



# Temperature-based activity estimation accurately predicts surface activity, but not microhabitat use, in the Endangered heliothermic lizard *Gambelia sila*

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**Abstract.**—With the existence of many endangered terrestrial ectotherms now being threatened in the face of climate change, effective tools to aid in the management of their conservation are necessary. Temperature-based activity estimation (TBAE) is an automated method for predicting surface activity and microhabitat use based on the temperature of an organism and its habitat, and TBAE may be used to reduce the monitoring effort for sensitive species. However, its efficacy has not been assessed in heliothermic species. We hypothesized that heliotherapy would facilitate the accurate prediction of surface activity due to the rapid changes in temperature effected by exposure to solar radiation, but that TBAE would not accurately predict microhabitat use because heliothermic lizards shuttle too frequently among microhabitats. In this study, we assessed how well ambient air temperature and lizard physical model temperature predicted surface activity and microhabitat use of a federally-listed Endangered lizard, Blunt-nosed Leopard Lizard, *Gambelia sila*, by comparing these variables to continuously logged active lizard body temperatures in the field. While surface activity was correctly predicted 93% of the time using either ambient or physical model temperatures, the accuracy in predicting microhabitat use only ranged from 47–72%. Finally, TBAE allowed us to predict the time of morning emergence from burrows to within approximately 11 minutes. TBAE is a promising means for remotely monitoring surface activity and morning emergence of heliotherms, however its utility in distinguishing microhabitat use in heliotherms is limited.

**Keywords.** Automated data collection, microhabitat selection, Reptilia, surface activity, TBAE

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## Introduction

Refugia constitute a major resource for terrestrial organisms because they provide protection from predators (Martin and López 2004; Manicom et al. 2008) and escape from extreme temperatures (Schwarzkopf and Alford 1996; Polo et al. 2005), and can buffer animals from extreme aridity and precipitation events (Bulova 2002; Burda et al. 2007; Ivey et al. 2020). However, essential behaviors like mate-searching and feeding typically require surface activity, which can be problematic for xerophilic animals due to the especially harsh conditions they often encounter on the surface (Martin and Pilar 1999; Krause et al. 2000; Webb and Whiting 2005; Amo et al. 2007; Davis et al.

2008; Munguia et al. 2017). Animals that inhabit arid environments are at risk of extinction due to the increased temperatures and longer periods without precipitation associated with climate change (Archer and Predick 2008; Barrows 2011), and such conditions force these animals to seek refuge more frequently and potentially reduce their ability to obtain resources (Buckley et al. 2015; Grimm-Seyfarth et al. 2017). Heliothermic (sun-basking) lizards are particularly at-risk (Sinervo et al. 2010) because they already thermoregulate at high temperatures (Cowles and Bogert 1944; Huey 1982), and further increases in ambient temperatures will force them into refugia. Heliothermic lizards typically have limited plasticity in their thermal tolerance (Gunderson and Stillman 2015). Because they are so adept at behavioral

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thermoregulation by shuttling among the sun, shade, and refugia, they have a low potential for adapting to higher temperatures (Huey 1982; Huey et al. 2003; Angilletta 2009; Muñoz and Losos 2018). Therefore, heliothermic lizards are excellent candidates for studying how shifts in climatic events will impact organisms that rely on their thermal environment and for understanding how we can use temperature to model their activity.

A direct approach for studying how climate change influences vulnerable ectotherms relies on robust methods for collecting continuous data on body temperature and microhabitat use, but continuous sampling of small, heliothermic lizards is logistically challenging. Most of these studies employ the “grab and jab” technique, in which a lizard is captured, and a point sample of its body temperature is collected using a cloacal thermometer (Taylor et al. 2020). However, point-sampling of body temperature is highly biased in that it provides a small number of data points which only reflect those time periods in which animals are active and accessible (Taylor et al. 2004). Furthermore, tracking small individuals over time is difficult due to limitations in radio-transmitter size and battery life. Even in cases where telemetry is possible, tracking these animals on a regular basis over time presents financial and logistical challenges. Researchers might be able to accurately predict activity and microhabitat use based on body temperature data for small, heliothermic lizards in arid, hot environments if those data can be collected continuously and subjected to robust validation. Temperature-based activity estimation (TBAE) has been tested in two large-bodied reptiles, a lizard and a snake (Davis et al. 2008). The use of TBAE allowed researchers to predict surface activity 96% of the time in the Gila Monster (*Heloderma suspectum*), which forages actively on the surface, but only 66% of the time in the Western Diamond-backed Rattlesnake (*Crotalus atrox*), which tends to hide in the shade and therefore thermoconforms more than the Gila Monster. In this study, we investigated whether TBAE could be used to successfully predict not just surface activity, but also microhabitat use, in a smaller, heliothermic lizard.

