birds (e.g., *Lanius excubitor*; Orr et al., 1979). The activity patterns of the species are limited by hot temperatures in the summer and cold temperatures in the winter, which, together with abundant rocks and sparse vegetation cover in the Judean Desert, make this ecological system ideal for our study.

2.3. Animal collection and preparation for experiment

We sampled lizards from Nahal Mishmar and Parking Tse'elim River during winter (December-February) and summer (June-August) in 2021 and 2022. A total of 30 lizards were collected (15 males during summer and 15 males during winter) – 13 from Nahal Mishmar and 17 from Parking Tse'elim River. To eliminate the effects of ontogeny or egg production on behaviour, we collected only adult males for our experiments. Overall, the mean mass of all lizards collected was 1.5 grams and ranged from 600 milligrams to 2.2 grams (summer range: 0.6–2.2 g, winter range: 1–2 g). The SVL (snout-vent length) ranged from 32–47.5 millimetres (mm) with a mean of 41.3 mm (summer range: 32–47.5 g, winter range: 36–45.5 g).

Upon capture, each lizard was placed in a 1 m^2 enclosure built from wooden planks (Fig. 1). Three enclosures were set up in the area around Ein Gedi and Nahal Arugot reserves (31°27′39.7″N 35°23′10.8″E) with each including a 40 × 40 cm wide rock and a 40 × 40 cm wide bush, as rocks and bushes are typical features used by the species in their natural habitat (Fig. 1).

Fig. 1. We tracked the microhabitat selection of lizards under semi-natural conditions. Top panel — an example of an arena. Each arena included a rock, a bush, and an open area. Bottom panel — an example of camera footage from within the arena.

To monitor the thermal conditions of microhabitats within the enclosures, we placed miniature iButton temperature loggers (DS1923; Maxim Integrated, San Jose, California, USA) beneath each rock and bush and in the centre of the arena on open ground, covered by a small rock to prevent direct exposure to sunlight. Loggers recorded the temperatures at each location at 10-min intervals throughout the experiment, thus capturing the thermal profiles of the microhabitats available to lizards. All experiments were conducted in compliance with the regulations of the National Parks Authority, under Permit no. 2021/42778.

2.4. Microhabitat choice experiment under semi-natural conditions

At the beginning of each trial, we placed an individual lizard in the middle of the arena and then tracked their activity for 24 h with a motion detection camera (Ltl Acorn, Model: Ltl-5310). To minimize observational effects and give each individual time to habituate (e.g., to reduce records of unnatural behaviours such as attempted escapes from the arena, etc.), we did not use data from the first hour of these videos in either season (Kalyuzhny et al., 2019). Due to the activity time of these lizards (diurnal all year round), we included only recorded daytime activity. The cameras used in this experiment are activated by motion, i.e., start to record only when a movement is detected and then record 1 min of video. Videos recorded due to other movements (e.g., birds flying nearby or wind) were discarded, leaving 855 videos of lizard activity for analysis.

Due to several SD card failures in the cameras, we were able to record activity data for only 25 of the 30 lizards in the experiment. We analysed videos to quantify each lizard's daytime movement patterns, including transitions between microhabitats and time spent in each microhabitat throughout the day. Since the open ground within the enclosures could be directly exposed to the sun or covered by shade cast by the enclosure walls, we recorded whether the lizard was in the open ground under sunny or shaded conditions and excluded shade-covered open areas from our analysis to focus specifically on the influence of temperature on microhabitat selection. We analysed microhabitat selection by individual lizards at 1-min intervals beginning when the lizard was first spotted by the camera and ending when it was last spotted by the camera, omitting data for lizards that were observed for less than 3 h during the 24-h trial. This enabled us to specifically track the lizards' movements between microhabitats, while also accounting for the time spent staying in each one.

We validated the accuracy of the motion-sensing cameras in capturing lizard activity by positioning a handheld gimbal camera (DJI Pocket 2) to a motion-sensing camera within an arena. We then compared the activity patterns of a lizard recorded for 24 h by both cameras, which confirmed that the motion-sensing camera accurately recorded the use of all microhabitats (Appendix S1). However, both cameras only captured activity occurring within the range of the microhabitats and the cameras' field of view.

