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REVIEW

How dryland mammals will respond to climate change: the effects of body size, heat load and a lack of food and water

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ABSTRACT

Mammals in drylands are facing not only increasing heat loads but also reduced water and food availability as a result of climate change. Insufficient water results in suppression of evaporative cooling and therefore increases in body core temperature on hot days, while lack of food reduces the capacity to maintain body core temperature on cold nights. Both food and water shortage will narrow the prescriptive zone, the ambient temperature range over which body core temperature is held relatively constant, which will lead to increased risk of physiological malfunction and death. Behavioural modifications, such as shifting activity between night and day or seeking thermally buffered microclimates, may allow individuals to remain within the prescriptive zone, but can incur costs, such as reduced foraging or increased competition or predation, with consequences for fitness. Body size will play a major role in predicting response patterns, but identifying all the factors that will contribute to how well dryland mammals facing water and food shortage will cope with increasing heat loads requires a better understanding of the sensitivities and responses of mammals exposed to the direct and indirect effects of climate change.

KEY WORDS: Dehydration, Homeostasis, Osmoregulation, Starvation, Thermoregulation

Introduction

Drylands, which comprise about 45% of the Earth's land surface (Fig. 1) and support substantial biodiversity (Mirzabaev et al., 2019), have warmed and dried more strongly than other ecoregions over the last 40 years (Zhou et al., 2015). As a consequence of climate change, warming and drying will probably continue, with precipitation predicted to become more variable, and droughts and heatwaves more frequent (Mirzabaev et al., 2019). Because there is a strong link between primary productivity and precipitation in drylands, drying results in reduced productivity that permeates across trophic levels (Chesson et al., 2004). Warming may alter the

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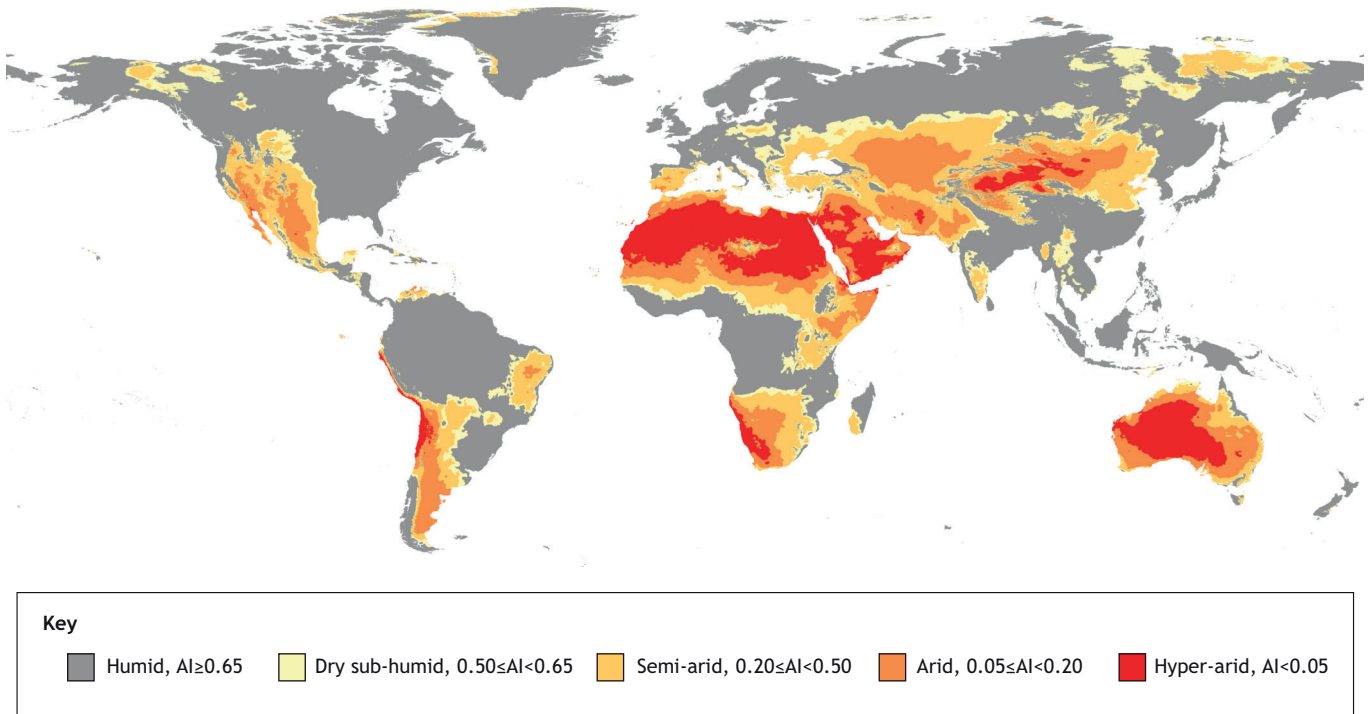
temporal distribution of food availability through phenological shifts (for example, earlier plant growth), resulting in trophic mismatches (Post et al., 2008). Altered vegetation composition with climate change may also result from increasing spread of invasive plants, bush encroachment and wildfires (Mirzabaev et al., 2019). Mammals in drylands will therefore be affected not only by the direct effect of increasing heat, but also indirectly through the impact of climate change on their habitats and resources.

Mammals provide important 'ecosystem services' in drylands, including roles as ecosystem engineers, seed dispersers and apex predators (Lacher et al., 2019). While many mammal species have adaptations that allow them to survive in the harsh and often unpredictable current dryland environment (Fuller et al., 2014; Walsberg, 2000; Withers et al., 2016), further climate change may severely challenge their physiological welfare, and ultimately, their fitness (Fuller et al., 2016). Dryland mammals typically have to contend with high diurnal heat loads, as a consequence of high air temperatures and high solar radiation (Fig. 2). As environmental heat load increases, mammals become more reliant on evaporative cooling to maintain homeothermy (Mitchell et al., 2018). The low water vapour pressure in dry environments facilitates a high rate of evaporative heat loss, which is beneficial and sustainable provided that mammals can replace the lost body water. Many mammals in drylands, and particularly small mammals that can dehydrate rapidly, avoid the costs associated with activity in the heat by being active at night or crepuscular. Indeed, the majority of dryland mammal species are active nocturnally (Bennie et al., 2014). Being active nocturnally is not without thermal cost, however. At night, even if air and substrate temperatures remain relatively high (Walsberg, 2000), clear dry skies create a substantial radiative heat sink (Fig. 2), resulting in a greater demand for endogenous heat production, and hence energy intake, to maintain body temperature (Mitchell et al., 2018). Dryland mammals therefore often face high water and high metabolic energy demands. These demands can be attenuated by manipulation of the 24 h activity pattern and the use of microclimates. The aardvark *Orycteropus afer*, for example, typically remains within a thermally buffered burrow during the day and is active at night (Fig. 2), but in the face of insufficient food it shifts its activity to the warmer day, thereby reducing energetic costs (Weyer et al., 2020), but probably at the cost of increasing water loss.

