

Time and ecological resilience: can diurnal animals compensate for climate change by shifting to nocturnal activity?

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Abstract. Considerable research is aimed at developing predictions of ecosystem responses to climate change, focusing on the spatial scale, such as range shifts and contractions, as well as activity restrictions to shaded microhabitats. On the other hand, the ability of species to shift their activity times during the diel cycle, and consequently to alter the environment in which activity occurs, has been largely neglected. Daily activity patterns are perceived as fairly fixed; however, natural changes in activity patterns have been reported in increasing numbers of species. Here, we present a framework that explores how shifts in activity patterns may buffer impacts of climate change. To demonstrate our framework, we simulated costs of activity of diurnal and nocturnal rodents and showed that future summers may decrease the energetic demands of nocturnal mammals while increasing water demands of diurnal mammals. Climate projections suggest that vegetation cover and water availability will decrease under future climate scenarios, especially in areas where water demands are expected to increase the most. These changes are expected to limit the ability of diurnal animals to restrict activity to shaded microhabitats and to keep a positive water balance. Our analysis shows that by shifting to nocturnality, diurnal mammals may mitigate the high water costs of future summers. We suggest that future research should explore the role of the diel time axis as an ecological resource when predicting the impacts of climate change.

Key words: activity times; biophysical modeling; climate change; competition; diurnal; energy expenditure; mammals; microhabitat; nocturnal; predation; water loss.

INTRODUCTION

Global concern regarding climate change and its projected effects on biodiversity have triggered a significant volume of scientific research. As climates change, animals respond in various ways, including shifts in phenology (Parmesan and Yohe 2003, Root et al. 2003, Kearney et al. 2010, Diamond et al. 2011, Todd et al. 2011) and in geographic ranges (Porter et al. 2000a, b, Parmesan and Yohe 2003, Root et al. 2003, Mathewson et al. 2016). To better understand how future climates may affect ecosystems, ecologists are using statistical and process-based models to make predictions based on biological and environmental data. Most of the predictions, however, explore how species may track their preferred climatic niches through responses in the spatial dimension: from microhabitat selection (e.g., Kearney et al. 2009, Sears et al. 2011) to range shifts and contractions (e.g., Clark et al. 2001, Humphries et al. 2004, Marshall et al. 2008, Franklin 2009). Underestimating alternatives to spatial shifts, such as shifts in temporal,

morphological, and physiological traits may cause one to potentially overestimate the impacts of climate change (Jenouvrier and Visser 2011, Buckley 2013, Valladares et al. 2014). Although previous models suggest that animals may restrict their activity times to avoid thermal stress (Sears et al. 2011), they limit temporal responses to the current temporal niches, either day or night. However, many species are able to switch their activity patterns from diurnal to nocturnal activity (Table 1, Hut et al. 2012). Although such behavioral responses may occur with climate change, no framework was developed to estimate the probability or the results of such responses, and we lack understanding of their ecological and evolutionary implications.

Theoretically, such shifts can begin with a widening activity trough during the hotter hours of midday and culminate with complete inversion into nocturnal activity, allowing organisms to maintain their current geographic range or to change it only in a limited manner while remaining in the climate to which they are adapted. Similar to behavioral thermoregulation, shifts in activity times may enable animals to be active within a range of temperatures suitable for activity (e.g., Porter et al. 1973, Kearney et al. 2009, Kearney 2013). Here, we present a conceptual framework that integrates the diel temporal niche axis into climate change research to better understand how shifts in activity patterns may occur and

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TABLE 1. Examples of species that switch temporal niches under natural conditions.

| Common name | Species | TNS | Condition | References |
|--------------------------|--------------------------------------|-----------|------------------------------------|-------------------------------|
| House mouse | <i>Mus musculus</i> | N > D | natural conditions | Daan et al. (2011) |
| Golden spiny mouse | <i>Acomys russatus</i> | N > D | interspecies competition | Shkolnik (1971) |
| Field vole | <i>Microtus agrestis</i> | N > D | winter | Bäumler (1975) |
| Montane vole | <i>Microtus montanus</i> | N > D | short photoperiod | Rowsemitt et al. (1982) |
| Tundra vole | <i>Microtus oeconomus</i> | N > D | winter | Erkinaro (1969) |
| Syrian hamster | <i>Mesocricetus auratus</i> | N > C, D | natural conditions | Gattermann et al. (2008) |
| Kangaroo rat | <i>Dipodomys spectabilis</i> | N > D | drought | Lockard (1978) |
| Ord's Kangaroo rat | <i>Dipodomys ordii</i> | N > D | drought | Boal and Giovanni (2007) |
| Rat | <i>Rattus norvegicus</i> | N > D | predation | Fenn and Macdonald (1995) |
| Rabbit | <i>Oryctolagus cuniculus</i> | N > D | also diurnal under high predation | Bakker et al. (2005) |
| Blind mole rat | <i>Spalax ehrenbergi</i> | D > N | high temperature, summer | Ben-Shlomo et al. (1995) |
| Roe deer | <i>Capreolus capreolus</i> | N > D | winter | Pagon et al. (2013) |
| Coyote | <i>Canis latrans</i> | D > N | hunting | Kitchen et al. (2000) |
| Bat-eared fox | <i>Otocyon megalotis</i> | D > N | high temperature | Lourens and Nel (1990) |
| Geoffroy's cats | <i>Leopardus geoffroyi</i> | N > D | food shortage | Pereira (2010) |
| Owl monkey | <i>Aotus azarai</i> | C > N | moonlight | Fernández-Duque et al. (2010) |
| Fat-tailed dunnart | <i>Sminthopsis crassicaudata</i> | N > D | winter | Warnecke et al. (2008) |
| Cane toad, metamorphs | <i>Bufo marinus</i> | N > D | cannibalism | Pizzatto et al. (2008) |
| Atlantic salmon | <i>Salmo salar</i> | N > D | reduced food | Metcalfe et al. (1999) |
| Atlantic salmon | <i>Salmo salar</i> | N > D | growth demand | Metcalfe et al. (1998) |
| Atlantic salmon | <i>Salmo salar</i> | D > C > N | winter > summer | Eriksson (1973) |
| Brown trout | <i>Salmo trutta</i> | D > C > N | winter > summer | Eriksson (1973) |
| Golden-lined rabbit fish | <i>Siganus lineatus</i> | D > N | shore > reef | Fox and Bellwood (2011) |
| Mediterranean lobster | <i>Nephrops norvegicus</i> | N > D | deep water (>200 m) | Chiesa et al. (2010) |
| Fruitfly | <i>Drosophila melanogaster</i> | C > D | short photoperiod, low temperature | Dubruille and Emery (2008) |
| Midge | <i>Chironomus thummi</i> | N > D | low temperatures | Kureck (1979) |
| Seed-harvesting ants | <i>Pheidole</i> spp. | D > N | high temperature | Whitford et al. (1981) |
| Crawfish Frogs | <i>Lithobates areolatus</i> | D > N | winter > summer | Stiles et al. (2017) |
| Neotropical otter | <i>Lontra longicaudis</i> | D > N | Pantanal > Atlantic Forest | Rheingantz et al. (2016) |
| Kudu | <i>Tragelaphus strepsiceros</i> | N > D | predation | Tambling et al. (2015) |
| Warthog | <i>Phacochoerus africanus</i> | N > D | predation | Tambling et al. (2015) |
| Buffalo | <i>Syncerus caffer</i> | N > D | predation | Tambling et al. (2015) |
| African elephant | <i>Loxodonta africana</i> | N > D | predation | Tambling et al. (2015) |
| Sitka black-tailed deer | <i>Odocoileus hemionus sitkensis</i> | D > N | predation | Bonnot et al. (2016) |

Notes: TNS, temporal niche switch. Switch in the dominant temporal niche indicated as N, nocturnal; D, diurnal; C, crepuscular. Most of the examples were taken from Table 1 in Hut et al. (2012).

their possible effects on individuals, populations, and communities. Our framework addresses how animals may shift their activity times toward nocturnality in response to climate change, allowing them to remain in their current habitats and geographic locations.

Accumulating evidence suggests that behavioral flexibility in activity patterns (i.e., temporal flexibility) in response to ambient temperatures is common in animals (Shkolnik 1971, Bacigalupe et al. 2003, Rezende et al. 2003, Aublet et al. 2009). Research indicates that animals may shift their activity patterns on the diel niche axis and may even invert them (night to day and vice versa) in response to ambient temperature (Whitford et al. 1981, Rowsemitt et al. 1982, Lourens and Nel 1990, Levy et al. 2007, Daan et al. 2011). Competition, predation, parasitism, and food availability have also been invoked to explain such phase shifts (Kronfeld-Schor and Dayan 2003, 2008, Hut et al. 2012, Kronfeld-Schor et al. 2017); while circadian rhythmicity appears to be somewhat constrained, clearly such evolutionary pressures had strongly influenced current activity patterns (Roll

et al. 2006, Hut et al. 2012). A recent global analysis has shown that although nocturnality is the global norm in mammals, there is a strong effect of climate on the distribution of activity patterns: diurnal activity patterns dominate regions where nighttime temperatures are low and the energetic costs of nocturnality are prohibitively high (Bennie et al. 2014). Moreover, crepuscular species are more abundant in regions where climate is preferable during twilight and nocturnal species are more abundant in arid regions (Bennie et al. 2014).

Performing well in multiple temporal niches is a challenging task for most animals. In particular, given that natural selection has crafted anatomical, behavioral, sensory, and physiological adaptations to day or night environmental conditions, organisms can often optimally exploit only one temporal niche. The retinal structure of a well-adapted diurnal animal, for example, would poorly capture the low light levels of the night, reducing its efficiency of activity (Jacobs 1993, Van Schaik and Griffiths 1996) and its ability to avoid predators (DeCoursey et al. 1997). Many species, however,

were found to exhibit flexible patterns of activity (Table 1). In reptiles, for example, ratsnakes (*Elaphe obsoleta*) are active at times when temperature is optimal regardless of light levels (DeGregorio et al. 2014). Among amphibians, young cane toads (*Bufo marinus*) have been shown to change activity patterns from nocturnal to diurnal, probably to avoid cannibalism by nocturnal conspecifics (Pizzatto et al. 2008). Nevertheless, if natural selection limits species to activity in a particular part of the day, or if climate change is too rapid for evolutionary responses, strictly diurnal species may be the more vulnerable to climate change, since in warm climates, increasing temperatures may constrain activity times to the point of extinction (Sinervo et al. 2010, Sears et al. 2011).

Diurnal mammals are an excellent model system to study the ability of animals to switch activity patterns. Evolutionary theory suggests that most early eutherian mammals were nocturnal (Wiens et al. 1986, Maor et al. 2017), avoiding predation and competition by the big diurnal reptiles, the dinosaurs (Clarke and Pörtner 2010, but see Schmitz and Motani 2011). Many nocturnal adaptations evolved in mammals during the Mesozoic Era, until the extinction of the dinosaurs allowed the radiation of mammals into day-time niches (Gerkema et al. 2013). Even today, after 65 million years, most mammals are still nocturnal, and most diurnal mammals still possess nocturnal features, such as a nocturnal structure of the retina (Gerkema et al. 2013). In fact, under controlled laboratory conditions, diurnal mammals show a large variety of activity patterns that include nocturnal, diurnal, and arrhythmic behavior (e.g., Blanchong et al. 1999, García-Allegue et al. 1999, Bacigalupe et al. 2003, Cohen and Kronfeld-Schor 2006, Refinetti 2006, 2008, Hagenauer and Lee 2008, Cohen et al. 2010a, b, Tomotani et al. 2012, Barak and Kronfeld-Schor 2013, Tachinardi et al. 2015), and the ability to spontaneously switch from diurnal activity under natural conditions to nocturnal activity in the laboratory (e.g., Blanchong et al. 1999, Levy et al. 2007, Gattermann et al. 2008, Barak and Kronfeld-Schor 2013). In nature, some diurnal mammals switch their activity patterns to nocturnal in response to competition, predation, and environmental conditions (Kronfeld-Schor and Dayan 2003, Vieira et al. 2010, Shuai et al. 2014, Tambling et al. 2015, Kronfeld-Schor et al. 2017). The shift of activity between different phases of the day may offer an important adaptation for reducing environmental heat stress (Hetem et al. 2012, Fuller et al. 2014, Davimes et al. 2017).