2.5. Statistical analysis

We fitted a Bayesian hierarchical logistic regression model to examine how microhabitat choice was affected by temperature and previous microhabitat. In the model, microhabitat choice is the response variable, having a multinomial distribution where a lizard can choose between the open, bush, or rock. We included the ground temperature for each modelled microhabitat and the ground temperature at the previously selected microhabitat as continuous explanatory factors, and season (summer or winter) and the previous habitat type (open, bush, or rock) as categorical factors. We also included the interactions between each continuous factor and between the season and the previous microhabitat. To account for repeated measurements taken from the same lizard and enclosures, we included the lizard's ID and arena number as a nested random effect in the model. As in multinomial models, the fixed and random factors were separate for each microhabitat selection. We fitted the model using the PyMC python package (Salvatier et al., 2016), ran it using a No-U-Turn (NUTS) sampler (Homan and Gelman, 2014) with 1000 iterations and 3 chains, and assessed convergence using trace plots, the Gelman–Rubin $\hat{R}$ diagnostic, and the effective sample size. To evaluate the significance of the predictors, we examined the posterior distributions of the coefficients and calculated their 95% credible intervals. A coefficient was deemed significantly different from zero at the 5% level if its credible interval did not overlap with zero. For model selection, we used the backward-stepwise approach, where we iteratively removed terms that were not significant for all microhabitats. For each modelled microhabitat model, we also removed insignificant terms that were related to the conditions in other microhabitats (e.g., the ground temperature of all previously selected microhabitats that were different from the modelled microhabitat).

3. Results

Lizards selected microhabitats differently in winter and summer: preferring to stay in the open during winter and sheltering under rocks and bushes in the summer (Figs. 2, 3).

During winter, microhabitat selection was not significantly related to ground temperatures (Table 1, Figs. 3, 4), and lizards tended to stay within their current bush (95%), open (90%) or rock (94%) microhabitat. For example, winter lizards were only 20% likely to move to the bush from the other microhabitats, 18% likely to move from the rock to the open, and 14% likely to move from the bush to the rock.

During summer, however, ground temperatures significantly influenced lizards' microhabitat selection (Table 1, Figs. 3, 4). Specifically, for every increase by 1°C in ground temperature, lizards were 10% less likely to remain in the open or move into it and 10% or 9% more likely to remain under a bush or rock, respectively, if already there. As in winter, lizards were less likely to move from the open and rock to the bush, and between the bush to the rock, regardless of temperatures.

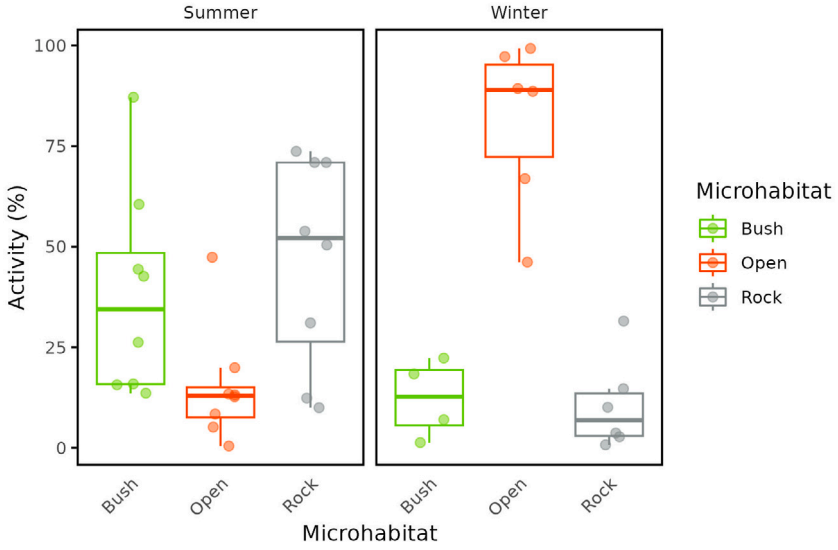

Fig. 2. The percentage of time lizards spent active in each microhabitat across summer (left) and winter (right). Bush is represented by green colour, open ground in red colour and rock in grey colour. Scatter points represent data of individual lizards.