In this study, the efficacy of TBAE for estimating surface activity and microhabitat use was assessed in the Bluntnosed Leopard Lizard (*Gambelia sila*), a federally-listed Endangered lizard found in a few isolated populations in the hot and arid San Joaquin Valley and Carrizo Plain in California, USA (IUCN 2017; Germano and Williams 2005; Germano and Rathbun 2016; Stewart et al. 2019). Substantial financial resources are invested annually in studying this species in order to inform management plans for its protection and recovery. *Gambelia sila* may be dramatically impacted by climate change in the coming years (Ivey et al. 2020), although these lizards may be able to shift their activity patterns to mitigate warming (Germano 2019). Nevertheless, documenting the thermal ecology and activity patterns represents an essential component in the continued assessment and

management strategy of *G. sila* as federal managers seek to understand how rising temperatures, drought, and other stressors impact lizard behavior, health, and recruitment. We tested the hypothesis that TBAE can accurately predict surface activity in a heliotherm, because of the rapid change in temperature effected by exposure to solar radiation when the lizards emerge from burrows, but that it will be less robust in predicting microhabitat use because heliothermic lizards shuttle frequently among microhabitats. To test this hypothesis, we evaluated three key predictions: (1) TBAE accurately predicts whether a lizard is underground or surface active, (2) the accuracy of TBAE in distinguishing microhabitat use (open sun, shade of plant, or inside burrow) is lower than in identifying surface activity, and (3) TBAE accurately predicts the time of day that a lizard first emerges from its overnight refugium.

## Materials and Methods

### Study Species and Sites

This study took place in the Elkhorn Plain in the Carrizo Plain National Monument, California, USA, at two different sites. The first site (“shrubbed”) has sparsely distributed *Ephedra californica* shrubs throughout the terrain (35.117998°, -119.629063°), while the second site (“shrubless”) lacks *Ephedra* shrubs or any other permanent ground cover and is located 6.1 km SW of the shrubbed site (35.0891800°, -119.5750100°). The Elkhorn Plain experiences arid summers (average high 30–40 °C) and cool winters (average low 5–9 °C, Raws USA Climate Archive, <https://raws.dri.edu/index.html>, accessed: 13 September 2019). Both sites are dominated by Giant Kangaroo Rat (*Dipodomys ingens*) precincts with extensive burrow networks that provide important refugia for *G. sila* (Ivey et al. 2020). TBAE analyses of surface activity and microhabitat use were performed using data from the shrubbed site in 2018, and analyses of the timing of morning emergence were performed using data from both sites in 2019.

Adult *G. sila* were captured by a hand-held lasso in early May 2018 at the shrubbed site ( $n = 30$ ), and in late April/early May 2019 at the shrubbed ( $n = 20$ ) and shrubless ( $n = 20$ ) sites. Lizards were fitted with VHF temperature-sensitive radio-transmitter collars (Holohil model BD-2T, Holohil Systems Ltd., Carp, Ontario, Canada) following the methods of Germano and Rathbun (2016). The collars weighed approximately 1.5 g and never exceeded 5% of a lizard’s body mass. We recorded standard morphometrics (mass, SVL, sex, gravidity, and tail length), released lizards at their sites of capture, and subsequently tracked lizards 1–3 times per day using a VHF receiver and a Yagi antenna (R-1000 Telemetry Receiver, Communications Specialists, Inc., Orange, California, USA). Observations were taken daily between 0700 and 1900 h, for a total of 147 observations

for all 30 lizards. During each tracking event, behavioral observations, microhabitat description, GPS coordinates, and a timestamp were recorded. In mid-July (the end of their active period), the lizards were recaptured, the radio-transmitters were removed, and the lizards were released at their location of capture to allow estivation for the remainder of the summer.