Most predictive models of mammalian responses to climate change have focused on the direct effects of higher ambient temperatures. In this perspective article, we argue that while a higher heat load on mammals in drylands will be detrimental, and heatwaves may indeed be catastrophic, the compound effects of reduced water and food availability will result in far greater decrements in performance (reflected by performance measures such as growth, body condition and reproductive output) than heat alone. We consider how the interplay between these stressors will result in mammals facing competing demands on homeostatic

Fig. 1. Global distribution of drylands in 2019. Drylands are defined as areas with an aridity index (AI) of less than 0.65, with AI defined as the ratio of average annual precipitation to potential evapotranspiration. Note that there is considerable annual variability in the distribution of drylands, as climatic factors vary, and that drylands are expected to expand further with climate change. Data were sourced from Abatzoglou et al. (2018).

systems, and the implications of body size for their responses. Finally, we reflect on how those understandings will contribute to improved predictions of how dryland mammals facing heat, water and food shortage will cope in a changing world.

Effect of increasing ambient temperature

As a consequence of climate change, mammals are facing long-term changes in climate trajectories with extreme events overlaid (Harris et al., 2018). The capacity of mammals to cope with heat stress has
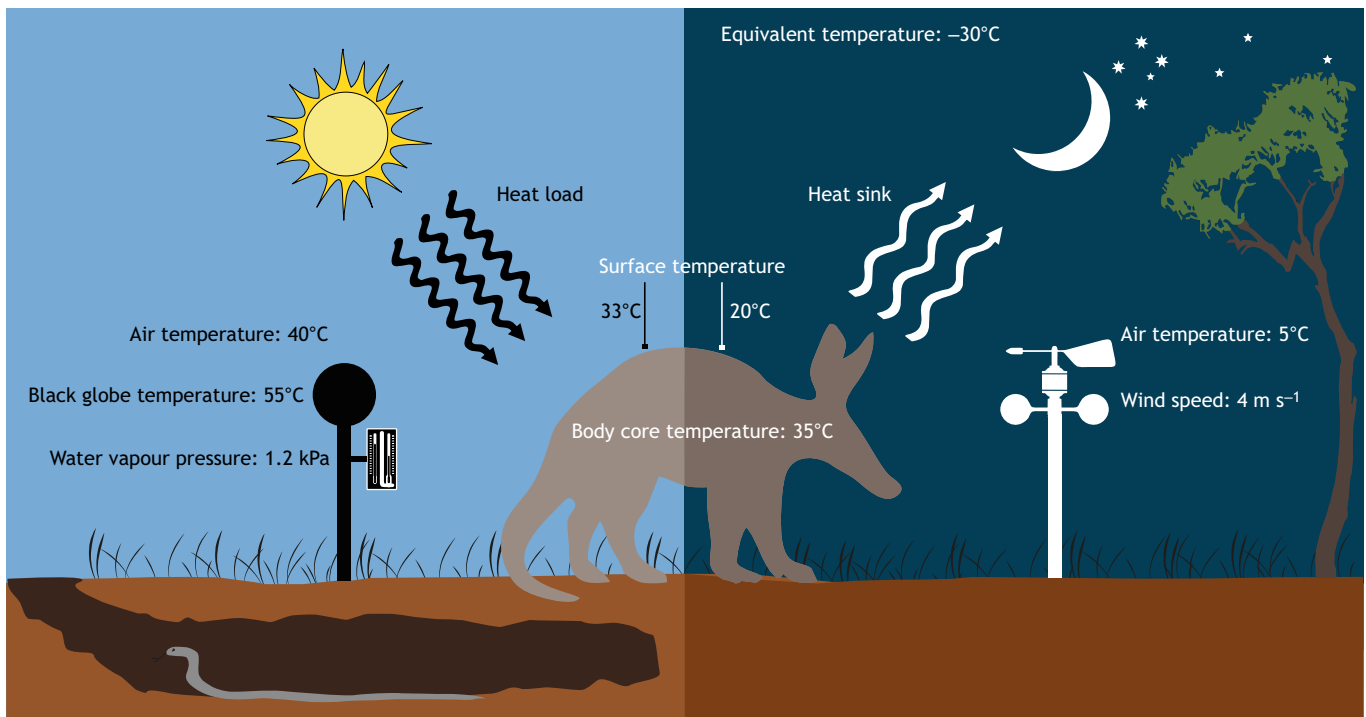

Fig. 2. Major gradients for heat transfer between a mammal and its dryland environment during the day and at night. Left, day; right, night. Illustrative climatic measurements and animal temperatures are shown.

been studied for many years, but only recently, against the background of climate change, have the consequences of chronically increasing ambient heat loads and heatwaves started to become evident for free-living mammals. Only since the 1980s have mass mortality events across taxa, attributed to heat extremes, been reported (Fey et al., 2015). Mean annual air temperatures in drylands may increase by as much as 6.4°C by the end of this century (Wei et al., 2019), while heatwaves are likely to occur more often and with greater intensity and longer duration (Perkins-Kirkpatrick and Lewis, 2020).

Mammals respond to high ambient heat loads by changing their behaviour and by increasing heat dissipation through peripheral vasodilatation and evaporative cooling (Bartholomew, 1964; Schmidt-Nielsen and Schmidt-Nielsen, 1952; Withers et al., 2016). Dry heat loss facilitated by peripheral vasodilatation occurs only if the operative temperature of the environment is lower than the body surface temperature. Once operative temperature exceeds body surface temperature, mammals require evaporative cooling to dissipate both the heat gained from the environment and their metabolic heat production, to maintain a stable body core temperature (Mitchell et al., 2018). If ambient heat load continues to increase, there comes a point when the heat load exceeds the mammal's capacity for evaporative cooling, and body core temperature will rise. In addition, as a result of the Q_{10} effect, metabolic rate will increase exponentially as body temperature increases, further increasing metabolic heat production (Withers et al., 2016). When body temperature increases beyond its normal range with increasing ambient heat load, a mammal will be forced outside its prescriptive zone (Fig. 3A) and into the tolerance zone (Mitchell et al., 2018), where physiological malfunction is more likely to occur, resulting in reduced performance. If ambient heat load increases further, resulting in a continued increase in body temperature, a mammal may be forced out of its tolerance zone and into the survival zone, where its life is threatened (Mitchell et al., 2018). The degree of compromise of physiological function, and risk of death, is likely to depend on the duration of time that a mammal spends outside its prescriptive zone. Many mammals, particularly small diurnally active desert mammals (Walsberg, 2000), tolerate transient episodes of high body temperature.

