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LETTER

Too hot to hunt: Mechanistic predictions of thermal refuge from cat predation risk

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Abstract

Many threatened species depend on climatic microrefugia, but places with harsh climates for predators may also play a refugial role. Feral cats threaten many native species in arid Australia. Although cats can persist in regions with no free water, their abundance should depend on the availability of microclimates that protect them from harsh environmental conditions. We developed a biophysical model of feral cat heat stress and used it to explore how behavior and microhabitat features influence water requirements and activity. Tests of model predictions against fine-scale GPS and microclimate data highlight the importance of refuges, particularly rabbit burrows. Continent-wide simulations show large but temporally varying areas of the arid zone that would be lethal for cats without access to deep or shaded burrows. Our approach can identify locations that may act as natural refuges for native prey, and where habitat management strategies may be effective in controlling cat abundance.

KEYWORDS

ecophysiology, *Felis catus*, heat stress, mechanistic niche models, predator management, thermoregulation, threatened species management

1 | INTRODUCTION

Models that predict species distributions are used widely to inform the conservation and management of biodiversity (Guisan et al., 2013; Whitehead et al., 2017). At finer scales, an understanding of how species persist in particular landscapes can assist in developing targeted management plans (Keith et al., 2008; Magadzire et al., 2019). Refuges—locations that enable species to persist in times of stress (Keppel et al., 2012)—are an attractive target for managers because these locations can have disproportionate impacts on species' long-term persistence (Reside et al., 2019; Scheele et al., 2017). Although refuges are often thought of at relatively broad spatial and temporal scales, they can also operate over shorter time periods, and include habitats that buffer species against extreme heat, cold, humidity, or other stressors (McLaughlin et al., 2017). Considerable focus has been given to enhancing or protecting refuges to aid conservation of threatened species (e.g., Heard et al., 2015; Reside et al., 2019), but management directed at refuges relied on by invasive species may also be an effective means of reducing their distribution and abundance (Florance et al., 2011). An understanding of when and where the activity, distribution, or abundance of invasive species is constrained by stressors could also be used to help identify refuges for native species (Letnic et al., 2009).

Introduced predators, including the feral cat *Felis catus*, have been implicated in population declines of native species globally (Doherty et al., 2017; Woinarski et al., 2015). In Australia, feral cats are estimated to occur across 99% of land area (Legge et al., 2017), including arid areas where cats have been implicated in the demise of many threatened species (DEWHA, 1999).

Feral cats are likely to be physiologically challenged in Australia's arid zone, despite occurring at high densities during wet periods (Legge et al., 2017). Laboratory studies of cat physiology found that water loss rates increased rapidly at air temperatures exceeding 35°C, and prolonged exposer to air temperatures of 41°C and 75% humidity resulted in a breakdown of thermal homeostasis (Robinson & Lee, 1941). Air temperatures across the global distribution of this species—including parts of arid Australia—frequently exceed these limits, and in the wild, cats must also contend with substantial heat loads from solar radiation.

Directly applying thermal limits identified in the laboratory to field conditions is problematic, because other factors (e.g., wind speed, solar radiation, infrared radiation) influence heat exchange in complex environments. Furthermore, animals have a range of behavioral strategies for coping with thermally stressful environments, including postural adjustments and seeking cool microclimates (Huey et al., 2012). Biophysical models of energy and mass exchange represent powerful tools for understanding climatic constraints on species distributions and how species persist in particular environments (Briscoe et al., 2016; Porter et al., 2000; Porter & Gates, 1969). These models use physical principles to explicitly model how microclimates experienced by animals influence their energy and water requirements and core temperature, as a function of their morphology, physiology, and behavior. They can quantify how behaviors such as the use of cool microclimates influence energy and water requirements (Briscoe et al., 2014) and determine climatic constraints on activity patterns and habitat use (Kearney et al., 2016; Mathewson et al., 2017).

Here, we develop a general biophysical modeling framework for computing cat sensitivity to heat stress. We coupled this with field microclimate measurements and GPS data to gain a better understanding of how feral cats persist across the arid zone of Australia and map the potential importance of fine-scale refuges, such as rabbit burrows, in facilitating feral cat persistence across the arid zone to identify options for management.

2 | METHODS

2.1 | Cat biophysical modeling

We modeled feral cats using the endotherm mode in the R package NicheMapR (Kearney et al., 2021; Kearney & Porter, 2017; see Figure 1). We adapted the *endoR* function of NicheMapR to capture thermoregulatory responses of cats and used it to estimate hourly energy and water requirements and core temperatures under different microclimatic and behavioral scenarios. Model parameters were obtained by measuring feral cats from two study sites (n = 16–18 per site), with additional morphological, physiological, and behavioral data collated from the literature (Table S1.1). We tested the model against published laboratory data and our own field observations.