### **Body Temperature ( $T_b$ )**

The body temperature ( $T_b$ ) of each lizard was continually recorded (every ~5–10 minutes) as the temperature of the radio-collar via relay to a Telonics TR-5 receiver with a data acquisition system (Telonics Option 320) and ~3-m tall omni antenna (Telonics model RA-6B). The transmitters record surface temperature and not core  $T_b$ , so the recorded temperatures will change more rapidly upon exposure to solar radiation than they would using surgically implanted transmitters. We programmed the system to log the interpulse intervals for each radio-transmitter about every 10 minutes, and used the manufacturer-provided calibration equations to convert interpulse intervals to surface  $T_b$ .

### **Characterizing the Thermal Habitat: Air Temperature and Physical Models**

The thermal habitat at the shrubbed site was characterized in 2018 using two methods: air temperatures and the temperatures of physical models. First, mean hourly data were downloaded from the RAWs weather station at Cochora Ranch (station ID: CXXC1), 3.7 km due east of the shrubbed site, and used as a proxy for air temperature ( $T_{air}$ ). Second, physical models were deployed from 1–19 July 2018 ( $n = 6$  in the sun,  $n = 6$  in the shade of *Ephedra* shrubs, and  $n = 6$  in burrows) following the methods of Ivey et al. (2020). Briefly, the models consisted of 1 inch (2.5 cm) diameter copper pipes fitted with a Thermochron iButton (DS1921G-F5) that was programmed to record the temperature every 10 minutes. The pipes were filled with water and secured with PVC caps screwed onto the male copper ends. The total length of the model was 15.3 cm. The models placed above ground were fitted with “legs” made from copper wiring to prop them onto one end, mimicking a basking lizard. The models placed in burrows did not have legs.

### **Temperature-Based Activity Estimation (TBAE)**

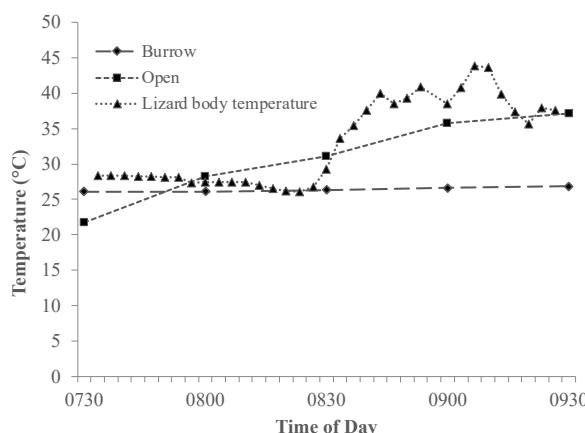
First, the difference between  $T_{air}$  and  $T_b$  was used to predict when a lizard was surface active or below ground. When lizards are above ground, their  $T_b$  often exceeds  $T_{air}$  as they bask in the sun, and this difference equals the “positive temperature differential.” Positive temperature differentials of 2, 4, 6, 8, 10, 12, and 14 °C were tested to determine which differential best predicted when the lizards were surface active. A solo researcher created a

spreadsheet with the  $T_b$  of each lizard at each of its radio-telemetry observations along with data on its activity (above or below ground). The “IF THEN” function in Microsoft Excel was used to predict whether the animal was above or below ground based on the positive temperature differential. For example, if  $T_b$  was above  $T_{air}$  by 2 °C, then the lizard was predicted to be above ground; if not, it was predicted to be below ground. After making the predictions, the predicted and actual data were merged to examine how the various positive temperature differentials impacted the accuracy of the predictions.