The ambient heat load that defines the upper limit of a mammal's prescriptive zone, and is associated with increasing risk of physiological malfunction, will be influenced by its body size. Smaller mammals have a greater surface area to volume ratio than larger mammals, and therefore they gain environmental heat more rapidly, per kilogram of body mass, when under ambient heat load (Fig. 4). Smaller mammals also have a greater mass-specific metabolic rate, and hence metabolic heat production per gram of tissue, and a greater mass-specific rate of evaporation required to maintain homeothermy (Fig. 4). Consequently, dissipating heat by evaporative cooling results in more rapid dehydration in smaller mammals than in larger mammals (Schmidt-Nielsen and Schmidt-Nielsen, 1952). As heat load increases, therefore, smaller mammals exposed to the elements will experience a greater increase in body temperature and will probably be forced out of the prescriptive zone at a lower ambient heat load than a similarly exposed larger mammal. As might be expected, most small mammals avoid detrimental exposure to heat by escaping into cooler and shaded microclimates like those offered by burrows. Ground squirrels *Ammospermophilus leucurus* and *Xerus inauris*, for example, which can be active across hot days with high solar radiation, avoid severe hyperthermia by shuttling in and out of burrows (Chappell and Bartholomew, 1981; Fick et al., 2009). Outside the burrow,

body core temperature rises rapidly, as the squirrels can gain heat from their hot environments at a rate of about 6-fold that of their basal metabolic heat production (Chappell and Bartholomew, 1981). In the cool burrows, the high mass-specific dry heat loss rate of small-bodied squirrels allows them to lower body temperature rapidly (Taylor, 1977) and they also can implement conductive cooling by direct contact with the substrate. Smaller mammals shuttling between variable microclimates will have a much more labile body temperature than a larger mammal like an elephant (Fig. 4), which remains predominantly exposed to the prevailing macroclimate, and buffered by its greater thermal inertia. Nonetheless, African (savanna) elephants *Loxodonta africana* seek shade under trees with increasing ambient heat load (Mole et al., 2016), but their larger size does mean that fewer thermal refuges are available to them (Liow et al., 2008; Schmidt-Nielsen and Schmidt-Nielsen, 1952) and they have to balance shade-seeking with the need to traverse a large area to satisfy their higher absolute energy and water requirements (Fig. 4).

Given the consequences of small body size for the rate of heat gain under heat load, and the risk of dehydration, one would expect that heatwaves would cause greater mortality in smaller, than in larger, mammals if they are unable to escape from the heat. Extreme heat events in Australia have killed many thousands of flying foxes (*Pteropus* spp., 0.1–1.5 kg body mass), koalas (*Phascolarctos cinereus*, 4–15 kg) and possums (*Trichosurus vulpecula*, 1.2–4.5 kg; *Pseudocheirus peregrinus*, 0.5–1.1 kg) (Bird, 2009; Gordon et al., 1988; Ratnayake et al., 2019; Welbergen et al., 2008). The koala deaths were associated with a heatwave during a drought, and it is more likely that koalas, and other medium-sized or larger mammals, will succumb to heatwaves when they occur with drought or insufficient water availability. Common to most of the Australian mammal species that have died in large numbers in heatwaves is an arboreal lifestyle (Turner, 2020), a habit shared with most birds, which also experience high mortality during heatwaves (McKechnie et al., 2012). Flying foxes succumb when air temperature exceeds 42°C, although the heat load they experience also will be influenced by other factors like solar radiation (Ratnayake et al., 2019).

Birds and mammals exposed to an acute heat load may conserve body water, at least for a short time, by suppressing evaporative cooling, which results in body temperature rising (Gerson et al., 2019; Turner, 2020). That rise can be somewhat advantageous if body surface temperature also rises, because whenever body surface temperature exceeds operative temperature, there is a gradient for heat loss to the environment, and even when operative temperature exceeds body surface temperature, a higher surface temperature will reduce the rate of heat gain from the environment. The rise in body temperature, however, places mammals at risk of rapidly reaching a fatal body temperature, particularly for small mammals if ambient heat load continues to increase, or if dehydration ensues when evaporative water loss eventually is increased (Turner, 2020).