Here, we develop a framework to estimate the climatic, physiological, and ecological factors that may cause diurnal species to shift their activity patterns in response to climate change. By using hourly microclimate data and an endotherm model to calculate energy and water costs of diurnal and nocturnal activity (see Climate data and Model description sections for detailed description of the microclimate data and endotherm model), we show that animals in some regions can adapt to a warmer environment by shifting to nocturnal activity patterns. Our framework may explain how flexibility in the timings of activity patterns may offer a mechanism other than spatial responses to buffer environmental conditions. In mammals, the benefits of temporal flexibility remain unclear, but a recent analysis of 73

mammalian species in North America suggests that species that are strictly diurnal or nocturnal are twice as likely to spatially respond to climate change (McCain and King 2014). If some species are responding to climate change by shifting to nocturnality, this phenomenon has generally been excluded from climate change studies. Importantly, such shifts may have significant ecological consequences on individuals, populations and ecological communities, by altering interspecific interactions and by increasing competition at night (Fig. 1). We suggest that empirical and modeling efforts can be applied to test our framework and improve our understanding of the consequences of such shifts by explicitly considering the impacts of climate change.

THE TEMPORAL-SHIFT FRAMEWORK: WHERE DIURNAL SPECIES MAY BECOME NOCTURNAL

The temporal-shift framework links between variation in thermal costs of activity throughout the day and the availability of ecological resources to understand the effects of climate on organismal choice of activity times. In particular, we suggest that heat input, availability of shade, and availability of water are three major factors that act to determine the tendency of individuals for diurnal or nocturnal activity (Fig. 2). First, we show how climate change may impact the relative metabolic costs of activity for diurnal and nocturnal organisms and how diurnal species may avoid increased costs of evaporative cooling by shifting to nocturnality. Second, we discuss how ecological resources may buffer high water costs of diurnality and eliminate the need to shift activity patterns toward nocturnality: for example, animals can avoid shifts by either choosing shaded microhabitats for activity or, when shade is less available, by balancing the costs of thermoregulation through increased consumption of water. Finally, we highlight how remaining diurnal or changing activity patterns may affect intra- and interspecific relationships (Fig. 1).

Heat input and costs of activity patterns

During activity, mammals maintain their body temperature at a certain range, and the amount of heat input determines the two metabolic costs of balancing heat exchange: energy expenditure and evaporative water loss. By estimating the differences in costs between day and night, we may identify the activity times that minimize these costs, and how they may shift under climate change. In particular, the climatic challenges of diurnality and nocturnality may increase or decrease based on the current climate and the magnitude of change as climate change will bring animals toward or further away from the thermoneutral zone (TNZ; i.e., the range of temperatures and other climatic conditions such as radiation, wind velocity, and humidity that minimize energy and water costs; Hill et al. 2016; Fig. 3). Activity below or above the TNZ will force an animal to increase its energy expenditure to avoid hypothermia (followed by a relatively small increase in water loss due to high rates of ventilation; Scholander et al. 1950), or increased evaporative water loss to avoid hyperthermia (an active process that requires energy expenditure), respectively (Porter and Kearney 2009, Hill et al. 2016). For example, at cold locations or

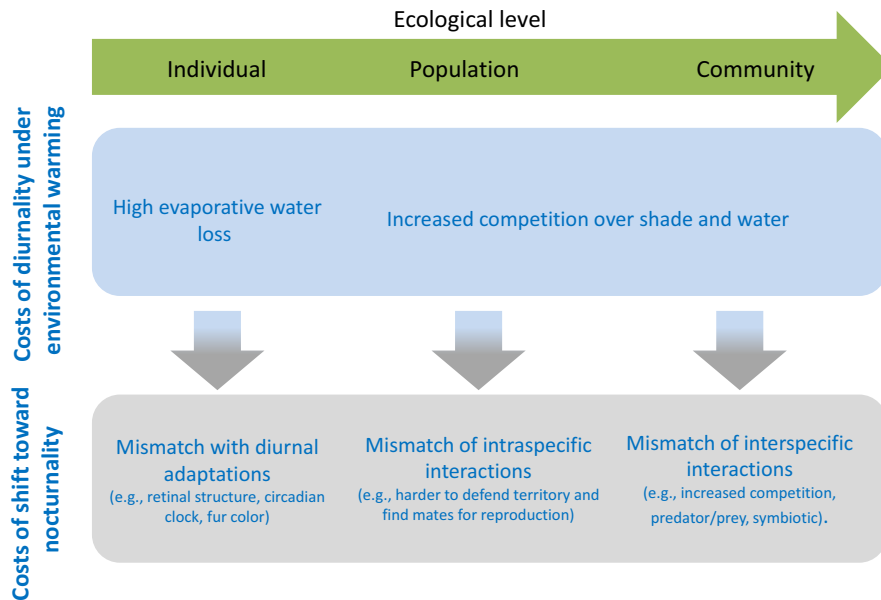


FIG. 1. Climate change will alter the costs and benefits of diurnal and nocturnal activity patterns. Daytime temperature will demand higher rates of water loss to avoid hyperthermia, forcing individuals to seek shade and increase water intakes, enhancing the inter- and intra-specific competition over these resources. We suggest that such conditions may attract individuals toward nocturnal activity patterns when water costs are lower. Importantly, such shifts will bring new challenges to ecological systems, such as mismatches between diurnal adaptations and night-time conditions, between conspecifics, and between species.

during colder days, a nocturnal animal may experience temperatures that are lower than the TNZ, and activity during daytime should be preferred (van der Vinne et al. 2015). At warmer locations, on the other hand, as temperatures increase with climate change, the magnitude of the distance from the TNZ will be lower during the night, while daytime activity may require increased rates of water loss, hence activity during nighttime should be preferred (Fig. 3).

To demonstrate how climate change may shift the activity patterns that minimize metabolic costs of activity, we used an endotherm model to estimate heat input and metabolic costs of diurnal and nocturnal activity under past and future climatic conditions (Appendix S1: Fig. S1). The endotherm model is part of the Niche Mapper (Portet and Mitchell 2006) and solves biophysical equations of heat and mass transfer as a function of the local microclimate and the characteristics of an animal to calculate the energy and water costs of maintaining a preferred body temperature during activity. It has the advantage of accounting for ecologically relevant variables that may affect energy expenditure and water loss but are not accounted for in laboratory measurement. In particular, the model can account for many environmental (e.g., temperature, radiation, wind velocity, and humidity), behavioral (e.g., activity times, microhabitat use, foraging strategies, social thermoregulation, and posture), morphological (e.g., body mass, size, shape, fur reflectivity, and fur density), and physiological variables (e.g., body temperature and minimal metabolic rate). As input for the model, we used (1) a microclimate data set that describes past and future conditions and (2) a model diurnal rodent, the golden spiny mouse (*Acomys russatus*), for which the model was previously parameterized and validated to study the effect of energy on water costs on activity patterns and foraging preferences (Levy et al. 2012, 2016c). Here, we used the model to

estimate hourly energy and water costs of thermoregulation of an active rodent and analyzed how the differences of costs between diurnal and nocturnal activity may change in the future and affect activity patterns (Appendix S1: Fig. S1).

Climate data.—We used a published data set of hourly microclimates (Levy et al. 2016a) to calculate energy expenditure and evaporative water loss during activity. The data set includes 11,407 locations covering the North American region at a resolution of 36×36 km for the past (1980–2000) and the future (2080–2100, assuming a radiative forcing of $+8.5 \text{ W/m}^2$ by year 2100; Riahi et al. 2011); with estimates of humidity near the ground surface, as well as temperatures and wind speeds at various heights, and soil temperatures at various depths and shade intensities. Moreover, the data set includes parameters that vary across latitudes, longitudes, and altitudes, such as length of daytime, temperature, humidity, and surface air pressure (e.g., Appendix S1: Figs. S2, S3). Thus, the data set is an excellent resource to study how day and night variations in environmental conditions may affect activity patterns. Although the golden spiny mice are not native to North America, we used the species as a model organism that is diurnal, well adapted to warm temperatures (Shkolnik and Borut 1969, Kam and Degen 1993), and has the ability to switch activity patterns (e.g., Levy et al. 2007). These adaptations should make the golden spiny mouse, and hence our model results, less sensitive to increasing temperatures compared to other, less adapted species.

Calculating heat input and metabolic costs of activity.—We used the endotherm model to calculate hourly environmental effects on metabolic costs during activity and resting. This model was previously used to predict the climatic