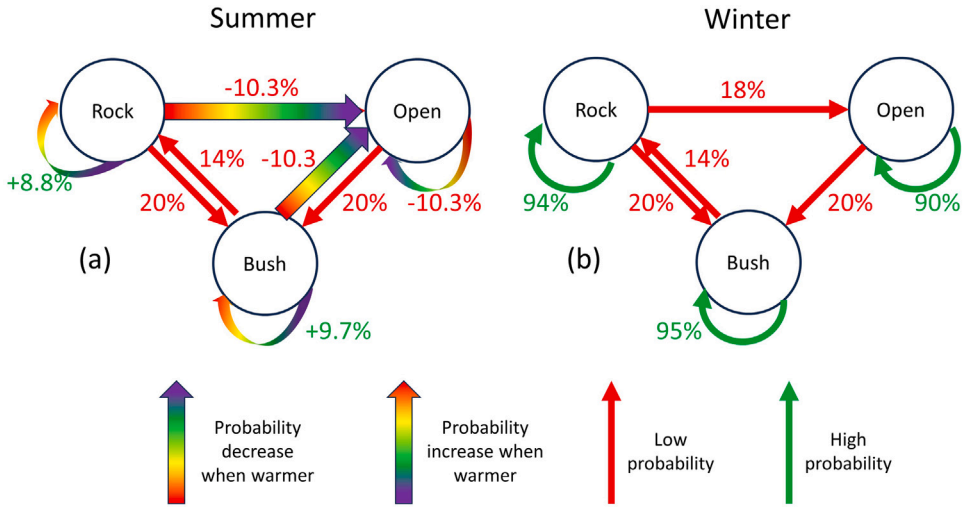

Fig. 3. A lizard's choice of microhabitat was determined by its current microhabitat in both seasons, and by ground temperature in summer. Here, green and red arrows represent a high or low probability of movement between microhabitats, respectively. Gradient-coloured arrows represent a positive (blue to red gradient) and negative (red to blue) effect of temperature on movement, respectively. U-shaped arrows represent probabilities of remaining in the same microhabitat. Numbers near green and red arrows represent the probability of movement between microhabitats. Numbers near gradient-coloured arrows represent the change in the odds of movement per °C increase in temperature.

Table 1
Summary statistics of microhabitat selection for the (a) bush, (b) open, and (c) rock microhabitats. Grey-marked lines represent statistically significant predictors.

(a) bush				(b) open				(c) rock			
Predictor	Mean ± SD	2.5%CI	97.5%CI	Predictor	Mean ± SD	2.5%CI	97.5%CI	Predictor	Mean ± SD	2.5%CI	97.5%CI
Intercept	−0.4 ± 0.7	−1.7	1	Intercept	0.9 ± 0.7	−0.4	2.1	Intercept	−0.4 ± 0.7	−1.7	0.9
T_g	0.1 ± 0.7	−1.3	1.3	T_g	−0.5 ± 0.5	−1.4	0.4	T_g	0.2 ± 0.7	−1.1	1.4
Summer	0.4 ± 0.7	−0.9	1.8	Summer	−0.8 ± 0.7	−2.1	0.5	Summer	0.4 ± 0.7	−0.9	1.8
Summer × T_g	−0.8 ± 0.7	−2.1	0.6	Summer × T_g	−2.5 ± 0.6	−3.7	−1.5	Summer × T_g	−0.1 ± 0.8	−1.5	1.4
P_{bush}	3 ± 0.7	1.7	4.2	P_{bush}	−1.2 ± 0.7	−2.4	0.1	P_{bush}	−1.8 ± 0.7	−3.1	−0.5
P_{open}	−1.4 ± 0.7	−2.7	−0.1	P_{open}	2.3 ± 0.7	1	3.5	P_{open}	−0.9 ± 0.7	−2.1	0.4
P_{rock}	−1.4 ± 0.7	−2.7	−0.1	P_{rock}	−1.5 ± 0.7	−2.8	−0.3	P_{rock}	2.8 ± 0.7	1.6	4.1
P_{bush} × T_g	−0.1 ± 0.7	−1.4	1.2	P_{open} × T_g	0.2 ± 0.5	−0.8	1.2	P_{rock} × T_g	0.7 ± 0.7	−0.5	2.1
P_{bush} × Summer	−1.5 ± 0.7	−2.8	−0.1	P_{bush} × Summer	0.5 ± 0.7	−0.9	1.7	P_{bush} × Summer	1 ± 0.7	−0.4	2.4
P_{rock} × Summer	0.7 ± 0.7	−0.6	2.1	P_{rock} × Summer	0.8 ± 0.7	−0.5	2.1	P_{rock} × Summer	−1.6 ± 0.7	−2.9	−0.3
P_{open} × Summer	1.1 ± 0.7	−0.2	2.4	P_{open} × Summer	−1.2 ± 0.7	−2.5	0.1	P_{open} × Summer	0.1 ± 0.7	−1.2	1.4
P_{bush} × Summer × T_g	1.9 ± 0.8	0.4	3.3	P_{open} × Summer × T_g	−0.8 ± 0.7	−2.1	0.5	P_{rock} × Summer × T_g	1.5 ± 0.8	0.2	3