Larger mammals, with a smaller surface area to volume ratio, gain environmental heat at a lower rate, per kilogram of body mass, than smaller mammals. They also have greater absolute capacities for evaporative water loss and water turnover (Fig. 4). Although a rise in their body temperature in the heat can result in significant water savings (Ostrowski et al., 2003), large mammals with free access to water generally employ evaporative cooling to prevent their body temperatures from rising excessively (Fuller et al., 2016). Body temperature patterns of baboons (*Papio ursinus*) with access to drinking water, for example, did not differ in a simulated hot desert environment compared with at an air temperature of 22°C (Mitchell et al., 2009). The maximum daily body temperature of free-ranging
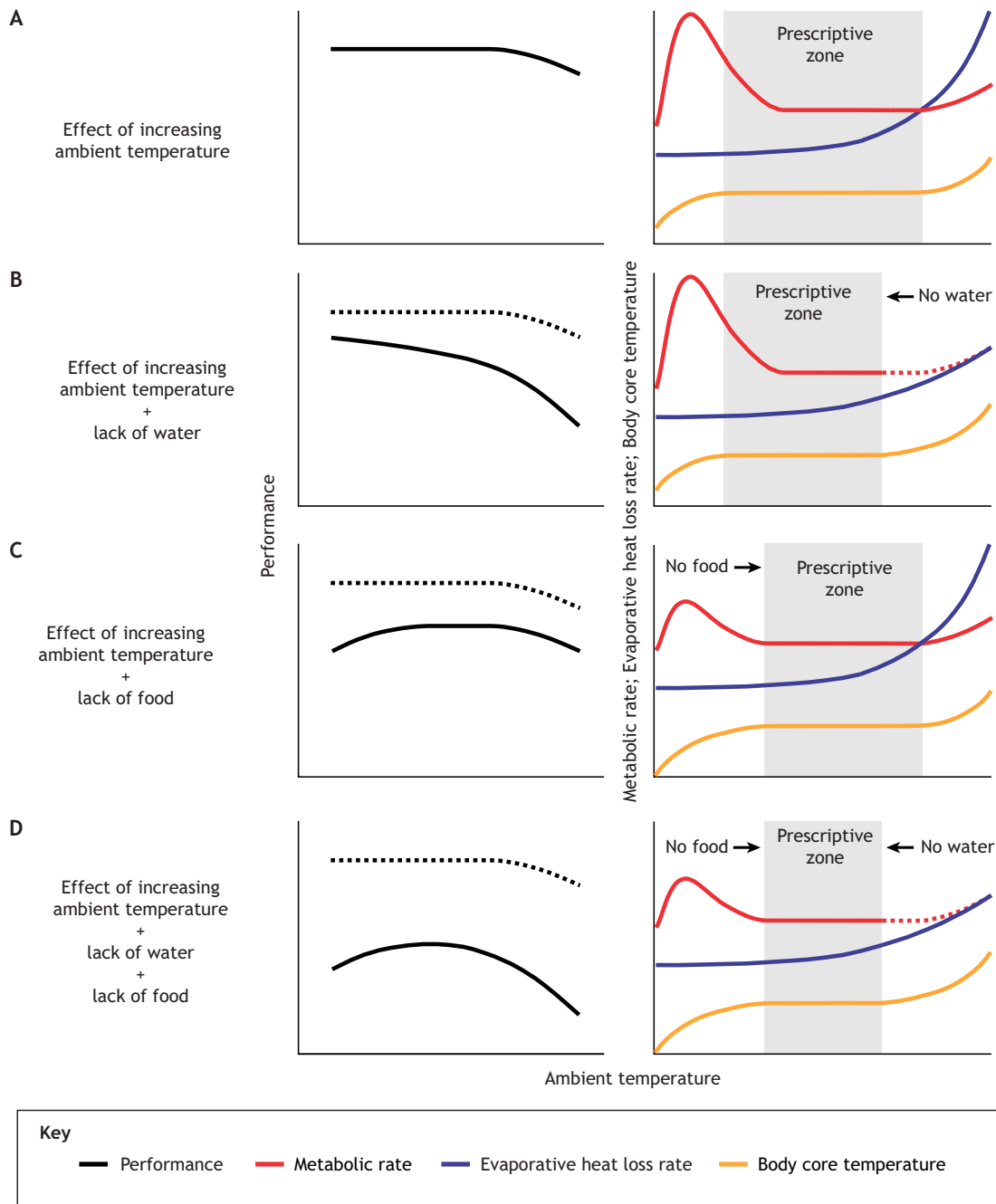
Fig. 3. Expected challenges facing mammals in drylands as a consequence of climate change, the associated predicted effects on mammal performance, and the likely implications for maintenance of body core temperature and width of the prescriptive zone. Left, consequence of climate change; centre, mammal performance; right, metabolic rate, evaporative heat loss rate, body core temperature and prescriptive zone. Performance can be measured as growth, body condition or reproductive output, for example. Mammals in drylands facing increasing heat load will experience a probable decrease in performance (A) that will become significantly worse when combined with lack of food and/or water (B–D).

savanna elephants also did not increase with increasing air temperatures, despite the elephants being under heat load from the environment for at least half of the study days (Mole et al., 2018). Indeed, contrary to what might be predicted from the physical principles of body size, when they have access to drinking water over hot summers, large free-living dryland mammals, ranging in size from about 15 kg to several thousand kilograms, maintain a remarkably similar endogenous 24 h rhythm of body temperature, with body temperature usually increasing by about 1°C over the course of a day (Fuller et al., 2016).

In support of the idea that well-hydrated large mammals routinely use evaporative cooling to maintain homeothermy is the finding that they implement evaporative cooling well before operative temperature approaches their body surface temperature (Mitchell et al., 2018). Cutaneous evaporative water loss of African elephants and Asian elephants (*Elephas maximus*), for example, increased exponentially from a relatively low air temperature of about 10°C, despite the elephants being sheltered from solar radiation (Dunkin et al., 2013). Exposure to solar radiation substantially increases the rate of evaporative water loss. Within an hour, the removal of shade
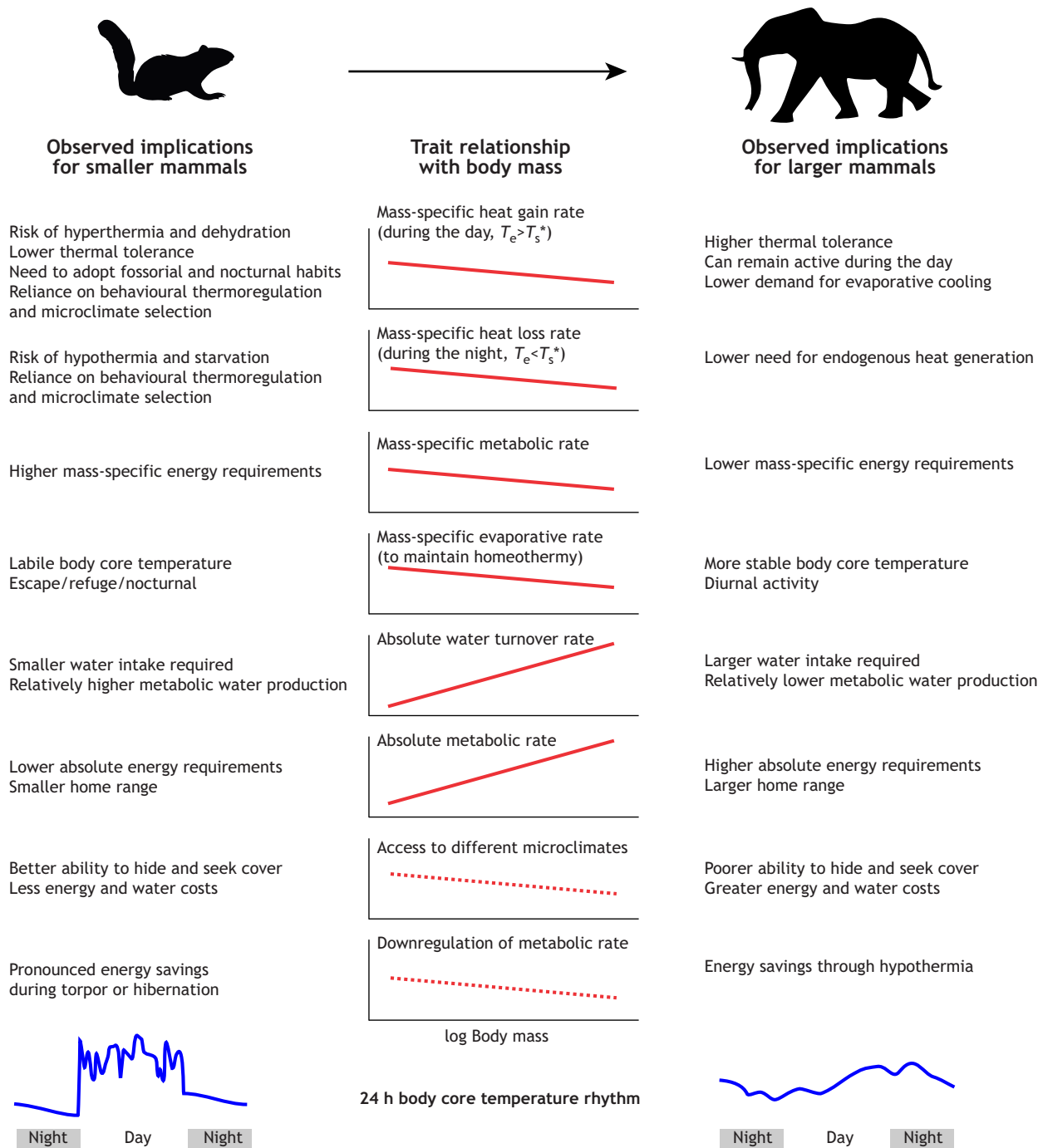
Fig. 4. Observed and predicted implications of body size (log body mass) for dryland mammals in terms of heat, metabolic energy and water balance. Relationships are derived from Fuller et al. (2016) and Withers et al. (2016). *T_e, operative temperature; T_s, surface temperature.