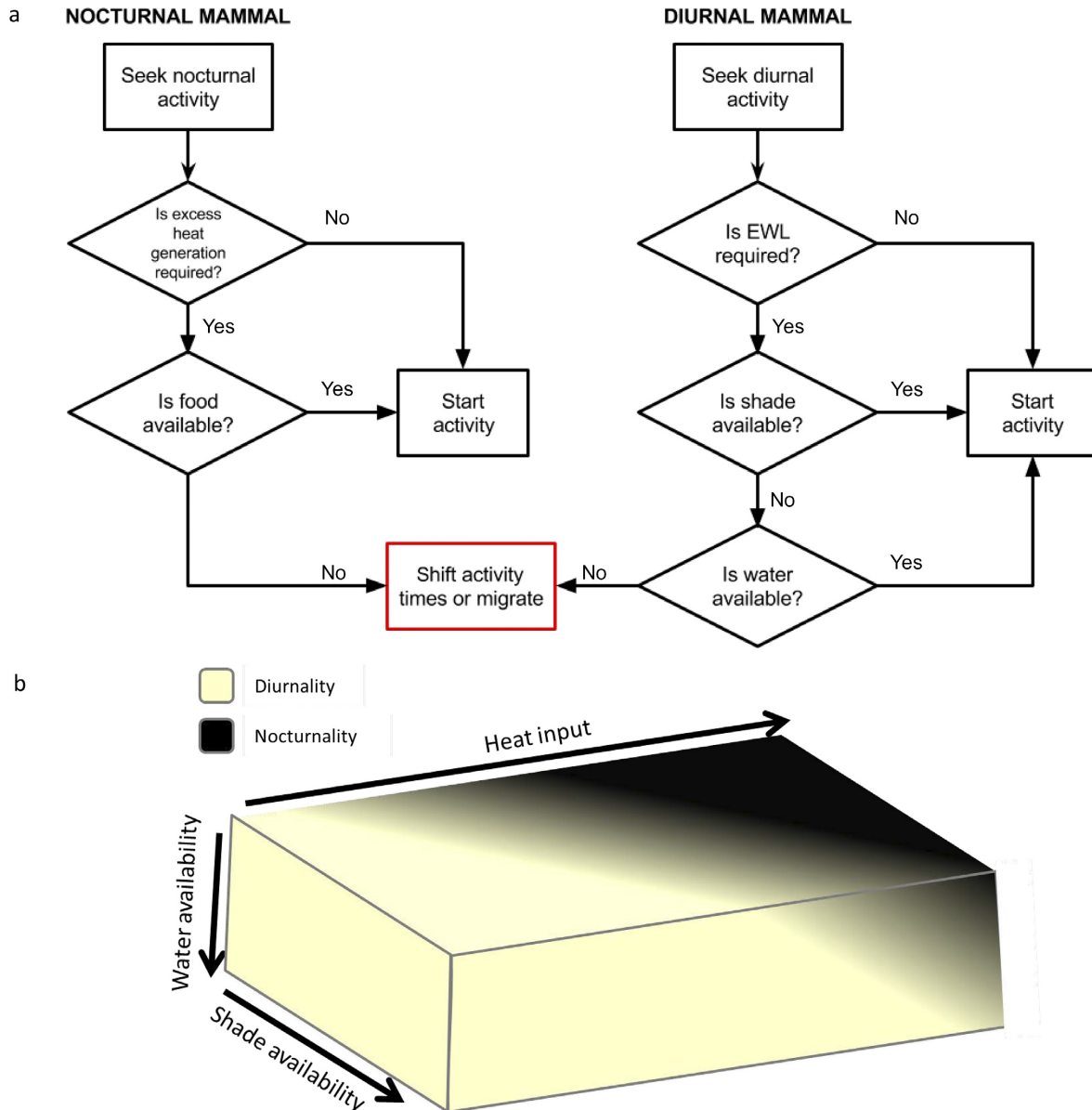


FIG. 2. (a) Heat input from the environment, shade availability, and nutrient availability interact to shape activity patterns. At cold locations, nocturnal animals may prefer diurnal activity when food availability is low since daytime offers higher temperatures and hence lower energetic costs of heat production to avoid hypothermia. As heat input increases, due to changes in temperatures and other factors such as wind and rainfall, diurnal animals may prefer nocturnal activity when excess loss of water is required to avoid hyperthermia. However, animals can also avoid high water costs by restricting their activity to shaded microhabitats. But the lower the abundance of shade microhabitats, the higher the competition and predation costs that animals will encounter at these patches. Moreover, when animals can easily access drinking water or water-rich food items, higher rates of evaporative water loss due to diurnal activity may not pose a risk of dehydration. But the lower the abundance of water, the higher the risk of dehydration, as well as the costs of competition and predation at water patches. (b) In a simplified three-dimensional cube, we demonstrate how the probability of diurnality and nocturnality may change under different levels of heat input, shade, and water. EWL, evaporative water loss.

constraints on the distribution of mammals (Natori and Porter 2007, Long et al. 2009, 2014, Mathewson and Porter 2013), as well as activity times (Levy et al. 2012, 2016c, Moyer-Horner et al. 2015, Mathewson et al. 2016). Importantly, this method enables predictions at a relatively high temporal resolution that is crucial when predicting temporal patterns of activity. In particular, we first ran a simulation for each location in the microclimate data set and calculated hourly rates of energy and water costs of activity for every

day and year. Then, we analyzed the spatial and temporal distributions of activity costs and the differences in costs between day and night activities.

1.. Model description.—The endotherm model solves biophysical equations of heat and mass transfer as a function of the local microclimate and the characteristics of the animal to calculate heat input and the corresponding energy and water costs of maintaining a preferred body temperature

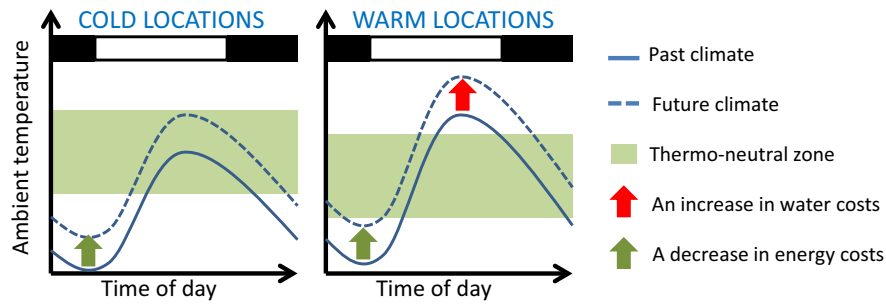


FIG. 3. The forces driving nocturnal activity patterns may differ between cold and warm locations. At cold locations (left panel), future climate will increase night temperatures toward an organism thermoneutral zone (green rectangles), decreasing the energetic costs of night activity (green arrow). For diurnal animals that prefer nocturnal activity (i.e., due to nocturnal adaptations such as retinal structure and circadian clock), such a decrease in costs may enable shifting toward nocturnality. At warm locations (left panel), higher temperatures will decrease costs of nocturnal activity (green arrow), but will also increase rates of water loss during diurnal activity, since daytime temperature will rise further above the thermoneutral zone (red arrow). Bars at the top of panels represent the diel cycle (black, night; white, day).

during activity (Porter et al. 1994, 2000a, 2006, Porter and Mitchell 2006, Porter 2016). In the model, properties of the environment (such as air temperature, wind velocity, and surface reflectivity of the ground) and those of the animal (such as size, shape, body temperature, activity level, and fur depth, density, reflectivity, hair diameter, and length) are used to calculate heat exchange with the environment via convection, conduction, solar radiation, longwave infrared radiation, respiratory evaporation, and cutaneous evaporation. The model assumes a skin-to-core temperature gradient within the animal body, with heat generation in the flesh from the animal's metabolism and an optional layer of fat between the flesh and skin surface that insulates the core body and from the skin surface. A layer of fur acts as a second insulation layer, where heat transfer between the environment and the skin of the animal is assumed (Mathewson and Porter 2013). For the code of the model used in this study, see *Data Availability*.

2.. Parameterization.—We parameterized the model using the golden spiny mouse as a model animal, and assumed that active mice are foraging with an ellipsoid posture ($a = 2b$, where a and b are the semi-major and semi-minor axes of the ellipsoid, respectively) and with a fixed, empirically measured body temperature (Appendix S1: Table S1; Levy et al. 2012, 2016c). We used our own measurements of body mass and fur properties and the values found in or estimated from the literature for other physiological and allometric properties (Appendix S1: Table S2). In the model, thermoregulation as a response to heat stress was initiated when the estimated metabolic rate was below the empirically measured activity metabolic rate (based on Gutman et al. [2006], 8 mW/g; Levy et al. 2016c). Gutman et al. (2006) measured metabolic rates of activity during feeding, hence rates include the costs of thermoregulation, food handling, and digestion, but do not include the costs of searching for food items (e.g., digging). During thermoregulation, the sequence of events aimed at regulating body temperature was set as (1) a minimization of the silhouette area exposed to the sun (the default animal orientation was normal to the solar radiation, maximizing exposure to the sun); (2) an increase in flesh conductivity (from 0.4 up to 2.8 $\text{W}\cdot\text{m}^{-1}\cdot\text{C}^{-1}$); and (3) heat loss by evaporative cooling (cutaneous evaporative water loss and licking fur). Since mice are relatively small, other postural changes may

not be possible without ceasing activity. We assumed that an active rodent is located on the ground surface, either in an open (exposed to the sky) or shaded (under canopy cover) habitat, and that a resting rodent is in a burrow 30 cm below the ground surface. For simplicity, we assumed that the rodent is not torpid during the inactivity phase. For burrows, we assumed that the temperature follows the temperature of the soil at 30 cm depth, that relative humidity is constantly 99%, and that wind speed is 0.1 m/s to allow free convection. Moreover, we assumed constant fur conditions (dry fur with constant depth and density), thus a wet animal should lose more heat to the environment than predicted in the model. To explore how the model's predictions may vary for different rodents, we quantified how costs of activity may differ for species with $\pm 50\%$ change in body mass, fur reflectivity, and resting metabolic rate during activity. Our analysis is thus limited to animals that are small enough to burrow and have relatively short fur.

3.. Validation.—Levy et al. (2012) previously validated the predictions of the endotherm model using empirical data from two previous studies of golden spiny mice (Shkolnik and Borut 1969, Gutman et al. 2006). The validation shows that the endotherm model successfully predicts changes in energy expenditure and evaporative water loss in golden spiny mice, both when compared to measurements taken at different temperatures (20°, 25°, and 30°C; Shkolnik and Borut 1969) and at various activity levels (Gutman et al. 2006, Levy et al. 2012; Fig. A2).

4.. Model predictions.—Our analysis suggests that climate change will generally reduce cold-related energetic costs for nocturnal activity while increasing warm-related water costs during diurnal activity, but with complex temporal and spatial patterns. Considering such shifts at a few locations that differ in climatic patterns may shed light on the range of outcomes (Fig. 4): In Arizona, where the current climate is warm, energy expenditure will decrease throughout the year, especially during winter and during summer nights, but evaporative water loss would increase during diurnal activity. In particular, warming would require evaporative cooling during more days each year and with higher rates of water loss. In Florida, where climate is warm but relatively tropical and