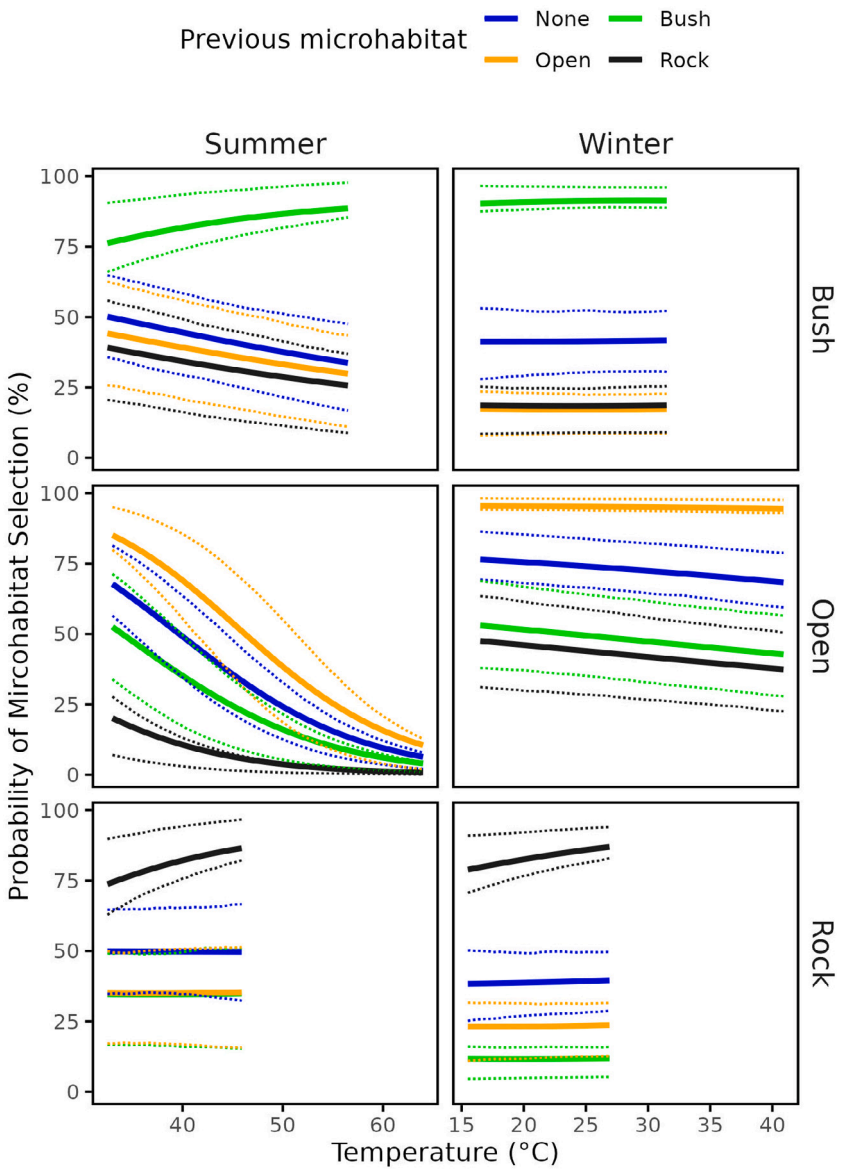

Fig. 4. Microhabitat selection by lizards was determined by ground temperature during summer, but not winter. Here, we show the relationships between ground temperature and microhabitat choice during summer (left panels) and winter (right panels). Solid lines represent model mean estimates, and dashed lines represent the model's 25 and 75 confidence intervals. Blue lines represent the effect of temperature where the previous microhabitat was not considered, while orange, green, and black colours represent the effect of temperature given that lizards were previously under the bush, rock, or in the open, respectively.