cover resulted in an approximate 4-fold increase in sweating rate in the eland (*Tragelaphus oryx*) and respiratory (panting) rate in the hartebeest (*Alcelaphus buselaphus cokii*) (Finch, 1972). Despite the demand for a large absolute water intake, the use of substantial evaporative cooling to prevent hyperthermia appears to be employed by many large mammals.

The option less costly than evaporative cooling, available to mammals when the environment imposes increased heat load, is to escape to cooler microclimates or be active at cooler times of the day. The advantage of avoiding exposure to high ambient temperatures is that a mammal may be able to remain within its prescriptive zone,

with less reliance on evaporative cooling than would be required had it not sought refuge. An environment analogous to that which many dryland regions will experience in a climate-changed future is the current Arabian Desert. In this environment, in severe summer heat with no drinking water, Arabian oryx (*Oryx leucoryx*) were inactive in shade during the day and shifted all their usual daytime activity to the night (Hetem et al., 2012a). Potentially, mammals will be able to reduce heat exposure with climate change by limiting their activity during the hottest part of the day, shifting to a crepuscular activity pattern, and eventually to a completely nocturnal activity pattern (Levy et al., 2019). One also might expect, if available, greater use of

cooler microclimates provided by structures like burrows, and the shade afforded by trees and shrubs (Fuller et al., 2016). Shifting activity to the night or seeking refuge during the day may not be without physiological and ecological costs, however. Shade-seeking or use of other cooler microclimates may compromise feeding unless the mammal can show a compensatory increase in nocturnal foraging, but the ability of mammals to shift activity to night may be constrained by factors such as the energetic costs of being active and exposed during the colder night, competition with nocturnal species, predation, or a lack of nocturnal adaptations like night vision (Fuller et al., 2016; Levy et al., 2019).

An advantage of reduced activity in the heat is lower metabolic heat generation, and therefore a smaller heat load to dissipate. Many diurnal mammals decrease feeding and activity in the heat (Withers et al., 2016). A small desert mammal, the golden spiny mouse *Acomys russatus*, ceased foraging when the rate of evaporative water loss exceeded water intake, despite its water being obtained from food (Levy et al., 2016). An advantage of lower metabolic heat production is that the upper limit of the prescriptive zone will increase, as shown for humans at different work rates (Lind, 1963). However, for mammals that are not able to compensate by feeding at night, reduced activity and feeding in the face of chronically high heat loads may ultimately threaten survival.

Indeed, the sub-lethal effects of chronic exposure to high ambient temperatures are likely to become more evident with continuing warming, as shown for birds (Conradie et al., 2019), and as revealed by two long-term data sets for the meerkat (*Suricata suricatta*) and African wild dog (*Lycaon pictus*) (van de Ven et al., 2020; Woodroffe et al., 2017). For meerkats, increasing air temperature over the past two decades has been associated with reduced daily body mass gain, and higher mortality of pups, probably partly as a result of chronic dehydration resulting from evaporative water loss over the day (van de Ven et al., 2020). For the larger wild dog, long-term records have revealed that higher air temperatures are associated with reduced activity, higher pup mortality, smaller litters, and longer inter-birth intervals (Woodroffe et al., 2017). Unlike another diurnal carnivore, the cheetah *Acinonyx jubatus*, which can hunt on moonless nights (Hetem et al., 2019), wild dogs facing high ambient heat loads appear to be able to shift activity to the night only when there is moonlight available (Rabaiotti and Woodroffe, 2019). While it is well known that exposure to high ambient heat load may directly compromise reproduction, by disrupting spermatogenesis, oocyte development and maturation, embryonic development and foetal growth (Hansen, 2009), the additional indirect effects of heat on recruitment, as demonstrated for meerkats and wild dogs, may threaten the continued survival of these mammal species, with climate change.

Effect of increasing ambient temperature and a lack of water
Mammals inhabiting drylands will be exposed to an increasing frequency of droughts and more variable precipitation superimposed on a warming climate (Mirzabaev et al., 2019; Naumann et al., 2018). Many mammals in drylands, particularly small mammals (Fig. 4) but some large species too (Williams et al., 2001), rely on preformed water in their diet and metabolic water produced from the oxidation of substrates (Withers et al., 2016). Most large mammals, however, have to supplement preformed and metabolic water with free water, and drinking water availability is also predicted to be reduced in drylands under climate change. Even for small mammals, high heat loads may require obligatory drinking (Walsberg, 2000) and therefore reliance on the diminishing free water.