Cats were modeled under a suite of behavioral scenarios relating to activity, microhabitat use, and associated thermoregulatory options (Table 1). Cats were assumed to be active nocturnally, or active for either 8 or 12 h per day (based on tracking results, see below), but we varied the timing of activity to minimize either energy or water costs. For each simulation, we assessed whether cats could meet their energy and water requirements based on daily energy intake estimated for adult male cats of 1297 kJ/day (Scott & Scott, 1967), with food properties based on those reported for rabbits (Fortun-Lamothe et al., 2002), and using digestive efficiencies suggested by Plantinga et al. (2011). For one set of simulations, we assumed that cats had access to drinking water if weekly rainfall exceeded 3 mm (i.e., not accounting for permanent water sources). Sites were deemed unsuitable if, over the period of a week, cats were predicted to be in negative energy balance or if they lost more than 10% of body weight as water. See Appendices S7–S9 for example code.

2.2 | Microclimate modeling

The microclimate model was used to calculate hourly air temperature, wind speed, relative humidity, and solar and long-wavelength thermal radiation in microhabitats available to cats (including down burrows). For empirical tests at study sites, we used for input local weather data measured with an automated weather station (WeatherHawk, Campbell Scientific, Inc.), as well as gridded weather data. Simulations based on gridded data used the *micro_aust* function in NicheMapR, with daily weather data obtained from Australian Gridded Climate Data (0.05° resolution; Jones et al., 2009) and daily wind speed from McVicar et al. (2008). Soil properties were extracted from the CSIRO Soil and Landscape grid of Australia (Grundy et al., 2015; see Appendix S2).

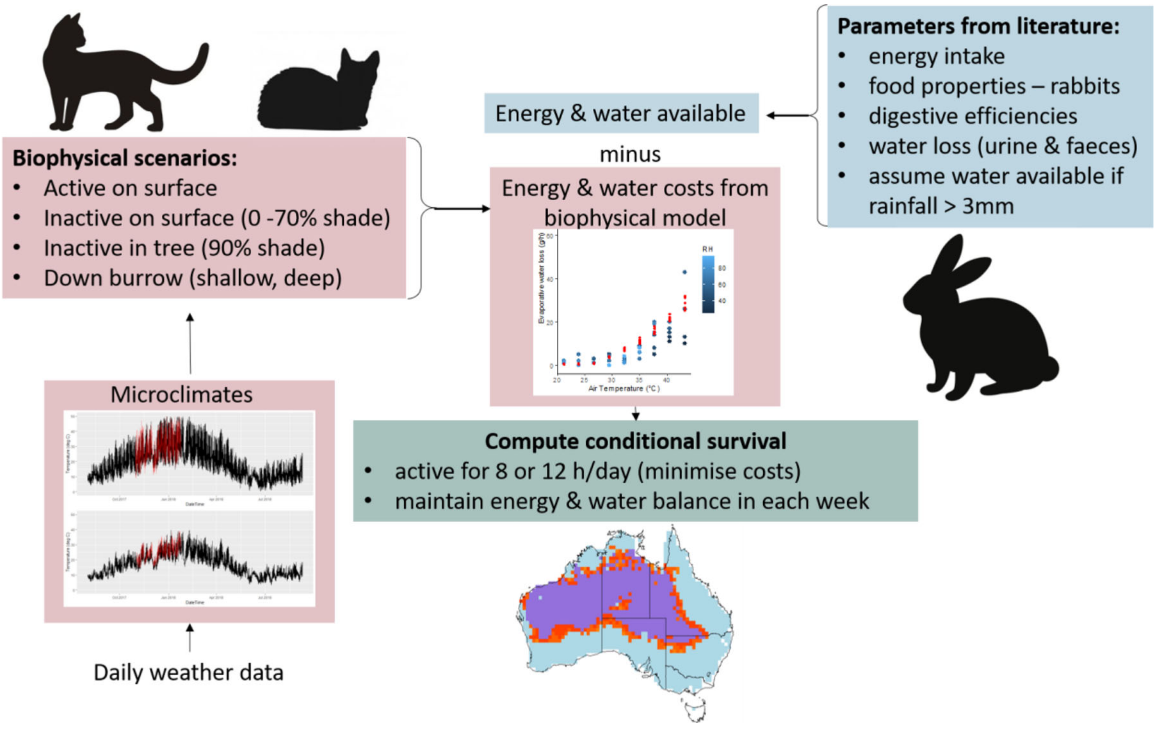

FIGURE 1 Overview of approach used to model feral cat reliance on refuges across Australia. Gridded weather data were used to compute microclimatic conditions in a range of microhabitat scenarios available to cats. Weekly energy and water costs of cats were then calculated via the biophysical model assuming different activity patterns, and the selection of microclimates to minimize water and energy costs. We then mapped where cats could meet their predicted costs with the energy and water available from food assuming cats ate a diet of rabbits