4. Discussion

Behavioural thermoregulation is a complex and interactive process, whereby animals continually weigh the ecological and physiological benefits and costs of shuttling between microhabitats. Using camera traps in custom enclosures, we found that shuttling between microhabitats is driven by behavioural thermoregulation in summer but not winter. This suggests that microhabitat selection by lizards in winter is probably shaped by either a relaxation of the benefits of thermoregulation or non-thermal, biotic factors (e.g., predation, food, mating). Importantly, by continuously tracking lizards' movements, we found a novel mobility bias, where lizards preferred to remain in their current microhabitat. This bias was independent of temperature in winter, but had a strong thermal effect during summer. Hence, our study demonstrates how the usage of camera traps in thermal behavioural studies of lizards can improve our knowledge of the temporal and spatial patterns of microhabitat use and the complex interactions between animals and microhabitats. Under climate change, this knowledge may be a critical step for developing better conservation plans and effective mitigation strategies.

In our study, seasonality played a significant role in the thermal biology of desert lizards. Similar outcomes have been shown in other lizard species (Huey and Pianka, 1977; Bauwens et al., 1996; Ortega and Pérez-Mellado, 2016). The substantial seasonal variation in lizard movements emphasizes the behavioural flexibility of lizards to adapt to standard climatic variation across the year (Grover, 1996; Ortega and Pérez-Mellado, 2016; Žagar et al., 2023; Huey and Pianka, 1977; Ortega et al., 2014). The driving forces behind this variation appear to differ between summer and winter. During summer, lizard behaviour was shaped by ground temperature across the arena, i.e., lizards sought shelter under rocks (and sometimes bushes) most of the daytime when temperatures were highest. During winter, however, lizards preferred to stay in whichever microhabitat they were in for a lengthier period, and in general preferred open ground to shaded microhabitats. Thus, microhabitats may serve different roles across seasons, as suggested in previous studies for this species (Stark et al., 2022, 2023), serving

as a thermal refuge in one season and take up other roles in another, such as protection from predators under rocks (Marshall et al., 2016; Chukwuka et al., 2021), proximity to food sources (e.g., ants or termites; Orr et al., 1979), or mating opportunities (Amo et al., 2007). Thermoregulation should also be considered in light of the thermal heterogeneity of the environment (Huey and Slatkin, 1976; Angilletta, 2009). For example, in a previous study (Stark et al., 2023), we found that lizards decreased the range of temperatures that enable activity during winter. This adaptive ability enables activity during the relatively cold winter season. Stark et al. (2023) also showed that winter temperatures are relatively uniform across microhabitats, and that activity is possible only in the open, since it enables warming through basking.

As lizards select when and where to move, they aim for the microhabitats that provide favourable abiotic and biotic conditions (in our case, either rocks, bushes, or open ground) (Belliure and Carrascal, 2002; Žagar et al., 2023). However, there is a dynamic tradeoff between staying at the current microhabitat and moving to another one (Basson et al., 2017; Rusch and Angilletta, 2017). On one hand, movement between microhabitats poses energetic or biotic costs, as energy is required for activity (Brewster et al., 2013; Basson et al., 2017) and exposure during movement may increase predation risk (Huey and Slatkin, 1976; Villén-Pérez et al., 2013). On the other hand, staying in the same location increases missed opportunity costs, such as finding food sources and defending territories (Basson et al., 2017). Our results show that lizards prefer to stay in their current microhabitat, even in the exposed open microhabitat, which may indicate that energetic savings are an important driver of behaviour in this species. We are not sure why lizards tended to move less between some microhabitats (see Fig. 3). For example, lizards were less likely to move to the bushes from both the open and rock microhabitats. This may happen due to predators of lizards hiding under bushes (Smith and Ballinger, 2001b; Martín et al., 1998; Vanhooydonck and Van Damme, 2003). In a previous study, we found that the positive effect of bushes on the body condition of lizards may be more indirect, as lizards' body condition was higher even when bushes were outside their home ranges (Stark et al., 2022); bushes may attract insects and other prey for the lizards (Johnson, 2000; Borkhataria et al., 2012). On the other hand, the benefits from rocks are more direct, through conductive heat transfer, shade, and cover from predators. Such insights are important for accurately predicting threats and mediating habitats for ectotherms as climates change, and underscore the importance of considering seasonal variation in animal behaviour and, thus, conservation strategies.