Insufficient replacement of body water causes dehydration. A common response of mammals to dehydration, particularly in larger mammals, is an inhibition of panting and sweating during heat stress (Fuller et al., 2016; McKinley et al., 2018). A reduction in evaporative water loss in a dehydrated mammal under heat load will cause body temperature to increase sooner and faster than it would have if the mammal was euhydrated (Hetem et al., 2016). Dehydration-induced hyperthermia, therefore, will result in the upper limit of the prescriptive zone decreasing, and therefore the width of the prescriptive zone reducing (Fig. 3B). While the inhibition of evaporative cooling serves to prevent hypovolaemia and hyperosmolarity, the additional heat storage and earlier rise of body temperature in the heat will ultimately compromise other functions and increase the risk of pathological hyperthermia. Indeed, with continued daily heat exposure, maximum daily body temperature progressively increases in dehydrated mammals, as demonstrated for baboons (*Papio hamadryas*; Mitchell et al., 2009), camels (*Camelus dromedarius*; Bouâouda et al., 2014) and sheep (*Ovis aries*; Strauss et al., 2015) in simulated desert environments.

The finding that large mammals cope well with heat when euhydrated but abandon homeothermy and become hyperthermic when they lack water, indicates that they are more likely to succumb to heatwaves if they face a concomitant lack of water. Indeed, there are reports of large mammals, such as goats, horses, donkeys and even camels, dying during heatwaves that they ought to survive, when they have insufficient access to drinking water (Cox and Wahlquist, 2019). Koalas obtain most of their water preformed from foliage, but during periods of extreme heat and aridity, leaf water content fails to meet their water needs and large-scale mortality can result (Mella et al., 2019). Most die-offs during drought, however, have been attributed to starvation rather than to dehydration or lethal hyperthermia (Young, 1994).

Without the ability to engage evaporative cooling, dehydrated mammals can maintain homeothermy only if dry heat loss is increased, or if heat gain from the environment or metabolism is reduced. The increasing body surface temperature that occurs in hyperthermic dehydrated mammals may serve to maintain a gradient for dry heat loss to the environment (Fuller et al., 2016). Bedouin goats deprived of drinking water and exposed to high air temperature and solar radiation had elevated body temperatures, but their body temperatures rose by less than 1°C (Jessen et al., 1998), and the contribution of that rise to the gradient for dry heat loss would be trivial. They were able to limit the effects of the high heat load not by dissipating the extra heat through enhanced dry heat loss, but through a decrease in metabolic heat production. Camels progressively decreased their food intake during a period of dehydration (Bouâouda et al., 2014). Indeed, although mammals that are adapted to arid environments typically have lower metabolic rates than other mammals (Withers et al., 2016), they commonly decrease metabolism further when they become dehydrated (Jessen et al., 1998).

The greatest sustained reductions in metabolic rate occur during torpor and hibernation. Torpor is usually triggered by low food availability, cold, and changing photoperiod, but it can also be triggered by a lack of water (Nowack et al., 2020). Golden spiny mice in outdoor enclosures expressed more torpor in summer than in winter, even when food was supplemented, implying that the main function of their torpor was to save water (Levy et al., 2011). Bats in drylands also appear to need torpor to maintain water balance (Bondarenco et al., 2016). Although there is evidence of daily hypothermia in large mammals during dry summers, it is probably driven primarily by low food availability. Summer torpor appears to

be limited to dryland mammals of low body mass (Fig. 4), and the extent of its function as a specific water conservation mechanism in them is not yet fully understood.

Similarly, little is known about the consequences of chronic or repeated, but non-lethal, dehydration for free-living mammals. Many desert-adapted mammals are resistant for several days to the effects of dehydration, for example by conserving their plasma volume at the expense of other body water compartments (Horowitz and Borut, 1970). In humans, plasma volume decreases during dehydration, and dehydration has been associated with reduced exercise, skilled task and cognitive performance (Cheuvront and Kenefick, 2014). In the heat, dehydration can impair performance through reduced blood flow to skeletal muscles, respiratory alkalosis, altered skeletal muscle motor recruitment and reduced motivation (Sawka et al., 2015). Repeated dehydration events, increasingly likely under climate change, have been implicated in a progressive decline in kidney function in humans, resulting in epidemics of chronic kidney disease (Glaser et al., 2016). Little is known about the chronic effects of dehydration in other mammals, but one would expect that reduced food intake when dehydrated, together with some catabolism of protein for water, is likely to result in reduced body condition and growth (McCue et al., 2017; van de Ven et al., 2020). The water-demanding process of lactation is also likely to be impaired, as demonstrated by the reduced milk output of dehydrated goats in the heat (Alamer, 2009). In summary, one would expect that a lack of water for mammals will increase the likelihood of dehydration and pathological hyperthermia as ambient temperature increases, resulting in a progressive reduction in performance associated with compromised reproduction, reduced growth, poorer body condition, and ultimately, greater mortality (Fig. 3B).

Effect of increasing ambient temperature and a lack of food

In drylands, vegetation biomass is associated closely with precipitation. Reduced precipitation with climate change, including drought, will reduce primary productivity, with a subsequent cascade across trophic levels. Food intake for mammals in drylands is also likely to be altered through other factors associated with climate change, including desertification, bush encroachment, wildfires, competition for limited resources, trophic mismatches and behavioural modifications to avoid heat (Fuller et al., 2016; Mirzabaev et al., 2019). A reduced or unpredictable food supply will affect not only daily energy intake, but may also compromise body water balance and reduce performance by impairing growth, health and reproductive success (Fig. 3C).

While the high solar radiation and air temperatures of drylands typically result in a heat load being imposed on mammals during the day, the direction of heat exchange between the environment and a mammal out in the open is usually reversed at night, especially in drylands where the night skies tend to be clear (Fig. 2). The low radiant temperature of clear night skies results in a substantial radiant heat loss (Swinbank, 1963), and convective heat loss also increases with falling air temperature over the night (Mitchell et al., 2018). An increase in air temperature at night by a few degrees Celsius, on average, as a result of climate change, will decrease heat loss by convection marginally, but will have little effect on radiant heat loss (Moen, 1968). In the coldest habitats on Earth, including cold drylands, mammals reduce heat loss by increasing their insulation (Withers et al., 2016). Mammals from hotter drylands, however, typically have little capacity to alter their insulation and the larger species, in particular, have thin pelages as a result of the need to facilitate rapid heat loss, particularly during exercise (Fuller et al., 2016).

The effect of cold stress at night for dryland mammals, however, has received far less attention than heat stress during the day. In the face of a heat sink at night, if they are to maintain homeothermy mammals must either take refuge in warmer microclimates, or expend energy through shivering or non-shivering thermogenesis, or increased activity. Decreasing energy availability as a consequence of climate change will reduce the capacity of mammals to defend their body temperature at night through energetically expensive processes. As a result, body temperature in exposed mammals will start to fall at a higher ambient temperature than in a well-nourished mammal. The lower limit of the prescriptive zone will therefore shift to the right, and performance is more likely to be compromised at lower ambient temperatures, as shown in Fig. 3C.