Next, the temperatures of the physical models were used to estimate microhabitat use and surface activity. We did not use  $T_{air}$  because we expected the temperatures of the physical models in the various microhabitats to be much more relevant to these variables (Dzialowski 2005). The average hourly temperatures of each physical model (sun, shade, burrow) during the active hours of *G. sila* (0700–1900 h) were plotted against each lizard’s  $T_b$  on the same day, and a researcher blind to the lizard’s actual microhabitat predicted its microhabitat based on three criteria (modified from Davis et al. 2008). (1) Lizards were predicted to be in the open if their  $T_b$  was equal to or higher than the temperature of the models in the open. (2) Lizards were predicted to be under shrubs if their  $T_b$  was equal to or higher than the temperature halfway between those of the models in burrows and under shrubs, but lower than models in the open. (3) Lizards were predicted to be in burrows if their  $T_b$  was lower than the temperature halfway between the models in burrows and under shrubs. The predictions of lizards in the open and under shrubs were combined to constitute total above-ground predicted activity, and the predictions of lizards in burrows constituted below-ground predicted activity. Next, the blind predictions were compared to the actual observations, and the proportions correctly predicted were calculated. A two-proportion Z-test in JMP (SAS Institute, Cary, North Carolina, USA, version Pro 14) was used to compare the efficacies of the two methods of TBAE ( $T_{air}$  versus the physical models) for predicting above- and below-ground activity.

### **Predicting Emergence Time**

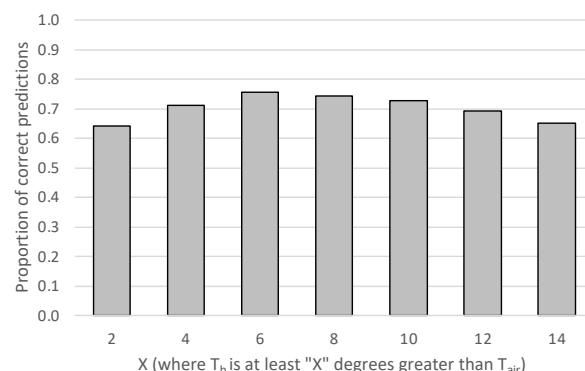
In 2019, new sets of physical models were deployed ( $n = 4$  in the sun,  $n = 4$  in burrows) at both the shrubbed and shrubless sites. The data for *G. sila*  $T_b$  and the physical model temperatures were used to predict the morning emergence time of lizards at each site. Each day from 23 June to 14 July 2019, two lizards were randomly selected as focal animals. Before dawn, each of two researchers radio-tracked one focal animal and waited at least 4 m away from the lizard’s burrow with binoculars trained on the burrow entrance. The emergence time was recorded in two ways: (1) the time of day when the lizard’s head was first visible emerging from the burrow, and (2) the time of day when the lizard’s entire body and tail had



**Fig. 1.** Methodology used to predict morning emergence time of *Gambelia sila*. Emergence was predicted as the time of day immediately preceding a distinct upward slope in the lizard's  $T_b$  (triangles and dotted line) based on the assumption that it would take several minutes for the radio transmitter to heat in the sun. The rising  $T_b$  was also typically associated with the departure from the burrow physical model temperatures (diamonds and long-dashed line) and the approach of the open (sun) physical model temperatures (squares and short-dashed line). In each case, the predicted time was then compared to the observed emergence time when the lizard's head first appeared outside its burrow. The average difference between observed and predicted emergence times was 11 minutes and 37 seconds.

emerged from the burrow. At the study sites, the June and July conditions are extremely hot and arid, and sometimes the lizards did not emerge from their burrows at all. If a lizard did not emerge by the time  $T_{air}$  reached 29.5 °C (since the optimum temperature for this species' activity is from 25–35 °C; CDFW 2019), the observation was abandoned, and that lizard was not included as a data point. These observations took place at both the shrubbed ( $n = 10$  lizards) and shrubless ( $n = 10$  lizards) sites. Two lizards observed at the shrubbed site were too far from the receiver array for associated  $T_b$  data to be collected, so the final sample for TBAE was 18 individual lizards (with no repeat observations).