Although there are many advantages of using camera traps in studies of ectotherm behaviour, this technology has yet to be widely adopted in studies of reptile ecology (Welbourne et al., 2015; Richardson et al., 2017), which typically rely on models based on temperature loggers rather than observations of lizards in semi-natural or natural conditions (Camacho and Rusch, 2017). Although other technologies such as acceleration loggers can be used to capture animal movements in the wild, these devices are still limited to large-sized reptiles such as the Burmese python (*Python bivittatus*) (Whitney et al., 2021) or the Snapping Turtle (*Chelydra serpentina*) (Rollinson et al., 2019). Currently, for smaller species, camera traps may serve as a powerful method for ecological research (Broeckhoven and le Fras Nortier Mouton, 2015; Hobbs and Brehme, 2017). Ultimately, incorporating camera trap data with other technologies (e.g., IR cameras, accelerometers, Artificial Intelligence modelling) will enable researchers to more accurately evaluate the microhabitat choices of species, analyse the importance of various microhabitats in natural ecological systems and better target them for conservation programs (Angilletta et al., 2009; Fleming et al., 2014; Hobbs and Brehme, 2017).

Future studies should explore the complex interaction between thermoregulation and movement preferences. Although we found a strong effect of temperature and current location on the movement of lizards, other factors – including competition or predation risk (Rusch and Angilletta, 2017; Black et al., 2019) – must be considered in models of lizard microhabitat choices and, thus, for species' conservation. Thermoregulatory behaviour and microhabitat choices are also likely to vary with life stages, sex, female reproductive condition, and state of hydration (Angilletta, 2009), so incorporating life history and physiological state into future experiments will increase our understanding of and ability to predict lizard behaviour. Moreover, long-term studies, such as those spanning across seasons, would more accurately capture the thermal preferences, movements, or microhabitat choices for this species. Finally, studying the natural behaviour of animals in small enclosures with cameras may simplify the biotic and abiotic conditions facing animals and constrain their behaviour. Thus, there is a need to find better methods of tracking animals in their natural environments while avoiding limiting methodologies that may change their behaviour. Regardless of these caveats, our study points to novel, understudied phenomena of microhabitat choice, such as the complex interactions between the current location and temperature.

In conclusion, our study demonstrates that – as was suggested in previous studies (Stark et al., 2022, 2023) – both rocks and bushes are important microhabitat resources for this species, differing in importance across seasons. Temperature significantly affected microhabitat choice only during summer, indicating that the thermal characteristics of microhabitats may only be useful for predicting habitat use during more thermally challenging periods. As such conditions may be more frequent and extreme under climate change, such knowledge can help formulate appropriate management plans for many threatened taxa (Scheffers et al., 2014), enabling conservation or habitat restoration programs to prioritize microhabitats in ways that effectively mitigate the negative effects of rapid temperature increases (Stark et al., 2023). Research and efforts are urgently needed in desert areas, where increasing extreme heat events are pushing desert species beyond their physiological limitations faster than animals living in different habitats (Sinervo et al., 2010; Vale and Brito, 2015), resulting in population declines (Iknayan and Beissinger, 2018; Riddell et al., 2021). Studies of the complex thermal, biotic, and abiotic drivers of animal movement will facilitate the integration of specific microhabitats into conservation planning, preserving refuges that will sustain lizards and other species living in this extreme ecosystem (Davis et al., 2013; Vale and Brito, 2015; Bachelet et al., 2016; Shi et al., 2016).

CRediT authorship contribution statement

Gavin Stark: Conceptualization, Data curation, Formal analysis, Visualization, Writing – original draft, Writing – review & editing. **Liang Ma:** Writing – review & editing. **Zhi-Gao Zeng:** Writing – review & editing. **Wei-Guo Du:** Writing – review & editing. **Ofir Levy:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Methodology, Project administration, Supervision, Visualization, Writing – original draft, Writing – review & editing.

Declaration of competing interest

There are no competing interests among all authors for this manuscript.

Data accessibility statement

Data and code can be found in https://github.com/levyofi/Stark_et_al_JTB_2024.

Acknowledgements

We are thankful to Rachel Schwarz, Ben Shermeister, Omer Ben-Zohar and Simon Jamison for their help in the collection of animals, assemblage of the arenas in the field and constructive discussion. The research was funded by the Israel Science Foundation (300/22) and the Joint Program between the Israel Science Foundation (ISF) and the National Natural Science Foundation of China (NSFC) [1276/19].

Appendix A. Supplementary data

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.jtherbio.2024.103841.

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