A decrease in body temperature and metabolic rate is a common response of mammals to energy deficit (Hetem et al., 2016; McCue, 2010). In dryland mammals, body temperatures are lowest in seasons with lowest food availability, but these are not always the coldest seasons. Arabian sand gazelles (*Gazella subgutturosa marica*) and oryx, for example, had their lowest 24-h minimum body temperatures in the hot, dry summer when forage quality was poor (Hetem et al., 2012b). Kangaroos *Macropus fuliginosus* had a lower 24 h minimum body core temperature at the end of a dry summer than at the end of the wet season in spring, despite minimum daily ambient temperature being higher in summer than in spring (Maloney et al., 2011). Studies that have reduced feed intake experimentally support the idea that an energy deficit induces hypothermia even in benign environments. In rats, for example, 24 h minimum body temperature dropped progressively as days of food deprivation progressed (Yoda et al., 2000), while sheep receiving only 70% of their maintenance diet also had lowered 24 h minimum body temperatures (Maloney et al., 2013).

The decrease in body temperature of food-deprived mammals does not appear to be a regulated fall in body temperature, like that seen in torpor, but rather an inability to maintain homeothermy. Indeed, with continued food deprivation and starvation, body temperatures fall progressively, in advance of mammals dying (Hetem et al., 2016). As a consequence of a drought that reduced the availability of their termite prey, aardvarks exhibited a decreasing 24 h minimum body temperature before they succumbed, despite shifting their activity from the night to the warmer day (Rey et al., 2017; Weyer et al., 2020). In contrast to the response to water deficit, when mammals may switch from diurnal to nocturnal activity, during periods of negative energy balance many nocturnal mammals shift their activity to the daytime to reduce energy costs to maintain homeothermy during the cold nights (van der Vinne et al., 2015). The increase in daytime activity is typically greater when mammals face additional energetic demands, such as lactation or exposure to low ambient temperatures (van der Vinne et al., 2015). Temporal niche shifting, where it is not constrained by other factors, offers a means for nocturnal mammals to conserve energy, although the energy saving may not be as high as that offered by torpor or hibernation.

Torpor and hibernation, however, are restricted mainly to mammals of small body mass, particularly in drylands (Fig. 4) (Nowack et al., 2020). Torpor is a regulated fall in rest-phase body temperature and metabolic rate, such that metabolic rate may decrease by 50–95% (Geiser, 2020). Hibernation is prolonged torpor over consecutive days, sometimes even lasting several months, but interspersed with regular bouts of arousals and a return to normothermic body temperature (Geiser, 2020). The degree to which body temperature falls, as well as the frequency and duration or torpor, differs widely among species and environmental

conditions (Levesque et al., 2016; Nowack et al., 2020). As a controlled process, associated with a change in body temperature set-point (Jastroch et al., 2016), the extreme body temperature fall during torpor should not be represented as a mammal being outside its prescriptive zone, as shown in Fig. 3. Torpor may manifest as a seasonal response or opportunistically as a response to emergency situations, helping small mammals cope not only with food shortage, but also with water shortage, cold spells, heatwaves, storms, wildfires and an increased presence of predators (Carey et al., 2003; Geiser, 2020; Nowack et al., 2020). Despite the many benefits of torpor, there are possible costs too, including interference with reproduction, reduced immunocompetence, slowed locomotor reactions, decreased sensory perception, and increased oxidative stress (Geiser, 2020; Levesque et al., 2016). Warming associated with climate change may also increase the frequency of arousals, increase energy expenditure through the Q_{10} effect and change the timing of hibernation for seasonal hibernators (Nowack et al., 2017).

While the energy savings of torpor or hypothermia may protect against unpredictable and sudden environmental change, prolonged drought or chronic loss of a food source for other reasons (for example, wildfires) may threaten the survival of many mammals under climate change. The lower mass-specific metabolic rate (Fig. 4) and relatively greater fat storage of large mammals will allow them to endure fasting for longer than smaller mammals (Fuller et al., 2016). Nevertheless, starvation (associated with drought or severe winter), together with disease, has been identified previously as the major factor leading to natural die-offs of large mammals, with herbivores experiencing droughts in drylands most affected by starvation (Young, 1994). In South Africa, deaths of large herbivores during droughts resulted from starvation rather than dehydration (Smit et al., 2020). Analysis of historical megadroughts reveals that they can result in widespread mortality and ecosystem collapse. An Australian megadrought from 1891 to 1903 resulted in bottom-up trophic collapse, from primary producer to herbivore and omnivore guilds, with the least mortality for the predators and mesopredators (Godfree et al., 2019). In contrast, an extreme drought in California from 2012 to 2015 resulted in a reduced mammal abundance with carnivores negatively affected (Prugh et al., 2018). How reduced food availability will affect mammals is likely to be ecosystem specific, even within drylands, and dependent on how food webs are altered. In addition, the flexibility of species to respond to reduced and unpredictable food resources, and to meet energy-demanding activities like reproduction, will be crucial to their long-term success under climate change.

Effect of increasing ambient temperature and a lack of water and food

The strong relationship between precipitation and vegetation in drylands means that mammals facing climate change in these regions will often have to contend with a concomitant lack of food and water. Dryland mammals in such circumstances, exposed to both increasing heat loads during the day and heat sinks at night, will abandon homeothermy sooner than they would have if they were well-nourished and euhydrated. The prescriptive zone will be narrowed by both the lower limit increasing and the upper limit decreasing (Fig. 3D). A mammal exposed to the prevailing macroclimate over 24 h may therefore exhibit heterothermy characterised by both a higher 24 h maximum and a lower 24 h minimum body temperature, as demonstrated for Arabian sand gazelles and oryx in the hot and dry summer of the Arabian Desert (Hetem et al., 2012b). Mammals may cope outside the prescriptive

zone for some time, but prolonged exposure when they are faced with both food and water shortage will result in greater decrements in performance (Fig. 3D). The narrowing of the prescriptive zone is likely to be accompanied by narrowing of both the tolerance zone and the survival zone (Mitchell et al., 2018).