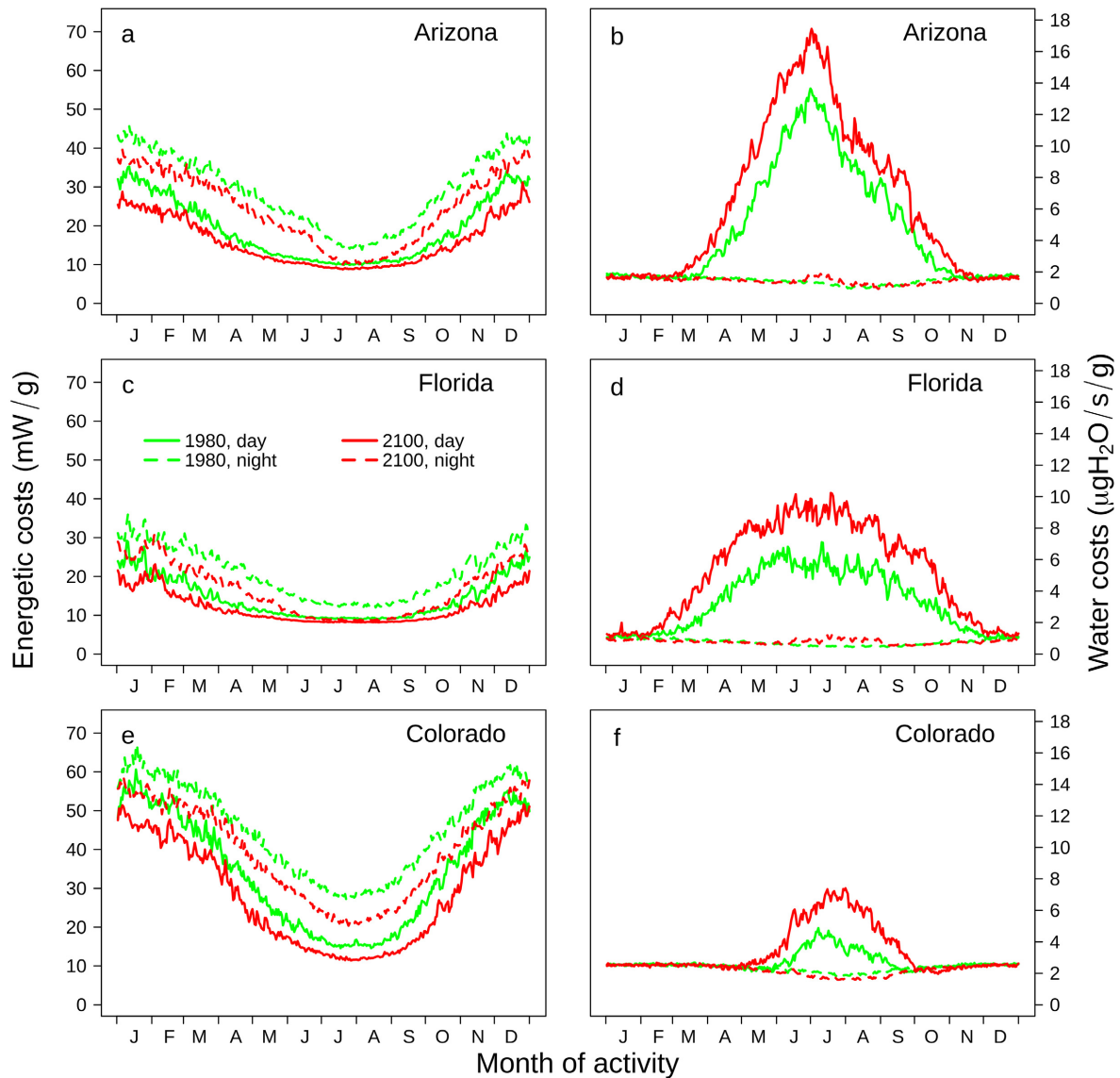
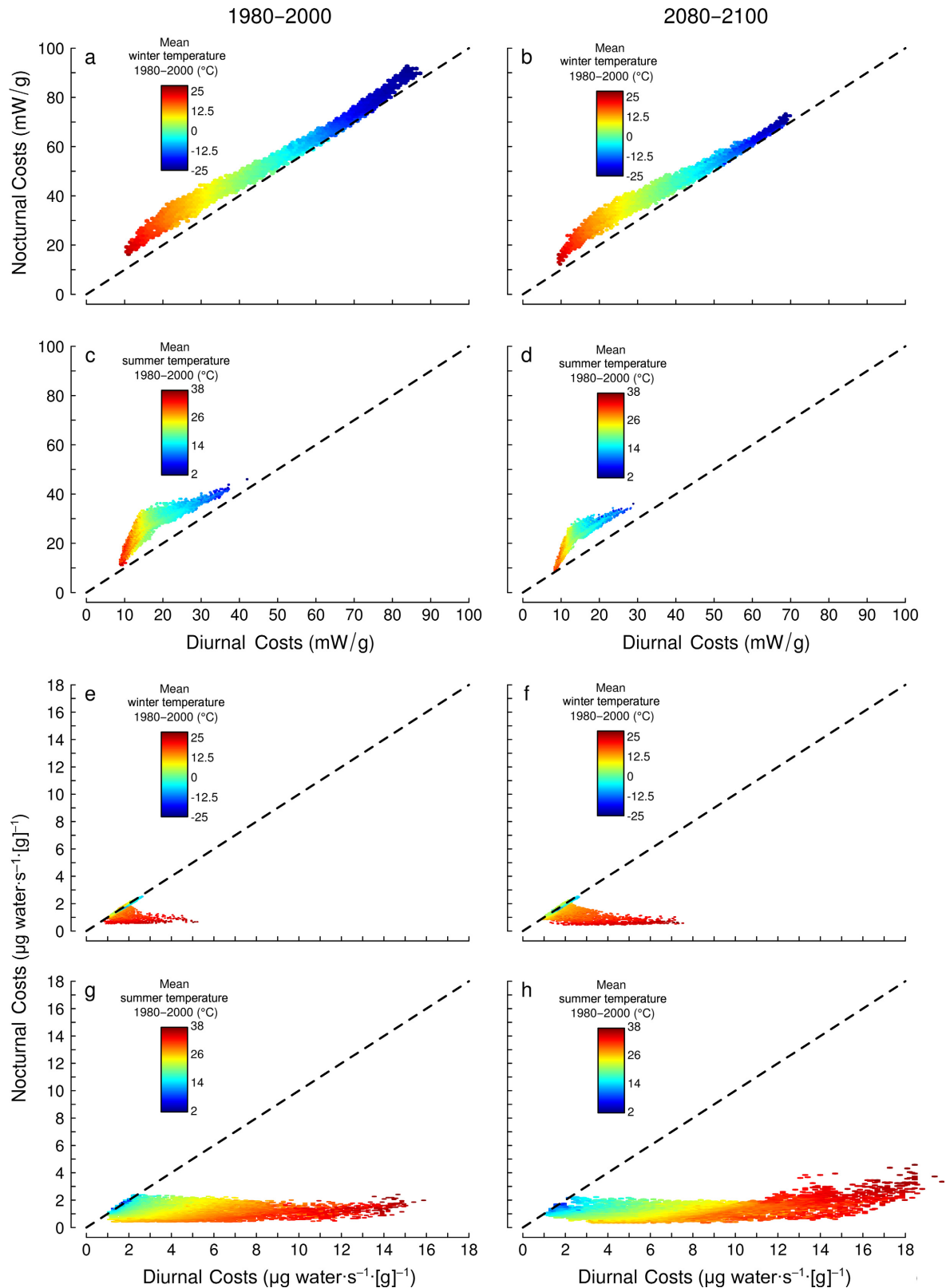


FIG. 4. Predicted effects of climate change on energy and water costs of activity in three locations that represent three types of climates: (a, b) Arizona (33.87° N, 111.47° E), which is relatively warm and dry; (c, d) Florida (29.85° N, 82.23° E), which has a subtropical climate (warm, humid, and low seasonal and daily variations in temperatures), and (e, f) Colorado (37.70° N, 104.85° E), which is relatively cold. Model predictions are per gram body mass.

therefore varies less than the climate in Arizona, further warming would decrease energy requirements of activity during winter nights, but would require an increase in water costs during diurnal activity. Moreover, a diurnal rodent in Florida would need to evaporate less water than in Arizona, but during more days each year. Finally, in Colorado, where the current climate is cooler, warming would simply decrease energetic costs of activity throughout the year and will increase evaporative water loss of activity during summer days. Each of these distinct scenarios occurs in some portion of the North American domain, and would probably occur around the globe, depending on the current climate and the anticipated change in climate (Fig. 5). In particular, rodents at lower latitudes and elevations experience warmer weather, and hence spend relatively less energy (Fig. 6) and more water (Fig. 7) for maintaining preferred body temperature

during activity. By 2100, the need of evaporative cooling will increase at these warmer locations, and expand to mid-range latitudes and elevations (Figs. 6, 7). Interestingly, our model suggests that the metabolic costs of resting do not vary throughout the day for burrowing mammals since burrows buffer diel cycles of temperature across the entire range of climates covered in our North American data set (Fig. 8). Our predictions were qualitatively robust to differences in body mass, fur properties, and minimal rates of energy expenditure, but values of predictions vary with these parameters, especially in the warmest and coldest locations (Tables 2–3; Appendix S1: Figs. S4–S9; see Appendix S1 for detailed analysis). Moreover, our analyses suggest that climatic factors other than temperature (e.g., humidity and wind speed; Gates 1980) also affect energy and water costs of activity as suggested previously by Gates (1980; e.g., humidity and wind



speed, see Appendix S1: Figs. S10–S16). For example, increases in wind speed can increase evaporative water loss, decreases boundary layer thickness, and promote water loss at higher temperatures.

From shifts in energy and water costs to changes in activity patterns.—Our predictions suggest that animals may shift their activity patterns to reduce the negative impacts of climate change. We believe, however, that such temporal shifts

FIG. 5. Costs of activity vary between day and night across climatic gradients. We show past (1980–2000) and future (2080–2100) energy (winter [a] past, [b] future; summer [c] past, [d] future) and water (winter [e] past, [f] future; summer [g] past, [h] future) costs of diurnal and nocturnal mammals. Energy costs are higher during nighttime activity, lower in warmer locations, and will decrease in the future. Water costs are higher for diurnal animals in both winter and summer. Future climate will increase rates of water loss for diurnal animals but not for nocturnal animals. We defined winter months as December, January, and February, and summer months as June, July, and August. Model predictions are per gram body mass. The color of each point indicates the mean air temperature (3 cm height) at one or more locations. Dashed lines represent equal diurnal and nocturnal costs of activity. For predictions for different values of body mass, fur properties, and minimal rates of energy expenditure, see Appendix S1: Figs. S4–S9.

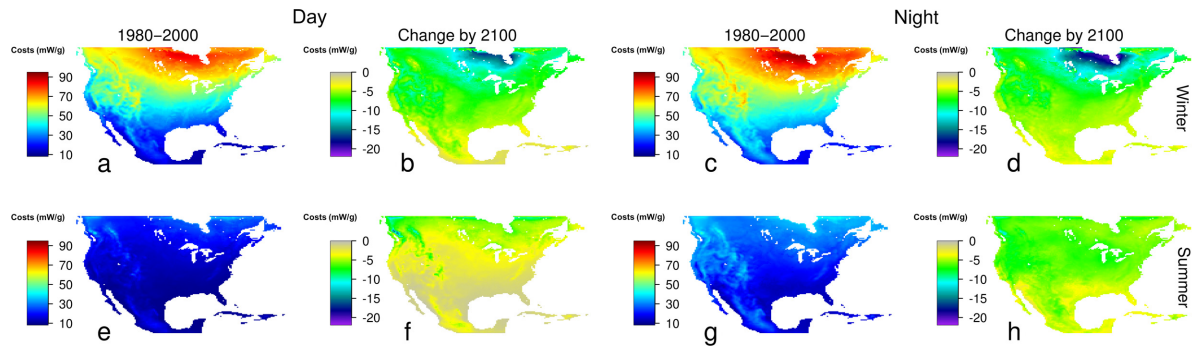


FIG. 6. Computed energetic costs of activity during past climate (1980–2000) and the difference in costs between past and future (2080–2100) climates. Data are mean values for a diurnal and nocturnal rodent active on the ground surface during winter (a and b, diurnal; c and d, nocturnal) and summer (e and f, diurnal; g and h, nocturnal). When averaged across the map, predicted energetic costs of activity were higher during the night than during the day at 100% of the locations, by 5.64 ± 2.88 mW/g (mean \pm SD) during winter and 8.79 ± 2.93 mW/g during summer under past climate (1980–2000). Under climate change (2080–2100, RCP 8.5 climate scenario), the difference between night and day are predicted to decrease to 5.32 ± 3.01 mW/g during winter and 6.46 ± 3.18 mW/g during summer. Model predictions are per gram body mass.

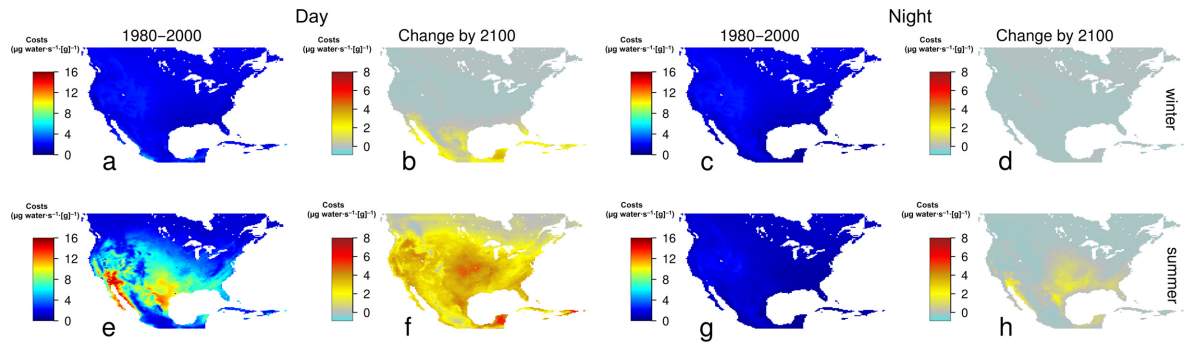


FIG. 7. Computed water costs of activity during past climate (1980–2000) and the difference in costs between past and future (2080–2100) climates. Data are mean values for a diurnal and nocturnal rodent active on the ground surface during winter (a and b, diurnal; c and d, nocturnal) and summer (e and f, diurnal; g and h, nocturnal). Predicted water costs of activity during past winters (1980–2000) were higher during the day than during the night by an average of 0.18 ± 0.43 $\mu\text{g water}\cdot\text{s}^{-1}\cdot(\text{g})^{-1}$ (mean \pm SD,) at 89% of the locations and lower by 0.03 ± 0.02 $\mu\text{g water}\cdot\text{s}^{-1}\cdot(\text{g})^{-1}$ at 11% of the locations. Under climate change (2080–2100, RCP 8.5 climate scenario), the difference between day and night will increase at most locations, with winter water costs higher during the day than during the night by 0.39 ± 0.97 $\mu\text{g water}\cdot\text{s}^{-1}\cdot(\text{g})^{-1}$ at 91% of the locations and lower by 0.04 ± 0.03 $\mu\text{g water}\cdot\text{s}^{-1}\cdot(\text{g})^{-1}$ at 9% of the locations. During past summers, predicted water costs were higher during the day than during the night by 3.13 ± 3.03 $\mu\text{g water}\cdot\text{s}^{-1}\cdot(\text{g})^{-1}$ at 98% of the locations and lower by 0.03 ± 0.04 $\mu\text{g water}\cdot\text{s}^{-1}\cdot(\text{g})^{-1}$ at 2% of the locations. These differences are predicted to increase under climate change, with summer water costs higher during the day than during the night by 5.29 ± 3.86 $\mu\text{g water}\cdot\text{s}^{-1}\cdot(\text{g})^{-1}$ at 100% of the locations. Model predictions are per gram body mass.