To predict emergence time using TBAE, a researcher blind to a lizard's actual emergence time plotted the lizard's  $T_b$  data and the lizard physical model temperatures from that site for the duration of an emergence observation, and then predicted the lizard's emergence time as the time point immediately preceding a distinct increase in the slope of  $T_b$  (Fig. 1). The predicted emergence times were then compared with the observed emergence times, and the absolute value of the difference in predicted and observed emergence times (for each emergence criterion, i.e., head and entire body) was calculated. This value (in minutes) represents how close the predicted emergence time was to the actual emergence time. Observed emergence times (minutes after sunrise) of all lizards observed ( $n = 20$ , head only and full body) were compared between the shrubbed and shrubless sites using a Student's *t*-test, and all data were normally distributed and had homogenous



**Fig. 2.** Proportions of correct predictions using air temperature to predict surface activity versus below-ground refuge use of *Gambelia sila*. This method resulted in accurate predictions 64–76% of the time among the various temperature differentials shown on the x-axis. Predictions were maximized (76% correct) using the criterion that lizards are above ground when their body temperatures ( $T_b$ ) are at least 6 °C above the air temperature ( $T_{air}$ ).

variances. The sample size for head emergence was 20 and for full emergence it was 18 (since two lizards failed to fully emerge from their burrows after 1 h).

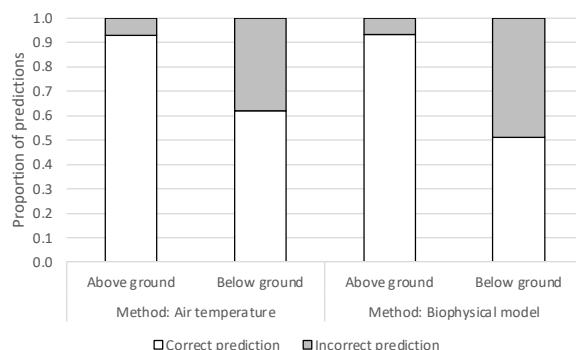
## Results

### Temperature Based Activity Estimation (TBAE)

The proportions of observations of *G. sila* correctly predicted to be above ground based on the criteria that  $T_b$  is at least  $X$  °C (where  $X = 2, 4, 6, 8, 10, 12$ , or 14 °C) above  $T_{air}$  ranged from 0.64 (for 2 °C) to 0.76 (for 6 °C). Thus, surface versus below-ground activity was correctly predicted 76% of the time when using the criterion that the lizards are above ground if  $T_b$  exceeds  $T_{air}$  by at least 6 °C (Fig. 2), and so a 6 °C differential was used in the subsequent analysis of the efficacy of TBAE based on air temperature for predicting surface activity.

In using TBAE to predict surface activity versus burrow occupancy, the calculation based on  $T_{air}$  (75.7% correct overall) was superior to the calculation based on the physical models (60.5% correct overall,  $Z = 3.43$ ,  $p = 0.0003$ ; Fig. 3). There was no significant difference in the accuracy of above-ground predictions using the two methods, as observations predicted to be above ground were correct about 93% of the time for both methods ( $Z < 0.001$ ,  $p = 1.00$ ). A significant difference was evident in the proportions of successful predictions for below-ground observations, with  $T_{air}$  (62% correct) significantly outperforming physical models (51% correct,  $Z = 1.78$ ,  $p = 0.037$ ). Predicting activity based on the physical models overestimated the time above ground specifically by misidentifying many lizards as being in the open when they were actually in burrows.

Of the 147 radio-telemetry fixes in 2018, 114 (77.6%) were in burrows, 19 (12.9%) were under shrubs, and 14 (9.5%) were in the open in the sun. Figure 4 shows the



**Fig. 3.** Temperature-based activity estimation resulted in accurate prediction of above-ground activity by *Gambelia sila* more often than accurate prediction of below-ground (burrow) occupation. Using air temperature ( $T_{air}$ ) was superior to using physical model temperatures when predicting below-ground occupation. For both methods, ~93% of observations predicted to be above ground were correct, whereas 62% (using  $T_{air}$ ) and 51% (using physical models) were correct for below-ground predictions.

relative success of predicting microhabitat use based on the physical model data. When lizards were observed in a given microhabitat, TBAE correctly predicted they were in that habitat with varying accuracy (79% correct when in the open, 47% when under shrubs, and 51% when inside burrows).