As we have discussed, one way for mammals to remain within their prescriptive zone is by accessing thermally buffered microclimates, such as burrows, but restriction to that microclimate may have costs, including reduced time for foraging and drinking. Another way to alter the microclimate while allowing greater behavioural scope is by shifting activity across the diel cycle, between night and day (Levy et al., 2019), as we have also discussed. Dryland mammals with insufficient food and water, however, will need to weigh up the energetic costs of being active on cold nights with the hydration costs of being active in the day. Based on their lower mass-specific heat loss rate and lower mass-specific evaporative water loss rate (Fig. 4), one would expect that large mammals deprived of water and food would be better suited to shifting activity across the diel cycle than small mammals. However, the relationship between body mass and the ability to alter the temporal niche is not simple. Both Arabian sand gazelles (ca 15 kg) and oryx (ca 70 kg body mass) in a hot and dry period shifted activity to the night in the same way, despite their modest size differences (Hetem et al., 2012b). Aardvark, on the other hand, despite being relatively large (ca 35 kg), prioritised energy conservation by shifting activity away from the cold night when they experienced a deficit of energy intake, and probably water too, given that they obtain all their water from their diet (Weyer et al., 2020). There also are records of relatively small nocturnal mammals shifting activity to the day during food shortage, including Geoffroy's cats (*Leopardus geoffroyi*; ca 3 kg) in Argentina (Pereira, 2010) and Ord's kangaroo rats (*Dipodomys ordii*; ca 70 g) in the USA (Boal and Giovanni, 2007). The activity pattern of mammals also is likely to be influenced by other factors like predation and competition, making it difficult to predict whether or how species will adjust their temporal niche. When mammals face increasing heat loads in combination with both food and water shortage, however, a shift in the activity pattern may not be sufficient to prevent a decrease in performance, and the decrement in performance is likely to be greater for mammals facing a combination of water and food shortage (Fig. 3E) than for mammals facing either water or food shortage alone. We predict that climate change in drylands will impair the performance of mammals through increasing ambient heat loads as well as the additive effects of inadequate food energy (Fig. 3C) and inadequate water (Fig. 3D).

Conclusion

While it may be possible to predict the effects of increasing ambient heat loads on free-living ectotherms with relatively good success (e.g. Rezende et al., 2020), it is much more difficult to do so for endotherms because of their greater control of body temperature through physiological and behavioural mechanisms. The thermal tolerance of a mammal cannot be estimated without understanding the capacity of the mammal to maintain homeothermy through water use and energy expenditure, as well as its ability to behaviourally modify the climate to which it is exposed. We have reviewed here how the effects of insufficient food and water alter the ability of dryland mammals to maintain homeothermy and perform optimally in changing environments. We have focused on dryland mammals because of the greater challenges of maintaining a positive energy and water balance in drylands than in humid zones, and because these challenges are set to become even greater as drylands become warmer and drier. However, the concepts we describe are generally applicable to mammals facing heat during

food and water shortage in other regions too (humid zones; Fig. 1), although responses may differ based on climate and habitat structure. For example, evaporative cooling may be precluded in the tropics by high water vapour pressure (Lovegrove et al., 2014), and climate warming may benefit mammals in colder regions in winter through increased food availability and reduced energy costs of keeping warm (e.g. Vetter et al., 2015).

We show how the prescriptive zone narrows with a deficiency of water or food, or both (Fig. 3), not as an attempt to define a specific range of ambient temperatures within which mammals can best function, but rather to illustrate the key role of food and water for a mammal in coping with a changing climate. In Fig. 3, as done previously (Mitchell et al., 2018), we use ambient temperature to define the prescriptive zone. However, although models predicting vertebrate function commonly use air temperature as the input variable, the complex thermal environment of free-living mammals cannot be quantified by air temperature alone, and, indeed, in hot environments air temperature is a relatively unimportant contributor to thermal load (Mitchell et al., 2018). In delineating the prescriptive zone, Lind (1963) recognised the complex thermal environment of humans by using the 'corrective effective temperature', an old index that incorporates air temperature, humidity, radiant heat and wind, to define the upper and lower limits of the prescriptive zone. For mammals in drylands, one of the most important routes of heat exchange is through radiation (Mitchell et al., 2018), so black globe temperature or operative temperature would provide a much better measure of the prescriptive zone than ambient or air temperature. Regardless of the defining climatic measure, the prescriptive zone cannot be delineated strictly for a particular species using thermal metrics only. It will differ not only with food and water availability but also with factors that influence energy and water expenditure, such as lactation, pregnancy, activity and acclimatisation, as well as body size and factors that influence size, such as sex and age.

Body size is a critical factor influencing how mammals respond to increasing heat loads, as we have outlined. In southern Africa, the largest of all mammals, the African elephant, uses a high absolute and surface area-specific rate of cutaneous evaporative water loss (Dunkin et al., 2013) to maintain homeothermy (Mole et al., 2018), despite inhabiting the hottest areas in the region (Mole et al., 2016). With ready access to free-standing water, it is probable that elephants will never attain the upper limit of their prescriptive zone in their current habitat. Without access to water, the upper limit would be measurable, and elephants would probably become hyperthermic frequently. Calculations of heat storage in Asian elephants, presuming they could not use cutaneous evaporative cooling, estimated that body temperature would reach a lethal limit of 43°C after 4 h of walking in full sun, at an air temperature of 31.4°C (Rowe et al., 2013). Smaller mammals in the same situation, even with access to evaporative cooling, would dehydrate and reach a lethal limit even sooner. Indeed, during summer, despite being inactive and in shallow burrows during the day in the Arabian Desert, Libyan jirds (*Meriones libycus*; ca. 60–160 g body mass) experienced body temperatures as high as 42°C (Alagaili et al., 2017). The advantage for mammals of small size in coping with unsuitable conditions is their ability to escape to a variety of cooler microclimates and to use torpor (Fig. 4), but it is a temporary advantage only.

In addition to the direct effects of increasing heat load and the compounding effects of insufficient water and food on mammals of varying body size, many other factors, such as dietary breadth, dispersal ability, reproductive rate, group size and social relationships, trophic relationships and disease, will influence the performance and survival of species facing climate change (Mirzabaev et al., 2019). Although it is not practical to study all species, further long-term studies of mammals in their natural environments, including physiological and behavioural measures, are needed for us to obtain a better grasp of how mammals will function with ongoing climate change. With the exception of mass mortality for some species, such as flying foxes during heatwaves, it is difficult to detect morbidity or mortality of mammals, especially in response to pervasive sub-lethal effects, without close monitoring. Aardvarks, for example, are listed as 'least concern' by the International Union for Conservation of Nature (IUCN), and, had we not been closely studying them over several years using biologging technology, we would not have detected mortality associated with drought, a potential threat to their continued survival (Weyer et al., 2020). Despite the allure of being able to predict the performance and survival of dryland mammals facing increasing heat, considerable uncertainty is likely to persist in modelling approaches without further knowledge of the sensitivity and responses of species in the face of decreasing water and food.

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