TABLE 1 Scenarios of activity and microhabitat use considered in biophysical modeling of cat energy and water balance

Scenario	Shade	Microclimate	Posture	Minimum metabolic rate	Panting	Licking
Surface active						
Long-distance	0%	15 cm	8	Q_{basal} × 2.07 (+ Q10 & pant)	16/2.07	20%
Walking	0%	15 cm	8	Q_{basal} × 1.40 (+ Q10 & pant)	16/1.40	20%
Sit-and-wait	0%	15 cm	5	Q_{basal} × 1.26 (+ Q10 & pant)	16/1.26	5%
Inactive						
Tree	90%	300 cm	4	Q_{basal} (+ Q10 & pant)	16	20%
Surface	0% or 70%	15 cm	2–8	Q_{basal} (+ Q10 & pant)	16	20%
Shallow burrow	0% or 70%	−20 cm	2–8	Q_{basal} (+ Q10 & pant)	16	20%
Deep burrow	0%	−50 cm	2–8	Q_{basal} (+ Q10 & pant)	16	20%

Note: Microclimates were computed for different heights/depths above/below ground. Posture was defined by the ratio of the length to radius of the assumed cylinder shape. The minimum allowable metabolic rate was the basal metabolic rate (Q_{basal}) with any additions imposed by the Q10 effect of core temperature rising, or the energetic costs assumed for panting, as well as any activity costs. The maximum panting rate (multiplier on basal breathing rate) was divided by the activity multiplier on basal metabolic rate to account for the already elevated breathing rate. Cats were allowed to increase their surface wetness to 20% by licking unless they were sit-and-wait foraging.

2.3 | Field tests

Field data were collected at two sites within the arid zone in Australia: Arid Recovery, a wildlife sanctuary approximately 20 km north of Roxby Downs in South Australia, and Scotia Wildlife Sanctuary, located near the border of NSW and South Australia and managed by the Australian Wildlife Conservancy. Scotia and Arid Recovery are characterized by hot, dry summers, with open shrubland vegetation and a mixture of sand dune and calcrete, or sand dune and solonized brown soils over clay. Feral cats are managed actively at both sites.

2.3.1 | Quantifying microenvironments available to cats

Field microclimate observations were used to test how well the microclimate model predicted environments available to cats. Hourly soil temperature profiles were measured in sand and calcrete/brown soils using a wooden stake with temperature loggers attached at a range of depths (~2.5–100 cm). Soil and local air temperatures at cat height were also recorded in open and vegetated environments using shaded temperature data loggers (Maxim iButton DS1922L or DS1923) mounted on stakes (0 and 15 cm height, shielded from solar radiation; Figure S2.1). At Scotia, measurements of temperature and humidity down four burrows were made from August 2017 to June 2020. At Arid Recovery, spot measurements of temperature and humidity down burrows (0–1 m from entrance) were recorded during hot weather (January 10–26, 2016; mean 1.2 m air temperature = 36°C) and compared to ambient conditions on the surface ($n = 28$ burrows).

2.3.2 | Refuge use and activity data

Cat activity and habitat use data were collected using GPS collars fitted to cats ($n = 6–9$ at each site) and set to record at fine (~2.5–20 min) time intervals. Cats were assumed to be inactive if the GPS collars indicated movement rates of less than 2 m/min. GPS collars were also fitted with a data-logger (Maxim hygrochron iButton DS1923) to record temperature and humidity data. At Arid Recovery, comparisons between vapor pressure calculated from data collected from cat collars and on the surface were used to identify when cats were likely to be using burrows, because burrows consistently had higher vapor pressure (Figure 2; Appendices S1–S3). Unfortunately, data loggers could not be retrieved from cats at Scotia. Instead, distances moved between sequential fixes were used to infer activity periods, which were then compared to predicted activity times and energy and water costs. GPS data from several individuals at Scotia were also used to identify the types of sites that cats were using during hot weather (i.e., air temperatures >35°C and solar radiation >800W/m^2).

