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Modeling the joint effects of body size and microclimate on heat budgets and foraging opportunities of ectotherms

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Running headline: Size and microclimate constraints on foraging ectotherms

Abstract

1. Body size affects the body temperature of an ectotherm by altering both heating rates and the microclimate experienced. These joint effects are rarely considered in analyses of climatic constraints on ectotherms but nonetheless influence body temperatures and thus activity periods and foraging opportunities.
2. Here we develop and test transient heat-budget models that use height-specific microclimatic forcing to compute the dynamics of size-dependent body temperatures

of ectotherms in sun and in shade. We incorporate a model of behavioural thermoregulation and use it to compute potential body temperatures and then to map these to ecologically relevant indices, including foraging opportunities and thermal constraints. To illustrate potential applications, we combine a microclimate model driven by a global climate database with the transient behavioural algorithm developed for lizards to explore how body size (10 g and 1000 g) and size-specific microclimate (at natural heights of 1 and 7.5 cm, respectively) interactively influence body temperatures and ecological indices at a warm, arid location in Australia in both spring and summer. To explore microclimatic effects, we contrast temperatures and indices for animals positioned at their natural versus reciprocal heights above the ground.

3. Our simulations show that the behavioural and ecological consequences of size can be strongly biased when joint effects of body size and size-imposed microclimate are ignored. For example, the two body sizes did not differ in total foraging time when compared at their natural heights, but did differ if compared at the same height, the direction of this difference reversing with the height at which they were compared. We show how computed foraging times can be translated to potential foraging radii from a central place (burrow or shade-providing bush), thereby illustrating how body size can be physiologically translated into habitat connectivity as a function of different shade configurations, e.g. as modified by fire regimes or shrub dieback.
4. All functions are now integrated into the biophysical modeling R package NicheMapR and as a Shiny app, which should provide new insights and avenues for investigation into functional interactions between body size and habitat structure for ectotherms.

KEYWORDS

scaling, heat exchange, microclimate, terrestrial ectotherm, foraging, thermoregulation, shade, fire

Introduction

Evaluating when, where, and for how long an ectotherm can safely forage in the open without overheating is a fundamental question in physiological and behavioural ecology. The empirical significance of this problem has been long recognized. For instance, Norris (1967) noted that hatchling *Uta stansburiana* lizards that are "*placed between bushes seven or eight feet apart at midday often will die before reaching shelter*." Similarly, Tinkle (1967) wrote that "*Less than one minute on the hot sand on a clear day was required to raise body*

temperature to a critical point" for adult *Uta stansburiana*. The configuration of shade in a habitat directly affects the thermoregulatory responses of ectotherms (Sears et al., 2016) and climate warming may alter activity budgets by increasing shade requirements (Sinervo et al., 2010; Michael R. Kearney, 2013). Shade configuration is being significantly altered on a global scale through habitat destruction and changed fire regimes, increasing the practical relevance of understanding the resulting thermal constraints on foraging in ectotherms such as lizards.

Biophysical (heat-transfer) models can quantify these dynamics, and they do so by determining how microenvironments experienced by an organism affect its body temperature (T_b) and in turn its potential movement and foraging options. Most biophysical models are steady-state and may be inappropriate for analyzing movement options and constraints for two reasons:

(1) They assume that T_b equilibrates instantly with environmental conditions (Buckley, 2008; Michael R. Kearney, Shine, & Porter, 2009; Sunday et al., 2014; Pinsky, Eikeset, McCauley, Payne, & Sunday, 2019; but see Christian, Tracy, & Tracy, 2006; Rubalcaba, Gouveia, & Olalla-Tárraga, 2019). However, T_b will not equilibrate instantly because all organisms have thermal inertia, especially as size increases over 100 g (Spotila, Soule, & Gates, 1972; Willmer & Unwin, 1981; Stevenson, 1985; Seebacher & Shine, 2004). We refer to this size-dependent lag as the 'Newtonian effect,' in reference to Newton's law of cooling (Figure 1a).

(2) Moreover, small and large organisms necessarily experience different microenvironments, simply because their bodies are at different heights above ground (Muth, 1977). At midday on the ground in the open sun, for example, a large animal will be in a cooler microenvironment than will a small animal simply because air temperature declines and wind speed increases with height above ground (Geiger, 1950). Thus, the animal's convective microenvironment is body size-dependent; we refer to this as the 'Geigerian' effect (Figure 1b) with reference to Geiger's (1950) classic treatise on microclimates.