in activity patterns will not only depend on the changes in activity costs throughout the day, but also on the underlying causes of the current activity patterns. In particular, for species whose diurnality has evolved to minimize its energetic costs, our predicted decrease in energetic costs due to climate change may lead to one of two outcomes: if the high energetic demands of night activity are the determining factor, a mere decrease in such demands may allow individuals to increase nocturnal activity or shift to it altogether. If, on

the other hand, the differences between day and night costs are the determining factor, daytime will remain the energetically advantageous temporal niche in the future. Furthermore, for diurnal species that cannot evaporate much water, or exist in arid habitats where water is scarce and evaporative cooling is too costly, our predicted increases in water costs of diurnality due to climate change may limit activity times significantly, forcing animals to restrict activity to shaded microhabitats or cooler hours and spend more time

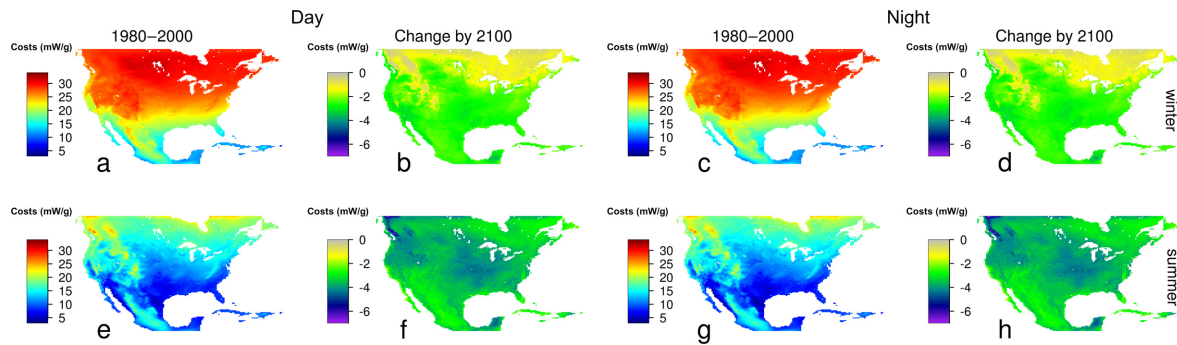


FIG. 8. Computed energetic costs of resting during past climate (1980–2000) and the difference in costs between past and future (2080–2100) climates. Data are mean values for a diurnal and nocturnal rodents resting in a 30-cm burrow during winter (a and b, day resting; c and d, night resting) and summer (e and f, day resting; g and h, night resting). Predicted energetic costs of resting during past winter (1980–2000) were slightly higher during the day than during the night by an average of 0.01 ± 0.01 mW/g (mean \pm SD) at 79% of the locations, and lower by 0.19 ± 0.15 mW/g at 21% of the locations. Under climate change (2080–2100, RCP 8.5 climate scenario), the difference between day and night will decrease at most locations, with winter resting costs higher during the day than during the night by 0.01 ± 0.01 mW/g at 97% of the locations, and lower by 0.19 ± 0.16 mW/g at 3% of the locations. During past summers, predicted energetic costs were higher during the day than during the night by 0.42 ± 0.11 mW/g at 100% of the locations. These differences are predicted to remain under climate change, with summer resting costs higher during the day than during the night by 0.43 ± 0.10 mW/g at 100% of the locations. Model predictions are per gram body mass.

in burrows in the daytime. For example, in the diurnal desert-dwelling golden spiny mouse, water requirements had the most substantial effect on observed foraging decisions, with mice gradually decreasing foraging behavior when climatic conditions required increased water costs (Levy et al. 2016c). In fact, mice often forgo even significant energetic returns when water loss is high (Levy et al. 2016c). Such behavior may cause a bimodal activity pattern during the summer season, in which individuals concentrate their activity during the morning and afternoon hours, and avoid foraging during the hottest hours of the day (Shkolnik 1971, Elvert et al. 1999, Kronfeld-Schor et al. 2001a). Other diurnal mammals such as *Psammomys obesus* (Ilan and Yom-Tov 1990), *Octodon degus* (e.g., Bacigalupe et al. 2003), *Xerus inauris* (Aublet et al. 2009), *Capra ibex* (Bennett et al. 1984), and *Spalacopus cyanus* (Rezende et al. 2003) may exhibit similar patterns.

For species that avoid or have minimal ability for evaporative heat loss, our model suggests that warmer regions (e.g., at lower latitudes and elevations) may offer only a few hours of diurnal activity during summer (Fig. 9). By 2100, these species will suffer from further decrease in time available for diurnal activity, especially at mid-range latitudes and elevations where evaporative heat loss was not previously required (Fig. 9). Nocturnality, on the other hand, offers many more opportunities for activity to such species, although future climates may also limit nocturnal activity times in warm regions (Fig. 9). Thus, species that are strictly diurnal, and unable to lose heat by evaporation, are at higher risks of population decline and distributional shifts. For example, a strictly diurnal species, the American pika (*Ochotona princeps*), is becoming extirpated at low-elevation sites across its range perhaps because activity at these warm locations is limited to the very few cool hours (Moyer-Horner et al. 2015, Mathewson et al. 2016). We suggest that if future climates further reduce the window of opportunity for activity, mammals may not be capable of meeting their metabolic and/or water demands, while also pursuing other fitness-enhancing activities (e.g., mating and defending

territories), analogous to predictions of diurnal ectotherm species (Sinervo et al. 2010). To maintain their current activity times, mammals may either restrict their activity to shaded and cooler microhabitats to avoid high water costs, or consume more water and food to maintain water balance.

Availability of shade

Shade is an important ecological resource that diurnal animals often use to limit the amount of heat input from solar radiation. Hence, exploiting shade patches may enable diurnal animals to maintain their activity patterns without high evaporative water costs. We explored the ability of shade to decrease water costs of diurnality by running the endotherm model with the same parameterization as described above but under full shade conditions. Our model predicted that activity in a shaded microhabitat drastically reduces stressful heat load and the need for evaporative heat loss under warm conditions. For example, by restricting activity to the shade, a diurnal rodent can reduce water costs in Arizona (warm), Florida (subtropical), and Colorado (cold) by an average of 75%, 73%, and 74% under recent summer conditions and by an average of 73%, 67%, and 80%, under future climate conditions, respectively (Fig. 10). Similar effects of shade occur across the North American region (Fig. 11), and predictions are robust to changes in body mass, fur properties, and minimal rates of energy expenditure (Appendix S1: Figs. S17–S22; Tables 2–3). Hence, the ability to avoid losing water behaviorally by being active in shaded areas may be critical to maintaining current spatial and temporal distributions of mammals in the future and will enable diurnal species to preserve their activity times, as was previously shown for ectotherms (Kearney et al. 2009).

In many ecosystems, however, shade is a limited resource that organisms cannot freely exploit. As temperatures increase, sparse shade patches will force diurnal individuals to confine activity to a relatively small fraction of their habitat. If future climates promote more vegetation cover, shade will be more abundant, allowing animals to thermoregulate

TABLE 2. Sensitivity analysis of the energy and water costs during recent climate conditions (predictions for 1980–2000).

| Season, habitat, parameter, and value | Figure | Energy expenditure (mW/g) | | Evaporative water loss ($\mu\text{g water}\cdot\text{s}^{-1}\cdot[\text{g}]^{-1}$) | |
|---|--------|------------------------------|-------------------|---|-----------------|
| | | Diurnal | Nocturnal | Diurnal | Nocturnal |
| Summer | | | | | |
| Open | | | | | |
| Original parameters | | | | | |
| Appendix S1: Table S2 | 5 | 16.02 \pm 5.42 | 24.82 \pm 6.92 | 4.24 \pm 3.02 | 1.19 \pm 0.35 |
| Body mass (g) | | | | | |
| 29.0 | S4 | 21.05 \pm 8.31 | 34.29 \pm 9.69 | 5.09 \pm 3.67 | 1.62 \pm 0.46 |
| 67.6 | S5 | 13.81 \pm 4.13 | 20.53 \pm 5.66 | 3.88 \pm 2.72 | 0.99 \pm 0.29 |
| Minimum energy expenditure during activity (mW/g) | | | | | |
| 4.0 | S6 | 14.48 \pm 6.31 | 24.75 \pm 7.01 | 3.41 \pm 2.53 | 1.16 \pm 0.35 |
| 12.0 | S7 | 17.93 \pm 4.52 | 25.00 \pm 6.70 | 5.24 \pm 3.52 | 1.25 \pm 0.35 |
| Fur reflectivity (% , dorsal/ventral) | | | | | |
| 20/17.5 | S8 | 15.59 \pm 5.17 | 24.81 \pm 6.92 | 4.81 \pm 3.33 | 1.19 \pm 0.35 |
| 60/52.5 | S9 | 16.50 \pm 5.67 | 24.83 \pm 6.93 | 3.73 \pm 2.72 | 1.18 \pm 0.35 |
| Shade | | | | | |
| Original parameters | | | | | |
| Appendix S1: Table S2 | 11 | 11.61 \pm 2.78 | 14.21 \pm 3.64 | 1.16 \pm 0.70 | 0.65 \pm 0.18 |
| Body mass (g) | | | | | |
| 29.0 | S17 | 14.97 \pm 4.49 | 19.21 \pm 5.24 | 1.22 \pm 0.65 | 0.82 \pm 0.23 |
| 67.6 | S18 | 10.23 \pm 1.96 | 12.03 \pm 2.78 | 1.20 \pm 0.74 | 0.61 \pm 0.20 |
| Minimum energy expenditure during activity (mW/g) | | | | | |
| 4.0 | S19 | 10.56 \pm 3.62 | 14.00 \pm 3.90 | 0.73 \pm 0.33 | 0.57 \pm 0.17 |
| 12.0 | S20 | 13.64 \pm 1.73 | 15.15 \pm 2.70 | 2.01 \pm 1.17 | 0.98 \pm 0.49 |
| Fur reflectivity (% , dorsal/ventral) | | | | | |
| 20/17.5 | S21 | 11.61 \pm 2.78 | 14.21 \pm 3.64 | 1.16 \pm 0.70 | 0.65 \pm 0.18 |
| 60/52.5 | S22 | 11.61 \pm 2.78 | 14.21 \pm 3.64 | 1.16 \pm 0.70 | 0.65 \pm 0.18 |
| Winter | | | | | |
| Open | | | | | |
| Original parameters | | | | | |
| Appendix S1: Table S2 | 5 | 48.21 \pm 18.80 | 53.85 \pm 16.90 | 1.80 \pm 0.38 | 1.65 \pm 0.38 |
| Body mass (g) | | | | | |
| 29.0 | S4 | 86.20 \pm 45.67 | 94.42 \pm 42.42 | 2.55 \pm 0.47 | 2.40 \pm 0.54 |
| 67.6 | S5 | 41.21 \pm 17.25 | 46.09 \pm 16.03 | 1.55 \pm 0.38 | 1.40 \pm 0.35 |
| Minimum energy expenditure during activity (mW/g) | | | | | |
| 4.0 | S6 | 48.07 \pm 19.04 | 53.85 \pm 16.90 | 1.74 \pm 0.34 | 1.65 \pm 0.38 |
| 12.0 | S7 | 48.44 \pm 18.44 | 53.85 \pm 16.89 | 1.91 \pm 0.54 | 1.65 \pm 0.38 |
| Fur reflectivity (% , dorsal/ventral) | | | | | |
| 20/17.5 | S8 | 47.75 \pm 18.97 | 53.84 \pm 16.90 | 1.84 \pm 0.45 | 1.65 \pm 0.38 |
| 60/52.5 | S9 | 48.65 \pm 18.61 | 53.85 \pm 16.89 | 1.78 \pm 0.35 | 1.65 \pm 0.38 |