3 | RESULTS

3.1 | Microclimate observations and tests

3.1.1 | Microclimates available to cats

GPS tracking data from Scotia revealed that feral cats used numerous hot weather refuges including rabbit burrows, disused fox dens, shallow depressions under *Triodia* hummocks, gaps under piles of refuge (branches, logs, and sand) adjacent to tracks, and under dense *Callitris* trees (Figure S2.2).

Recorded temperatures at cat height (15 cm) ranged from 5.5 to 54.5°C at Arid Recovery (January–April) and −7.5 to 55°C (January–December) at Scotia. Temperatures measured down burrows were consistently cooler than temperatures on the surface during hot weather. At Arid Recovery, mean temperatures recorded at depths of 25 and 50 cm were 3.6 and 5.7°C cooler, respectively, than 1.5 m air temperature in dunes, and 5.8 and 5.5°C cooler, respectively, in swales (Figure S2.3). At Scotia, burrows were on average 8.3°C cooler than 1.5 m air temperature during hot weather (air temperature >35°C and solar radiation >800 W/m^2), with a maximum difference of 19°C.

3.1.2 | Modeling feral cat microclimates

When run using local weather data, the microclimate model predicted air temperatures at cat height and soil temperatures well, with all correlation coefficients (r) >0.9, root mean square deviations (*rmsd*) between 1.6 and 13.4°C (Table S2.1). Burrow temperatures at Scotia were also well predicted (*rmsd*: 1.7–3.7°C, $r \sim 0.90$), while burrow humidity was predicted with lower accuracy (*rmsd*: 17.8%–24.1%, $r \sim 0.44$). Figure 2 provides example temperature and humidity observations and predictions for Scotia, with all tests provided in Appendices S3 and S4. Predictive performance generally decreased slightly when gridded, rather than local, weather data were used.

3.2 | Modeling feral cat physiology, burrow use, and activity patterns

Biophysical model predictions of cat responses to hot environments show good congruence with published laboratory data (Robinson & Lee, 1941; Figure S1.1), indicating rapid increases in evaporative water loss and core body temperature at chamber air temperatures >30°C.

At Scotia, cats were typically active for 12 h per day (mean = 11.9, monthly mean range = 9.7–14.3), but the diurnal pattern of activity varied through the year. Daily cat activity patterns were unimodal in winter, peaking at mid-afternoon and reaching a minimum between midnight and early morning, correlating inversely with predicted energy requirements associated with activity ($r = -0.43$, $P \leq 0.001$). Timing of activity gradually shifted so that by summer, daily activity was bimodal with maxima at dawn and dusk and reducing to near zero in the