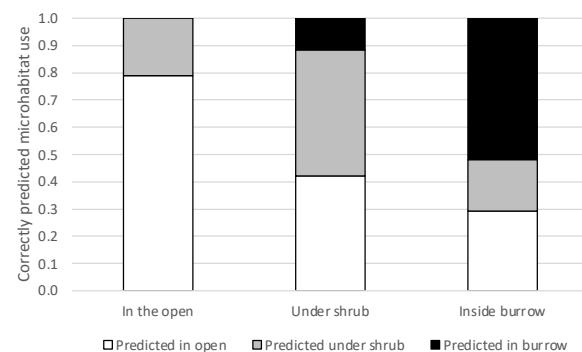
### Predicting Emergence Time

In summer 2019, lizards began emerging (head out of burrow) at about 0745 h (with no difference between shrubbed and shrubless sites in emergence time as minutes after sunrise:  $t_{18} = 1.28, p = 0.22$ ), and were fully emerged (body and tail out of burrow) by about 0813 h (lizards at the shrubless site tended to emerge later than lizards at the shrubbed site:  $t_{16} = 2.11, p = 0.05$ , Fig. 5). The difference between the predicted emergence and observed emergence (head out of burrow) was  $11:37 \pm 01:57$  (min:sec). Of the 18 observations, eight were underestimations of predicted emergence time and 10 were overestimations. The difference between the predicted emergence and observed full emergence was  $27:00 \pm 02:31$  (min:sec). Of the 18 observations, all predictions underestimated the time of the full emergence of the lizards.

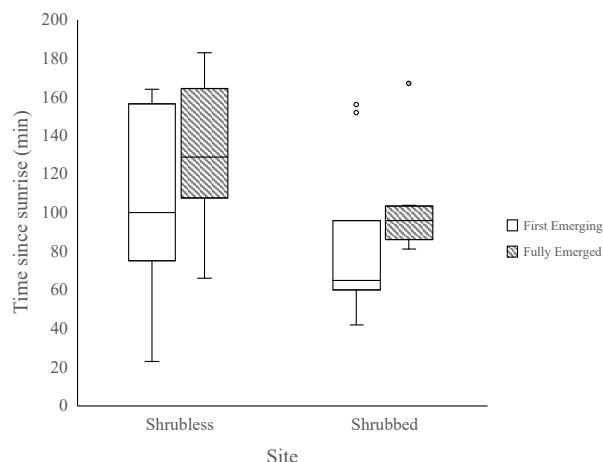
### Discussion

#### The Use of TBAE

A central goal of radio-telemetry monitoring studies is to quantify surface activity and microhabitat use in sensitive species like *G. sila* (e.g., Westphal et al. 2018), and determine how they are impacted by abiotic conditions such as weather and biotic variables such as prey abundance, predator behavior, and others (Germano and Williams 2005). Here we have shown that TBAE



**Fig. 4.** Proportions of correctly predicted observations of microhabitat use of *Gambelia sila* using temperature-based activity estimation based on physical model temperatures. Lizard microhabitat use was predicted correctly most often when they were in the open, but overall microhabitat use was not accurately predicted with TBAE in this heliothermic lizard.



**Fig. 5.** *Gambelia sila* emergence times (minutes after sunrise) at two field sites (shrubless and shrubbed). Initial emergence (head out of burrow) time did not differ between shrubbed and shrubless sites, while lizards at the shrubbed site tended to fully emerge (whole body and tail) earlier than lizards at the shrubless site.

correctly estimates surface activity 93% of the time for *G. sila*, a value very similar to the 96% accuracy rate obtained for TBAE of the Gila Monster by Davis et al. (2008). Both *G. sila* and the Gila Monster are active foragers, so they are likely to be exposed to a range of environmental temperatures as they forage, which can alter their  $T_b$  enough in comparison to their underground refugia to facilitate TBAE. Furthermore, since *G. sila* are heliothermic lizards, and because we used external radio-transmitters, their exposure to solar radiation should further help distinguish their surface-active  $T_b$  from their  $T_b$  when inside burrows (Stevenson 1985; Xiang et al. 1996). In contrast, TBAE failed to predict surface activity as accurately in an ambush-foraging rattlesnake (66% accuracy, Davis et al. 2008) because its body temperature in the shade of its ambush site was not sufficiently distinguishable from its body temperature inside a refugium. Therefore, TBAE is a potentially

valuable method for researchers interested in estimating surface activity of actively foraging species that are expected to be exposed to relatively high temperature variations in their environment.