Notes: To determine sensitivity, the values of body mass, fur properties, and minimal rates of energy expenditure (Appendix S1: Table S2) were increased and decreased by 50% from our original parameterization. Dependent variables are the mean \pm SD predictions over the North American domain of our model. Values are per gram of body mass.

behaviorally and to escape the warm temperatures of daytime. On the other hand, if vegetation cover decreases in the future, the distances between shaded patches will increase, limiting opportunities for diurnal behavioral thermoregulation, and driving both intra- and inter-specific competition over preferred thermal patches. To estimate how future climate conditions may impact vegetation cover, we analyzed regional estimates of past and future green vegetation cover (Levy et al. 2016a). These estimates were calculated using a dynamic vegetation model that simulates short-term vegetation dynamics by accounting for carbon budgets for soil and vegetation (leaf, wood, and root), as well as foliage dynamics caused by cold, drought, senescence, herbivory, and mechanical stress (Niu et al. 2011). Levy et al.'s (2016a)

predictions suggest that summers will offer less vegetation cover in large regions where high evaporative water loss rates are required (Fig. 12). Hence, less shade cover is expected where animals need it most to escape the heat of the day. Future climate warming will escalate these unfavorable conditions, with less vegetation cover at 65% of locations, especially during summer at relatively warm and vegetation-rich places (Fig. 13). Based on these predictions, we suggest that relying on vegetation cover for thermoregulation in warmer climates may be more challenging in the future, forcing individuals either to more crepuscular or nocturnal behavior to avoid foraging during the warm parts of the diel cycle or to fulfill the increased water requirements of avoiding hyperthermia.

TABLE 3. Sensitivity analysis of the effect of climate change on energy and water costs (predictions for 2080–2100 minus predictions for 1980–2000; positive values indicate increased costs under climate change) during diurnal and nocturnal activity.

| Season, habitat, parameter, and value | Figure | Energy expenditure (mW/g) | | Evaporative water loss ($\mu\text{g water}\cdot\text{s}^{-1}\cdot[\text{g}]^{-1}$) | |
|---|--------|------------------------------|--------------------|---|------------------|
| | | Diurnal | Nocturnal | Diurnal | Nocturnal |
| Summer | | | | | |
| Open | | | | | |
| Original parameters | | | | | |
| Appendix S1: Table S2 | 5 | -3.29 ± 1.83 | -5.62 ± 1.05 | 2.27 ± 1.32 | 0.03 ± 0.36 |
| Body mass (g) | | | | | |
| 29.0 | S4 | -5.08 ± 2.64 | -8.01 ± 1.33 | 2.78 ± 1.78 | -0.05 ± 0.35 |
| 67.6 | S5 | -2.49 ± 1.46 | -4.48 ± 0.99 | 2.03 ± 1.10 | 0.09 ± 0.37 |
| Minimum energy expenditure during activity (mW/g) | | | | | |
| 4.0 | S6 | -3.88 ± 1.90 | -5.86 ± 0.92 | 1.93 ± 1.33 | -0.08 ± 0.20 |
| 12.0 | S7 | -2.68 ± 1.72 | -5.07 ± 1.52 | 2.62 ± 1.30 | 0.26 ± 0.63 |
| Fur reflectivity (%; dorsal/ventral) | | | | | |
| 20/17.5 | S8 | -3.11 ± 1.77 | -5.61 ± 1.05 | 2.43 ± 1.29 | 0.03 ± 0.36 |
| 60/52.5 | S9 | -3.48 ± 1.87 | -5.62 ± 1.05 | 2.09 ± 1.34 | 0.03 ± 0.36 |
| Shade | | | | | |
| Original parameters | | | | | |
| Appendix S1: Table S2 | 11 | -1.73 ± 1.05 | -2.57 ± 0.93 | 0.69 ± 0.51 | 0.20 ± 0.40 |
| Body mass (g) | | | | | |
| 29.0 | S17 | -2.98 ± 1.37 | -4.04 ± 0.86 | 0.64 ± 0.63 | 0.06 ± 0.32 |
| 67.6 | S18 | -1.15 ± 0.85 | -1.84 ± 0.92 | 0.71 ± 0.44 | 0.30 ± 0.44 |
| Minimum energy expenditure during activity (mW/g) | | | | | |
| 4.0 | S19 | -2.53 ± 0.91 | -3.15 ± 0.49 | 0.32 ± 0.40 | -0.03 ± 0.14 |
| 12.0 | S20 | -0.94 ± 0.89 | -1.67 ± 1.16 | 1.08 ± 0.49 | 0.61 ± 0.62 |
| Fur reflectivity (%; dorsal/ventral) | | | | | |
| 20/17.5 | S21 | -1.73 ± 1.05 | -2.57 ± 0.93 | 0.69 ± 0.51 | 0.20 ± 0.40 |
| 60/52.5 | S22 | -1.73 ± 1.05 | -2.57 ± 0.93 | 0.69 ± 0.51 | 0.20 ± 0.40 |
| Winter | | | | | |
| Open | | | | | |
| Original parameters | | | | | |
| Appendix S1: Table S2 | 5 | -7.12 ± 2.65 | -7.43 ± 3.11 | 0.09 ± 0.55 | -0.11 ± 0.04 |
| Body mass (g) | | | | | |
| 29.0 | S4 | -18.29 ± 10.50 | -18.40 ± 10.31 | 0.02 ± 0.66 | -0.19 ± 0.06 |
| 67.6 | S5 | -6.99 ± 3.86 | -7.37 ± 4.17 | 0.08 ± 0.52 | -0.12 ± 0.04 |
| Minimum energy expenditure during activity (mW/g) | | | | | |
| 4.0 | S6 | -7.24 ± 2.50 | -7.43 ± 3.11 | 0.02 ± 0.42 | -0.11 ± 0.03 |
| 12.0 | S7 | -6.97 ± 2.82 | -7.41 ± 3.13 | 0.17 ± 0.67 | -0.10 ± 0.05 |
| Fur reflectivity (%; dorsal/ventral) | | | | | |
| 20/17.5 | S8 | -7.09 ± 2.71 | -7.43 ± 3.11 | 0.12 ± 0.61 | -0.11 ± 0.04 |
| 60/52.5 | S9 | -7.13 ± 2.59 | -7.43 ± 3.11 | 0.06 ± 0.49 | -0.11 ± 0.04 |

Notes: To determine sensitivity, the values of body mass, fur properties, and minimal rates of energy expenditure (Appendix S1: Table S2) were increased and decreased by 50% from our original parameterization. Dependent variables are the mean \pm SD change in predictions between 1980–2000 and 2080–2100 over the North American domain of our model. Values are per gram of body mass.

Availability of water

The ability of organisms to maintain water balance is crucial for survival (Fuller et al. 2014). As climates warm, diurnal animals may still be able to sustain activity if they can compensate for increased evaporative water loss by drinking water. For example, in free-ranging Arabian oryx (*Oryx leucoryx*), selection of thermal refuges was dependent not only on high ambient temperature but also on the availability of water (Hetem et al. 2012). Oryx sought thermal refuge less frequently during the rainy season than during the dry season, over a similar range of ambient temperatures, implying that microclimate selection was also enhanced by aridity. When both water and shade are scarce, such as in arid

regions, large mammals store the heat that otherwise would have been lost by evaporation during the day, resulting in body temperature rising by as much as 7°C (e.g., Schmidt-Nielsen et al. 1956, 1981, Fuller et al. 2014). Such dehydration-induced hyperthermia, however, brings an animal closer to heat death, or heat stroke in humans, and is not possible for small mammals due to their lower thermal inertia (Fuller et al. 2014). Access to water, by either drinking or by foraging for water-rich food items (e.g., arthropods and plants), may allow an animal to avoid hyperthermia by maintaining a positive water balance. Species from vegetated habitats, for example, were able to invade arid environments when water availability was increased by human settlements (Wasserberg et al. 2003, Letnic et al. 2014a, b).

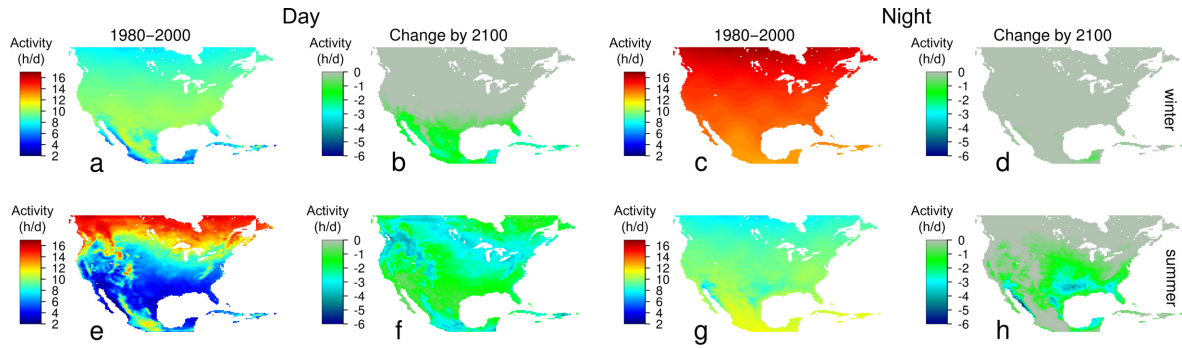


FIG. 9. Computed amounts of activity hours during past climate (1980–2000) and the difference in hours between past and future (2080–2100) climates. Data are mean values for a diurnal and nocturnal rodent active on the ground surface during winter (a and b, diurnal; c and d, nocturnal) and summer (e and f, diurnal; g and h, nocturnal). Each day, we counted the number of hours that did not require evaporative heat loss to maintain homeothermy. Predicted number of hours suitable for activity during past winter (1980–2000) was higher during the night than during the day by an average of 5.58 ± 1.58 h (mean \pm SD) at 100% of the locations with no effect of climate change by 2100 (night minus day, 5.92 ± 1.54 h). During past summers, the predicted number of hours suitable for activity was higher during the day than during the night by 4.36 ± 2.34 h at 43% of the locations, and lower by 3.85 ± 1.91 h at 57% of the locations. Under climate change, nocturnal activity will offer more hours of activity at 70% of the locations, with nights offering 4.03 ± 1.72 more hours of activity than days.