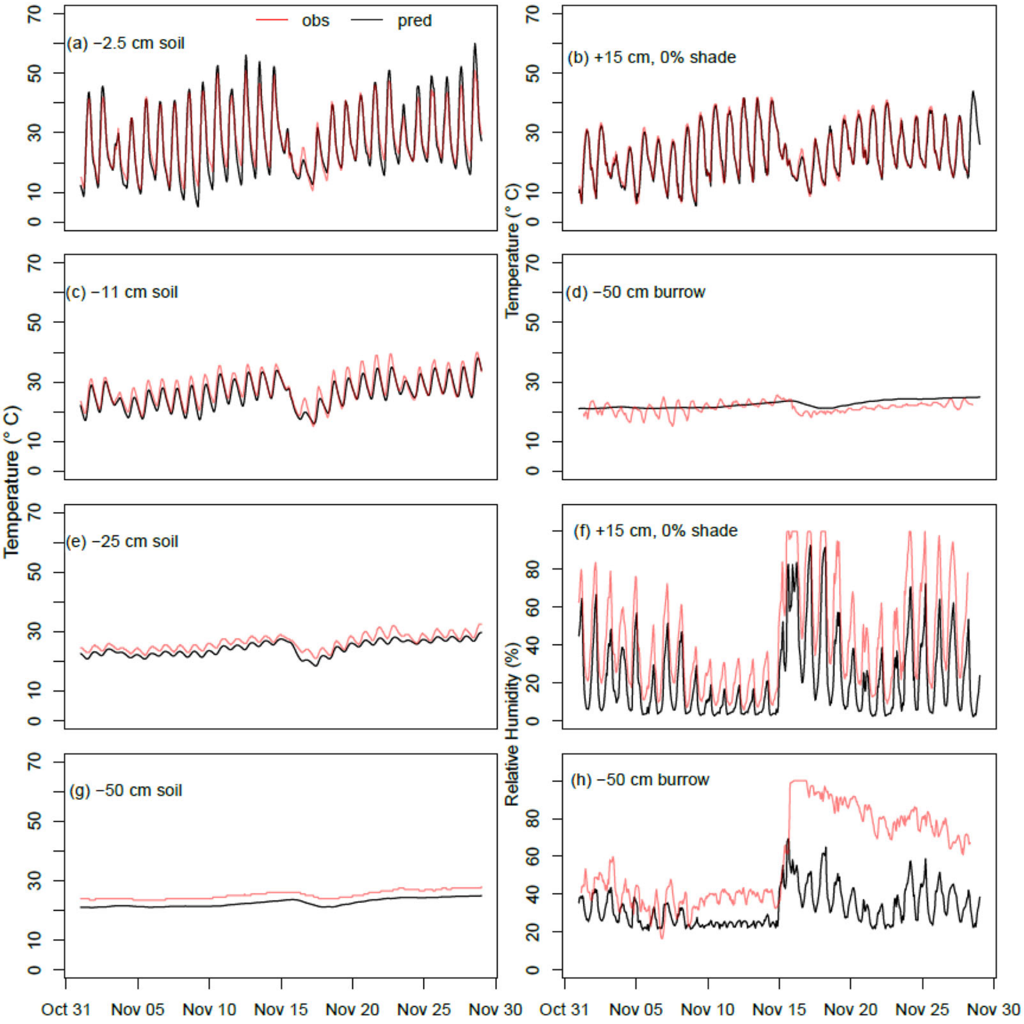

FIGURE 2 Example of modeled (black) and observed (red) microclimatic conditions relevant to cats at Scotia Wildlife Sanctuary in 2017

mid-afternoon, correlating inversely with predicted water loss rates associated with activity ($r = -0.62$, $P \leq 0.001$). Cats were predicted to rely on burrows when inactive. Overall, shifts in activity patterns across the year were captured well by simulations that assumed low or sit-and-wait activity, with activity timed to minimize energy costs (Figures 3 and S1.2–5).

At Arid Recovery, inferred burrow use by feral cats was reasonably well-predicted when we assumed that cats used burrows when predicted water savings from this behavior exceeded 20 g/h (Figure 4; Accuracy = 0.81, Precision = 0.42, Sensitivity = 0.43; compared to a null expectation of burrow use during daylight hours: Accuracy = 0.55, Precision = 0.25, Sensitivity = 0.91).

3.2.1 | Reliance on refuges across Australia

Plots of all landscape simulations are provided in Appendices S5 (allowing rehydration) and S6 (no rehydration). The effect of preventing rehydration from rainfall was minor, so we discuss only simulations allowing rehydration. Cold stress was also not found to be an important limiting factor, with energy deficits no greater than 2 kJ per week (Appendices S5 and S6), and is not discussed further.

Cats simulated to have access to deep burrows or shaded shallow burrows suffered minimal heat stress, and only in some years in small regions of the Gibson Desert and Simpson Desert in central and central-western Australia (Figure 5a–c; Appendix S5, simulations 1, 2, 5, 6, and 8). If access to deep or shaded shallow burrows was removed, heat stress was predicted, especially in the aforementioned regions, but rarely for more than two consecutive years (Appendix S5, simulations 3, 6, 9, 22, 25, and 28). However, if only surface shade and trees were available (no burrows), a large region of the arid zone became consistently unsuitable over multiple consecutive years (up to 27 years in some places), irrespective of whether a sit-and-wait or active hunting mode was assumed (Figure 5d–f; Appendix S5, simulations 4, 7, 10, 23, 26, and 28). Recent (post-1970)