The value of TBAE lies in its use of  $T_b$  data that are collected by an automated system, and therefore it does not require direct researcher sampling. In other words, researchers could deploy radio-transmitters on lizards to radio-track them as needed for the goals of a particular study, but allow TBAE to collect the data necessary for estimating surface activity. This could significantly save on time and resources by reducing personnel investment in radio-telemetry. An alternate method for collecting data on animal surface activity uses light level geolocators, which record the intensity of blue light (Wilmers et al. 2015) primarily as a means of tracking migration in birds (Lisovski et al. 2019), but they can also be externally attached to lizards (Refsnider et al. 2018) or other terrestrial wildlife to log diel exposure to light. The choice between TBAE and light level geolocators will depend on the goals and budget of the study, the secrecy and recapture rate of individuals of the species under investigation, and other factors. One advantage of TBAE over light level geolocators is that  $T_b$  data are collected continually by an automated receiver in TBAE, whereas geolocator tags must be retrieved from the animals so the data can be downloaded (Lisovski et al. 2019). Thus, any animals lost (e.g., to predation) represent lost data. Furthermore, in most studies on rare species such as *G. sila*, researchers would probably already be using radio-telemetry to facilitate repeated observations of known individuals, so it would generally be simpler and far less expensive to choose temperature-sensitive radio-telemetry over light level geolocators. On the other hand, light level geolocators would work very well for recording surface activity in systems where they could be feasibly attached to a large sample of animals with a high recapture rate.

In this study, TBAE was not as accurate when predicting below-ground activity. This limitation was primarily because TBAE misidentified certain observations as being “in the open” when the lizards were actually in burrows. Heliothermic lizards like *G. sila* maintain their  $T_b$  within a narrow range, typically within or near their laboratory-measured preferred  $T_b$  range, by shuttling between sun and shade (Lortie et al. 2015; Westphal et al. 2018; Germano 2019; Ivey et al. 2020). When a lizard moves from the sun into a burrow, its measured  $T_b$  could remain more than 6 °C above  $T_{air}$  or the physical model temperature for a short period of time; so, if such a lizard is tracked within that period of time, then TBAE would incorrectly assign it as being above ground. TBAE correctly predicted below-ground activity 62% of the time when using  $T_{air}$  and 51% of the time when using the physical models.

We had expected that the physical models would be more accurate than  $T_{air}$  because the models were in

the exact same field sites and mimic the size and shape of lizards to facilitate realistic heat exchange with the environment, whereas  $T_{air}$  data merely represent the air temperatures from a nearby weather station. The fact that  $T_{air}$  was a better estimate could be the result of several factors. First, predictions made using  $T_{air}$  have only two possible categories: above or below ground. In contrast, predictions made using physical model temperatures have three categories (open, shrub, and burrow), with open and shrub predictions then combined into above-ground predictions. In the latter case, predicting “shrub” use for a lizard that was actually underground because its temperature was intermediate between the two other options could result in overprediction of above-ground activity; whereas if the only options were assigning it to above or below ground, it may have been accurately assigned as below ground. In other words, if only above or below ground categories had been assigned using physical models like for  $T_{air}$ , then the two methods may have provided more comparable predictions. Alternatively, the lower accuracy of the physical models may reflect model design and radio-transmitter construction. Our radio-transmitters were on collars and therefore measured external temperature, not the deep  $T_b$  of the lizards, so the temperatures should change rapidly upon exposure to the sun. In contrast, our physical models were constructed with internal data loggers immersed in water, which would introduce a lag time for temperature changes due to high thermal inertia (Porter and Gates 1969). Additionally, the Giant Kangaroo Rat burrows used by the lizards are complicated in terms of depth, chamber size, and soil type, likely creating a labyrinth of thermal heterogeneity underground (Kay and Whitford 1978), and that heterogeneity is not captured by our physical models placed 1 m inside the burrows. The superior performance of  $T_{air}$  is good news because it means that researchers can simply download data from a nearby weather station rather than constructing physical models, and  $T_{air}$  data collected from a mini weather station deployed at the actual field site could provide even more accurate data. In summary, TBAE using  $T_{air}$  as a reference is a highly accurate means of estimating surface activity, but its ability to predict when lizards are underground during daytime hours is more limited.