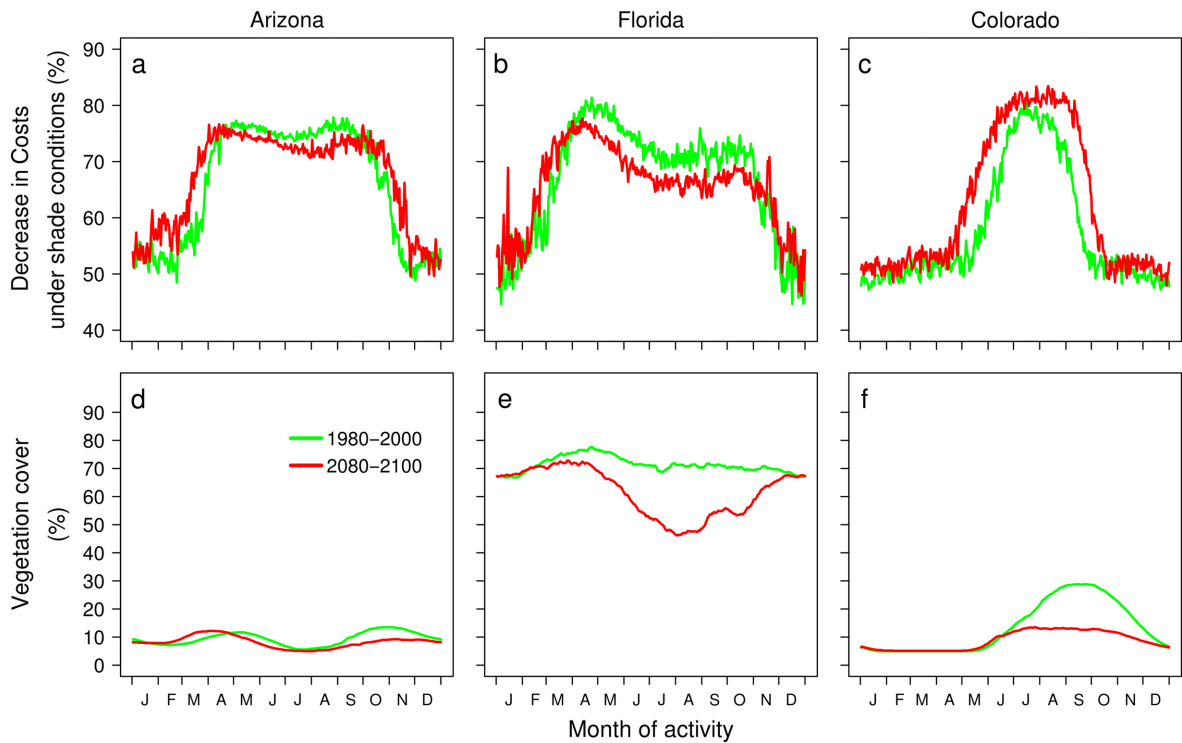


FIG. 10. Activity in the shade reduces the costs of water during activity. (a–c) We show the predicted percentage of water costs that animals may save by shifting activity to shaded microhabitats throughout the year. (d–f) We also show how percentages of vegetation cover vary annually and how climate change may reduce the availability of vegetation cover. Results are shown in three locations that represent three types of climates: Arizona (33.87° N, 111.47° E), which is relatively warm and dry; Florida (29.85° N, 82.23° E), which has a subtropical climate (warm, humid, and low seasonal and daily variations in temperatures); and Colorado (37.70° N, 104.85° E), which is relatively cold.

To estimate how water availability relates to water costs, and how future climate may change water availability, we analyzed estimates of past and future soil moisture (Levy et al. 2016a). Soil moisture may represent the availability of water for animals, since it reflects the relationship between the amount of water that reaches the ground as rainfall, and the amount of water that evaporates from the ground to the

atmosphere by factors such as temperatures, humidity, and radiation (Geiger 1965, Gates 1980, Ribot et al. 1996). For 1980–2000, we found that soil moisture is mostly lower at warm locations where high evaporative water loss is required during activity (Figs. 12g, 14a), with latitudinal and longitudinal gradients similar to the patterns of green vegetation cover (Fig. 12e). By 2100, soil moisture will decrease in the

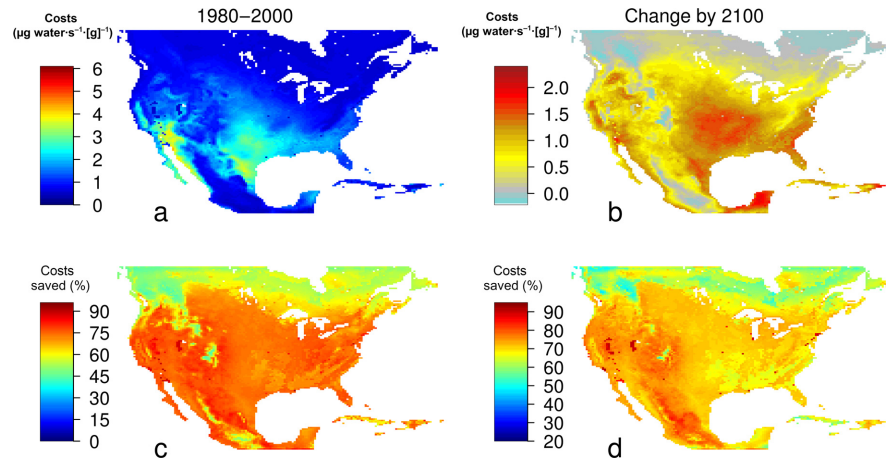


FIG. 11. Computed water costs of activity at shaded microhabitats during summer. Data are (a) mean values for a diurnal rodent active on the ground surface during past climate (1980–2000), (b) the difference in costs between past and future (2080–2100) climates, and (c, d) the percentage of water costs saved by activity in the shade. Under past climate, activity in the shade is predicted to reduce water costs by an average of 73% (c). Under climate change, activity in the shade may reduce 71% of the predicted increase in water costs (d). Model predictions are per gram body mass. For predictions for different values of body mass, fur properties, and minimal rates of energy expenditure, see Appendix S1: Figs. S17–S22.

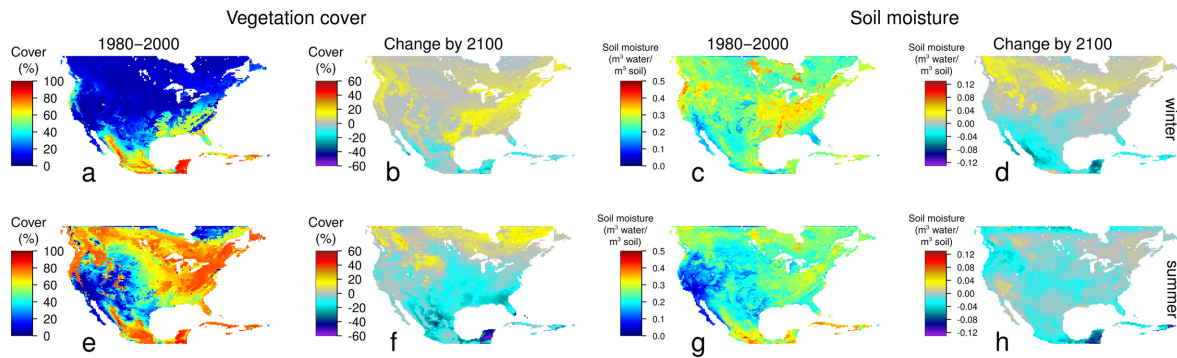


FIG. 12. Spatial distribution of natural resources that may buffer water costs of diurnal activity. We show predicted availabilities of vegetation cover and soil moisture under past climate (1980–2000) and the predicted shifts in resources between past and future (2080–2100). Data are mean values of vegetation cover and soil moisture during winter (a and b, vegetation cover; c and d, soil moisture) and summer (e and f, vegetation cover; g and h, soil moisture). Soil moisture values are for 0–10 cm depth below the ground surface.

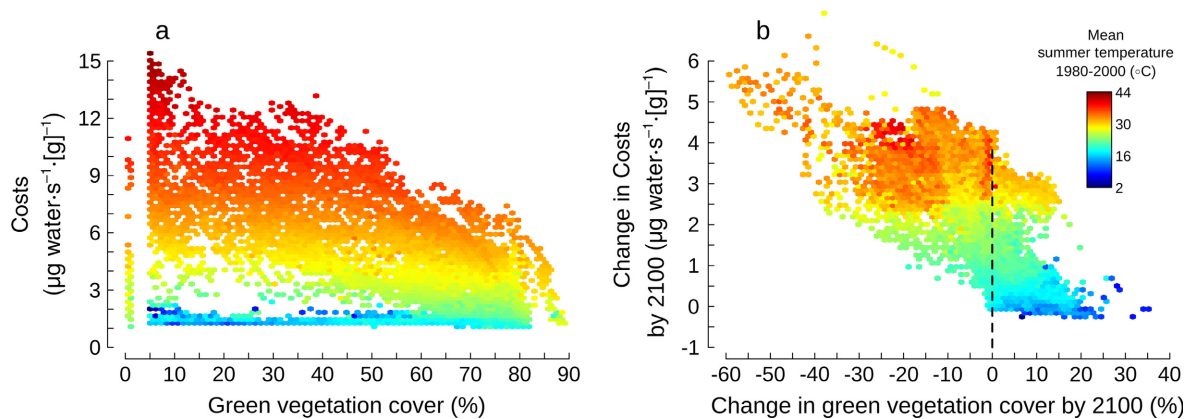


FIG. 13. (a) Past (1980–2000) vegetation cover during the summer is mostly lower at warmer locations, especially where water costs are predicted to be high. (b) By 2100, vegetation cover is predicted to mostly decrease at warm locations and increase at cold locations. In both panels, the color of each point indicates the mean air temperature (3 cm height) during summer at one or more locations. In panel b, the dashed line represents no change of green vegetation cover under future climate. Model predictions are per gram body mass.

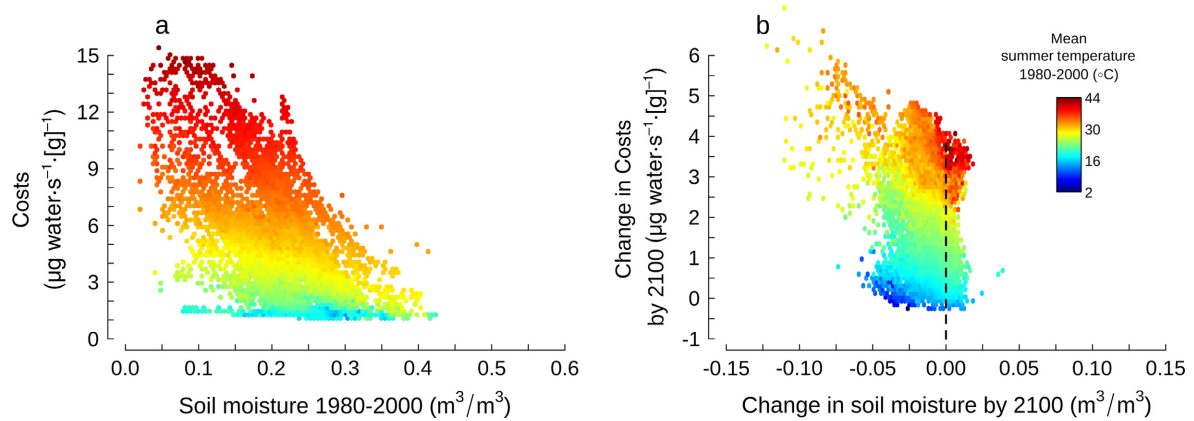


FIG. 14. (a) Past (1980–2000) soil moisture during the summer is mostly lower at warmer locations, especially where water costs are predicted to be high. (b) By 2100, soil moisture is predicted to mostly decrease, regardless of the summer temperatures. In both panels, the color of each point indicates the mean air temperature (3 cm height) during summer at one or more locations. In panel b, the dashed line represents no change in soil moisture under future climate. Model predictions are per gram body mass.

summer at 83% of the locations, both warm and cold (Figs. 12h, 14b).