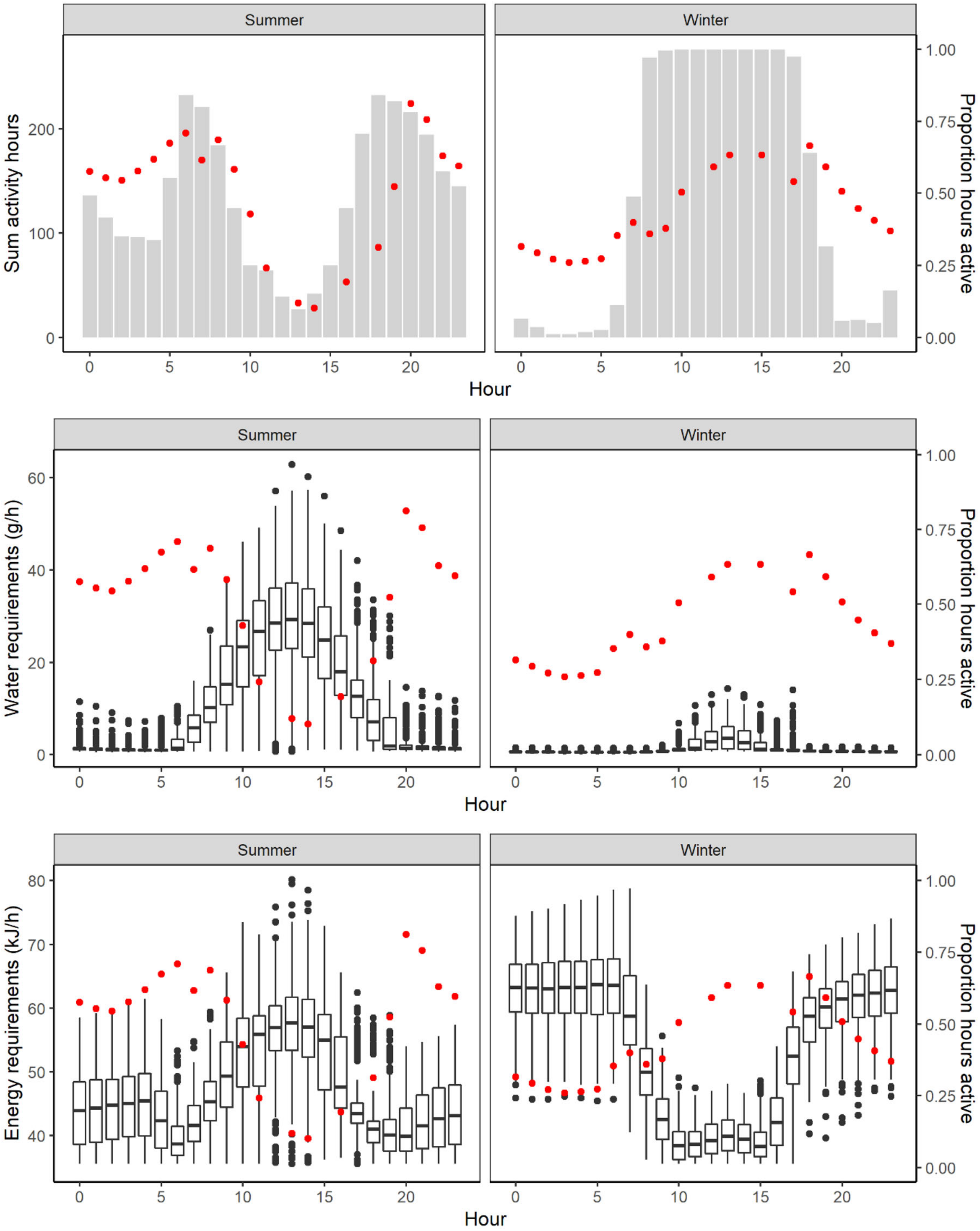

FIGURE 3 Predicted activity (sum of hours) (top), water costs (g/h) (middle), and energy costs (kJ/h) (bottom) of feral cats at Scotia in summer and winter for each hour of the day (2016–2018). Boxplots of water and energy requirements assume low-cost activity and show the range of values across days. Red dots indicate the proportion of hours that cat activity was observed across this period (right axis). Activity was inferred from GPS data

records of three native species impacted by feral cats correspond with areas with higher years of consecutive lethal conditions for cats (Figure 5g–i; Table S1.2).

4 | DISCUSSION

We found that potentially climatically lethal environments for cats exist throughout large parts of central and