### Microhabitat Use Predictions

To predict microhabitat use (burrow, shade, or open), TBAE using physical models accurately predicted 79% of the observations when the lizard was in the open (sun), 47% of the observations in the shade, and 51% of the observations inside the burrows. Of the observations for *G. sila* in the open, 100% of all predictions were above ground (79% correctly predicted as in the sun and 21% incorrectly predicted as under the shade of a shrub) and in no case was a lizard predicted to be underground. The accuracy of predictions for shade and burrows were

lower, probably for several reasons. First, as described above, *G. sila* shuttle among these three microhabitats regularly (Ivey et al. 2020), and an animal's temperature at a given radio-telemetry fix could be impacted by the microhabitat it occupied shortly before being observed. Second, the temperatures of the physical models in the shade and in burrows are necessarily more similar to each other than either is to the temperature of models in the open that are exposed to solar radiation, so errors in assigning shade or burrow microhabitat in TBAE are expected (Fig. 4). Our results suggest that accurate records of microhabitat use of heliothermic animals like *G. sila* require in-person radio-telemetry, as TBAE does not provide sufficiently accurate predictions.

The beginning of lizard emergence in the morning was predictable to within roughly 11 minutes, which supports the utility of TBAE as a means of remotely collecting data on the timing of morning emergence. Lizards at the shrubbed and shrubless sites began to emerge at approximately the same time, and lizards at the shrubbed site fully emerged slightly earlier in the day than lizards at the shrubless site. In the absence of shade-providing plants, lizards at the shrubless site may be more reliant on the protection offered by their overnight burrows than lizards at the shrubbed site, which can take advantage of shrubs for thermoregulation and protection from avian predators (Ivey et al. 2020). Lizards began emerging from burrows at about 0745 h and were fully emerged by 0830 h. These times agree with those reported by Germano (2019), who compiled data on the times at which lizards are active throughout the active season. These data are informative for practical use by managers; for example, California Department of Fish and Wildlife recently revised its guidelines for *G. sila* protocols based on these emergence times (CDFW 2019). As midday temperatures increase due to climate change, lizards may begin to emerge earlier in the morning, retreat to burrows earlier in the afternoon, and rely more heavily on plants for shade (Germano 2019), which could potentially buffer *G. sila* from experiencing the rising temperatures. Conducting TBAE annually would allow the testing of this prediction with reliability and with less effort than that required to radio-track lizards at dawn each day.

While animals must and should still be radio-tracked to obtain data relevant to the particular question being asked in a study and to validate TBAE and further delineate its limitations (as we have done here), adding TBAE to a radio-telemetry project could substantially improve inferences about animal activity patterns and microhabitat use while minimizing researcher effort and expense. For example, researchers could radio-track every other day or every third day, rather than the 2–3 times per day that is typical in studies of *G. sila*. To gain further insight into how abiotic factors like ambient temperature impact our ability to remotely predict activity and microhabitat use, TBAE in *G. sila* should be evaluated over the course of the season over multiple

years. We urge researchers to consider how adopting TBAE might augment their studies. TBAE has been used for a variety of applications ranging from studying maternal thermoregulation (Stahlschmidt et al. 2012) to examining usage of artificial refugia versus natural refugia in sympatric species (Lelièvre et al. 2010). TBAE can reduce the stress that endangered species experience by limiting their interactions with researchers in the field. Harnessing the power of temperature to predict animal activity has proven to be a useful resource to augment surveys and radio-telemetry studies, and it will assist managers and researchers in determining how to improve protocols for surveying and studying these species in the future, while minimizing the stress imposed on these sensitive species.

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## Estimating activity and microhabitat use in *Gambelia sila*



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