Integrating heat input, shade, and water availability

In sum, we predict that future estimates of changes in climate, vegetation cover and water availability will create an environment in which nocturnal activity is favored. As heat input increases, higher rates of evaporative cooling would be required to avoid hyperthermia during diurnal activity at more days every year and at more locations than before. Shaded microhabitats, in which animals can escape the heat and avoid excess water costs, will become less abundant, decreasing opportunities for behavioral thermoregulation while increasing their competitive and predation costs. Free surface water will be less abundant as well, hence reducing the ability of animals to maintain water balance without concentrating activity near areas of water such as waterholes, lakes, streams, and rivers. Animals so constrained spatially become easier targets for predators. At warm locations, species that shift their activity to the cooler hours of the night will avoid excess water loss and will not have to limit their activity to the vegetated patches or change their spatial distribution. Unless shifts in activity times emerge, animals will either shift their spatial ranges or compete for lesser shade patches and water resources.

ECOLOGICAL AND PHYSIOLOGICAL COSTS OF SHIFTING TO NOCTURNALITY

Although many organisms show some flexibility in choosing activity patterns, switching activity patterns poses challenges on every ecological level, from individuals to communities. To achieve an adaptive temporal shift, the benefits of shifting activity patterns should exceed the costs. For example, species may avoid shifting activity patterns if the decrease in water costs is only marginal relative to the ecological and physiological costs of shifting. For diurnal individuals, night-time activity may entail at least one obvious cost: they will be outperformed by nocturnal animals that possess sensory adaptations in vision, hearing, and

smell for sensing an environment under low light conditions (e.g., Bolen and Green 1997, Warrant 1999, Takahashi 2010), as well as other nocturnal adaptations. Nevertheless, in spite of the evolutionary constraints, species have shifted activity patterns in the past (Roll et al. 2006, Maor et al. 2017), suggesting that diurnal species could develop evolutionary adaptations to cope with the novel conditions of the night. However, given the rapidness of current climate change, the rate of climate warming may be too fast for diurnal species to gradually develop nocturnal adaptations. Unfortunately, we lack knowledge about the rates of genetic and plastic changes that may promote nocturnal adaptations, but it is possible that smaller species will be able to adapt more easily since their lifecycles are shorter, and they will have more generations in the same length of time.

Interestingly, some diurnal species already possess several nocturnal adaptations, often as a lasting legacy of their nocturnal ancestors. The golden spiny mouse, for example, possesses several morphological and physiological adaptations of a nocturnal animal, such as a rod-based retinal structure suitable for night vision (Kronfeld-Schor et al. 2001b), high capacity for non-shivering thermogenesis, an adaptation for cooler nights (Kronfeld-Schor et al. 2000), and an underlying nocturnal circadian rhythm (Levy et al. 2007). In fact, ~10% of diurnal mammals possess rod-cone densities that approach or even overlap densities in nocturnal mammals (Hut et al. 2012), which may enable them to use vision during night activity. Another strategy to increase performance during night-time is to rely on moonlight, as found in the central and South American owl monkeys (*Aotus azarae*) for example, which are nocturnal during moonlit nights and crepuscular during new moon nights (Fernández-Duque et al. 2010, Hut et al. 2012). Shifting activity patterns may cause activity to be out of synchrony with important physiological and biochemical processes (reviewed by Kronfeld-Schor and Dayan 2008). Such asynchrony, for example, may reduce the efficiency of physiological processes that are optimal during sleep, subsequently decreasing organismal performance during wakefulness (reviewed by Vyazovskiy and Delogu 2014). In humans, nocturnal activity has been associated with mental and physical disorders and can have a negative impact on

human safety, performance, productivity, and longevity (Turek and Takahashi 2001).

At the population level, temporal switching to nocturnality may disturb intraspecific interactions (Kronfeld-Schor et al. 2017). For species that rely on visual cues, finding and selecting mates for reproduction may be challenging, especially when color visual cues are important in sexual selection. The lack of light may also decrease the capacity of animals to forage in groups, an important anti-predatory behavior (reviewed by Beauchamp 2007). At the community level, similar to disturbance of interactions under spatial shifts of species (Araújo and Luoto 2007, Schweiger et al. 2008, Singer et al. 2013), interactions between species may become mistimed if species shift their daily activity patterns in different directions or magnitudes (reviewed by Buckley 2013, Kronfeld-Schor et al. 2017). Topographic impacts, such as north and south facing slopes, can also induce shifts in predator–prey interactions (Porter et al. 2002). Temporal partitioning, a separation in time that promotes coexistence among competitors, predators, and their prey, and parasites and their hosts (reviewed by Kronfeld-Schor and Dayan 2003, Castillo-Ruiz et al. 2012, Kronfeld-Schor et al. 2017), may collapse and leave subordinate species in danger of extinction (Buckley 2013). New competitive interactions may arise, with aggressive encounters occurring at higher rates as more species are simultaneously active, and with resources depleting faster if the ratio of predators and prey species increases. On the other hand, species that will stay diurnal may benefit from a diurnal niche that is relatively free from competition and predatory risks, especially if they develop water conservation adaptations, such as lower skin water permeability, high urine concentration ability, lighter color, or smaller body size.

It is important to note that, although inverting activity times poses challenges, animals may face challenges when shifting spatial distributions as well. In fact, we argue that many of the terms often used to describe ecological and evolutionary processes that occur at the spatial scale are also relevant to temporal scales, such as species distributions, fundamental and realized niches, gene flow, and range expansions (Table 4). For instance, species with specialized

niches and strong dependency on highly coevolved ecological interactions may not be able to establish populations in new habitats and ranges (reviewed by Lurgi et al. 2012). These species are at higher risk of extinction under climate change since their distribution is restricted to a certain environmental characteristics (reviewed by Colles et al. 2009). Generalists, on the other hand, should more easily find suitable resources and positive interactions in new locations (reviewed by Lurgi et al. 2012). We suggest that one of the only escape paths from climate change for habitat specialists is to shift their activity time. Whether or not the temporal niche of a species remains unchanged will depend initially on the factors or processes that currently limit its temporal flexibility, such as ecological interactions and evolutionary constraints. Restriction of activity patterns is most likely for diurnal species with a limited ability to perform in the dark. However, for species that are simply excluded from nocturnal activity times by ecological interactions, a shift in the temporal niche may occur under climate change when the ecological interaction is released.

DIRECTIONS FOR FUTURE RESEARCH

The ability of animals to buffer climate change by shifting activity times is largely unknown. We need a barrage of studies testing the ability of animals to shift activity times at both fine (hourly to daily) and coarse (seasonal and annual) scales in response to climatic stressors and other environmental conditions. Future studies should focus on comparing activity times under a gradient of vegetation cover, humidity, temperature, and water availabilities. Such measurements may highlight how the triangle of climate, vegetation cover, and water availability may contribute to activity patterns and affect ecological populations and communities. Mechanistic models, such as Niche Mapper, may be useful in searching for features that make species less vulnerable to warming scenarios.

We should also aim to better understand the interplay between the abiotic and biotic forces that determine activity patterns. Since the environments that animals experience

TABLE 4. Terms extensively used in studies of spatial species distributions, and their relevance to the temporal niches of species.

| Term | Spatial scale processes | Temporal scale processes |
|-----------------------|---|---|
| Species distribution | the latitudinal, longitudinal, and altitudinal limits of a species | the activity times of a species |
| Fundamental niche | the range of locations that offer abiotic conditions in which the species has a positive intrinsic growth rate | the range of activity times that provide abiotic conditions in which the species has a positive intrinsic growth rate |
| Realized niche | the range of locations in which the species has a positive intrinsic growth rate when coexisting with conspecifics and other species | the range of activity times in which the species has a positive intrinsic growth rate when coexisting with conspecifics and other species |
| Range limits | the locations at the border of a species distribution | the beginning and the end of a species activity phase |
| Range expansion | individuals are moving outside of the past range limits | individuals are active at times beyond their past activity phase. |
| Range shift | individuals are moving outside of the past range limits while disappearing from other locations | individuals are active at times before or after their past activity times while limiting their activity at other times |
| Maladaptive gene flow | species fail to adapt to conditions immediately outside their range limits because of gene flow from populations at the center of the range | species fail to adapt to activity at times outside of their activity phases because of gene flow from individuals that are highly adapted to current activity phase |

change rapidly throughout the day, the measurements of activity, environment, and costs should be at such fine scales. This is a challenging task, since, as far as we know, researchers cannot measure physiological costs such as energy expenditure and evaporative water loss at hourly scales under natural conditions. Moreover, activity costs can only be measured during activity, so we cannot measure activity costs at hypothetical times, although such differences can be explored in computational simulations (e.g., energy and water costs of night activity in a diurnal animal; Levy et al. 2012). As we demonstrated in our analysis, one way to tackle this challenge is by using heat- and mass-transfer physics to calculate energy and water costs (Levy et al. 2012, 2016c). Such costs can be estimated by calculating the amount of heat that an animal needs to generate or dissipate to maintain an optimal body temperature, given the morphological, physiological, and behavioral characteristics of the animal and the current climatic conditions (Porter et al. 1994, Porter and Kearney 2009). Theoretically, one can calculate how much energy and water costs may be saved by switching activity patterns, and use ecological data on each day phase (e.g., food availability, competition, predation, etc.) to estimate the ability of shifts in activity times to buffer the effects of climate change. As far as we know, our climatic data set and endotherm model are the only current approach to calculate how climate change may affect costs of activity. To decrease error propagation across calculations, we encourage the development of multiple climate data sets at hourly resolutions that include the important variables to calculate costs of activity (e.g., by downscaling the output of other global circulation models), and multiple modeling approaches to estimate energy and water costs.

We also lack understanding of the ecological and physiological costs of shifts in activity patterns. Measurements of temporal differences in foraging, anti-predatory, and communication strategies and their effect on growth, survival, and reproduction may shed light on the costs and benefits of shifts in activity. For example, the diurnal seabird, the Common Murre (*Uria aalge*), extends its activity into the night during the breeding season. At night, its diving depths decrease with light levels, probably resulting in reduced foraging efficiency (Regular et al. 2011). Although foraging success is lower at night, such extension of activity times may not have occurred if the costs of foraging at night outweighed the benefits. Future studies should also explore the interspecific consequences of temporal shifts, where temporal shifts in the activity of one species may cause responses in other species. For example, if a predator becomes nocturnal, nocturnal prey species may face a novel predator. On the other hand, if a prey species becomes nocturnal, the nocturnal predators will enjoy a new prey species while strictly diurnal predators will suffer from fewer prey items.

CONCLUSION: TREATING TIME AS A CLIMATIC LANDSCAPE IN CLIMATE CHANGE RESEARCH

Time is an ecological resource, a landscape-like space, where animals perform activities such as foraging, mating, sleeping, and other fitness-related actions. And like space, time offers gradients in climate, from the colder hours of the night to the warmer hours of the day, and from the warmer

summers to cold winters. But unlike space, repeated temporal climatic cycles at the diel scale may enable a species to behaviorally adapt to environmental warming, without shifts in distribution or preferred habitats. While ecologists extensively explored how climate warming may cause spatial shifts in geographic distributions (e.g., Ribot et al. 1996, Parmesan and Yohe 2003, Natori and Porter 2007, Marshall et al. 2008, Kearney et al. 2009, Kearney 2013), and how warming can shape life histories (e.g., Diamond et al. 2011, Levy et al. 2016b), shifts on the diel scale remained relatively unexplored (e.g., Moyer-Horner et al. 2015, Levy et al. 2016c, Mathewson et al. 2016). Since activity times are flexible in many species, integrating such shifts in climate change predictions can help in our understanding of extinction risks under global warming. Our framework presents how one can estimate the locations in which shifts in activity times are likely to occur, based on the energy and water climatic costs of activity, and environmental factors such as vegetation cover and water availability. We suggest that adopting time as a climatic landscape when predicting impacts of climate change can shed light on the fate of organisms, populations, and communities under climate change.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecm.1334/full>

DATA AVAILABILITY

Code is available from GitHub: https://github.com/levyofi/niche_mapper_activity_times and Zenodo: <https://doi.org/10.5281/zenodo.1404109>