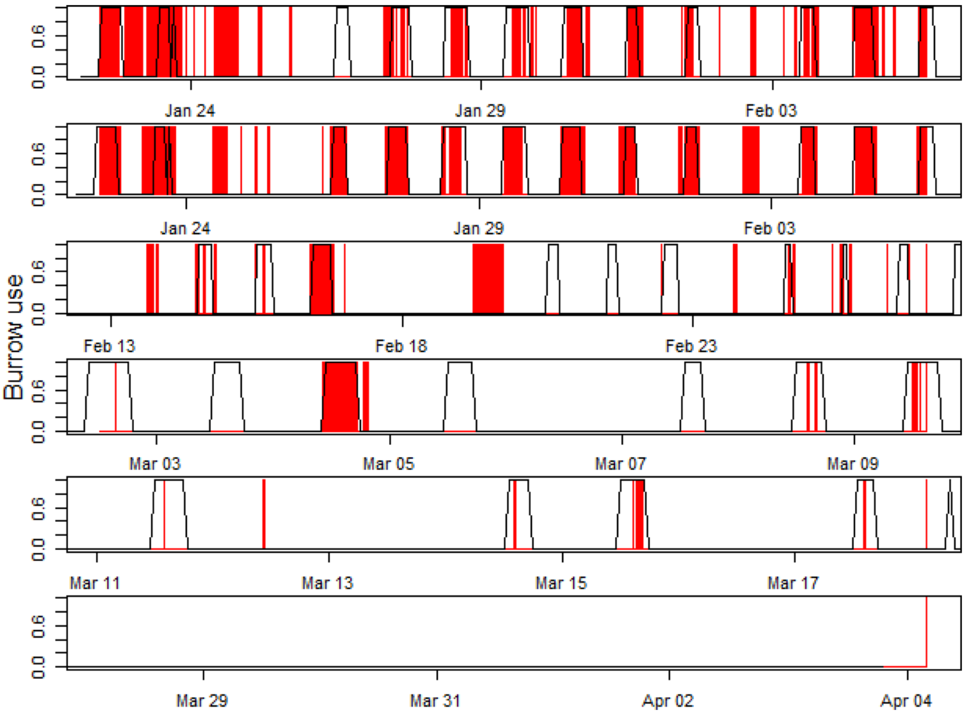

FIGURE 4 Predicted (black) and inferred (red) burrow use of six feral cats at Arid Recovery. Burrow use inferred from differences in vapor pressure between sensors mounted on feral cat collars and ambient on the surface. Cats were assumed to use burrows when the water savings from this behavior relative to sit-and-wait foraging on the surface exceeded 20 g/h

northwestern Australia's arid zone (Figure 5). However, continent-wide application of our model over 27 years of historical weather data shows that cats with access to deep or shaded shallow burrows can avoid exposure to potentially lethal heat stress at virtually all times and places. This is consistent with the cat's continent-wide distribution. Cats with access only to unshaded shallow burrows would experience lethal conditions in areas of Central Queensland and the Gibson Desert, and this zone expands to a large proportion of the arid zone if cats have no access to burrows and can only use shade from ground-level vegetation or climb trees to shaded, cooler (and windier) conditions. The magnitude and location of this stress zone varied from year to year (Appendices S5 and S6) but regions experiencing the greatest consecutive number of years of stress showed a broad association with remaining populations of several native species known to be vulnerable to cat predation (Figure 5). Regions with recent sightings of bilby and mulgara had significantly higher consecutive lethal conditions when compared to historic records (Table S1.2).

Data from two arid-zone field sites showed we could accurately characterize microclimates used by cats and underscored the importance of cool burrows as a refuge from hot weather. Our results are consistent with reports of cats using retreat sites such as rabbit burrows and shifting temporal activity patterns across seasons (e.g., Jones & Coman, 1982; Roshier & Carter, 2021)—suggesting that these behaviors are likely driven by thermoregulatory constraints. Over summer, cats at Scotia were more active at nighttime, with a low proportion of activity taking place during daytime hours that would place high energy and water demands on cats (Figure 3). By contrast, in winter, activity was spread across the day, although the highest activity levels occurred during the daytime when predicted energy costs of active cats were lowest. Other factors, such as prey or predator activity, are likely to influence feral cat activity patterns in the absence of strong thermoregulatory constraints (Wang et al., 2012). At the Arid Recovery site, cats generally used burrows at the times we predicted would be thermally stressful for them (Figure 4). Feral cat reliance on refuges such as burrows during the daytime could influence the types of native prey that face the most risk from cats in different seasons, and across different regions. Burrows from other native (e.g., bilbies, goannas) and introduced (foxes) species may also provide important thermal refuges.

Our study supports the hypothesis that some areas of Australia can become physiologically prohibitive for cats in some years if thermal refuges are not available. This result has several management implications. First, our predictions may help in the detection of populations of species threatened by cats but able to tolerate thermally harsh conditions, such as the night parrot. Searches could be

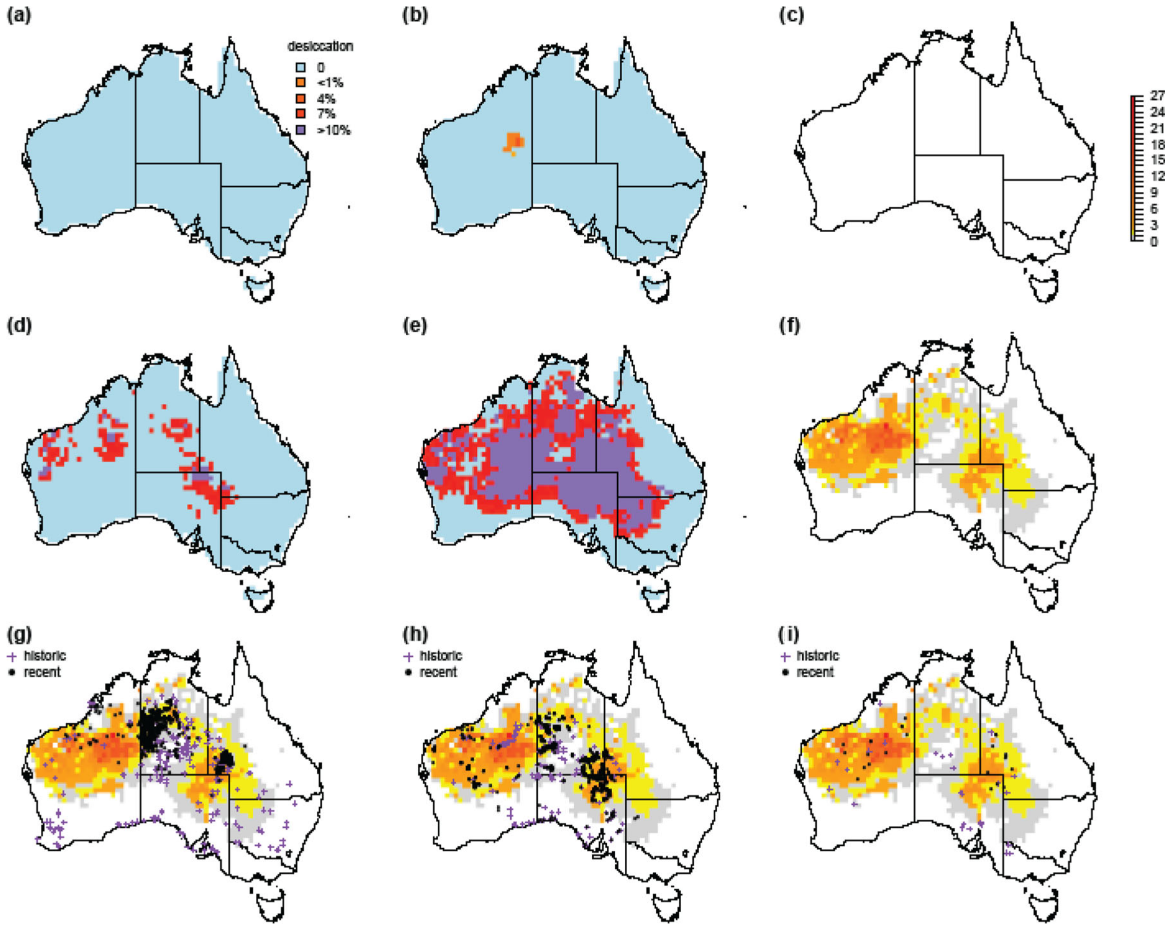

FIGURE 5 Summary plots of cat heat stress across Australia (1990–2017) when cats are assumed to be active for 8 h per day and all retreats are assumed to be available as refuge sites (a–c; Simulation 5) or no burrows are assumed to be available (d–i; Simulation 7). Example plots of desiccation stress (% of body mass) for (a, d) a mild year (1999), (b, e) a hot year (2012), and (c,f–i) the consecutive number of years of potentially lethal (10% of body mass) heat stress. Recent (since 1970, black dots) records of three cat-sensitive species: bilby (g), mulgara (h), and night parrot (i) are from areas with higher consecutive lethal conditions than historical records (purple crosses). See Appendix S5 for alternative simulations

prioritized to places that have a recent history of thermal stress for cats that are also naturally lacking in thermally buffered retreats for cats, such as burrows and caves. Second, our analyses show where removal of potential cat refuges can be most effective in limiting cat populations. For example, we found cats to be using piles of woody debris created in association with road management at Scotia. Removing such habitat features may substantially reduce the carrying capacity of cats in areas where threatened species occur, although consideration must also be given to the role such refuges play for native species (Read et al., 2008). Similarly, destroying rabbit warrens to limit refugia for cats will have greatest effect in areas of higher heat stress. These areas can be identified from our model, with outputs that allow site-based assessments available to managers through a web-based app (http://bioforecasts.science.unimelb.edu.au/app_direct/cat_oz/).

A key advantage of biophysical models is that they are generalizable: our model of feral cats could thus be applied to other parts of their global distribution where cats may threaten native prey, or the parameters adjusted to model other predators such as the red fox *Vulpes vulpes*. Our modeling could also be extended: while we focus here on identifying locations that would be physiologically challenging for cats assuming prey are available, data on spatial and temporal availability of prey and water sources (including artificial watering sources for livestock) could also be incorporated to further refine predictions.

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DATA AVAILABILITY STATEMENT

Data are openly available via Figshare at https://doi.org/10.26188/17031389.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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