We know of no biophysical modelling studies that jointly consider the 'Newtonian' and 'Geigerian' effects when evaluating the effects of size and microclimate on ectotherms. However, the importance of the Geiger effect is illustrated by reconsidering a classical result in biophysical ecology (Willmer & Unwin, 1981; Stevenson, 1985), namely that large ectotherms in sun have higher steady-state T_b than do small ones because large animals have relatively thick boundary layers and thus are less tightly coupled to the convective

environment than are small animals (Figure 1). The empirical (Willmer & Unwin, 1981) demonstration of this size effect was, however, based on insects suspended at a fixed height above ground (thus in same microclimates, P. Willmer, personal communication). Similarly the theoretical model also assumed that microclimate was independent of size (Stevenson, 1985). Nevertheless, if animals are heated at their normal height above ground, the classical size effect can be reversed, such that small ectotherms can have the higher steady-state T_b (justified below).

Here we develop a generic, transient heat-budget model for the R programming environment. The model is suitable for small to moderate-sized organisms and captures heat-flow via radiation and convection for different geometries. Using lizard-sized ectotherms as examples, we illustrate how this heat budget model can be forced with size-specific modelled microclimate inputs (Michael R. Kearney, Isaac, & Porter, 2014; Michael R. Kearney & Porter, 2017). We also develop an explicit model of behavioural thermoregulation that is incorporated into the Ordinary Differential Equation (ODE) solver routines such that, when T_b crosses a set-point threshold, an appropriate behavioural shift (e.g., thermoregulatory shuttling between sun and shade) is triggered. We then use the behavioural model to predict potential body temperatures of small (10 g) and large (1000 g) animals in sun or in shade at different times (day, season) in a hot, arid location.

Model derived estimates of T_b over time are relevant to ecology in several ways. First, because T_b affects an animal's physiological capacities, T_b can be mapped onto a performance or fitness index (Huey & Slatkin, 1976; Tracy & Christian, 1986; Vasseur et al., 2014). Second, the animal's current T_b and environment will also influence the animal's immediate behavioural options and constraints, such as how far it can safely forage away from shade without overheating or how soon it must shuttle to shade. Here T_b is mapped onto ecological or behavioural indices, a concept that traces to three papers published in 1967 (Janzen, 1967; Norris, 1967; Tinkle, 1967) and that anticipates the thermal safety margin (Heatwole, 1970; Deutsch et al., 2008). Third, the behavioural and movement options (above) can be overlaid on a habitat map with scattered patches of shade, and thus can measure the thermal quality and connectivity of the habitat from an ectotherm's perspective.

We show that values of all these indices can differ strikingly depending on whether a Newtonian vs. Geigerian perspective is adopted. We discuss the modelling framework in the contexts of interpreting thermoregulatory behaviour and of understanding shade-related habitat modifications, such as fire, land-clearing, or plant dieback.

Methods

Transient heat budget models

The transient heat budget models presented here are expansions on Porter et al. (1973), which developed equations based on an analogy of electrical circuits involving capacitors and resistors. A key decision is whether to assume that the body is at uniform temperature in a given moment and so can be considered as 'one lump', or whether the body must be broken into 'two lumps' with an inner core and outer shell, each of which may be at different temperatures in a given moment. One lump is adequate for small ectotherms but not for large ones (> ~1 kg), although exactly how large depends on the environmental context and specific organismal traits (Porter et al., 1973). In Supporting Information Appendix S1, we derive equations for solving one lump and two lump models.

In summary, for the 'one lump' scenario for an ellipsoid-shaped object with convective and radiative exchange without metabolic heat generation, the rate of change in body temperature is:

$$\frac{dT_c}{dt} = \frac{Q_{sol}}{C} + \frac{T_a}{CR_{conv}} + \frac{T_{rad}}{CR_{rad}} - \frac{T_c}{C}\left(\frac{1}{R_{rad}} + \frac{1}{R_{conv}}\right) \quad \text{(eq. 1)}$$

$$= \frac{1}{C}\left[Q_{sol} + A(h_{conv}T_a + h_{rad}T_{rad})\right] - \frac{A(h_{conv} + h_{rad})}{C} \quad \text{(eq. 2)}$$

where T_c, T_a, and T_{rad} are core, air and radiant environmental temperature, respectively (°C), $C = \rho V c_p$ is heat capacity (Joules, where ρ is density kg/m^3, V is volume m^3 and c_p is specific heat capacity J kg^{-1}), Q_{sol} is solar radiation absorbed (W), h_{conv} is the convective heat transfer coefficient (Watts m^{-2} °C^{-1}), $h_{rad} = 4\epsilon\sigma T_{ave}^3$ (Watts m^{-2} K^{-1}) is a Taylor-series approximation of the radiative heat transfer coefficient where ε is emissivity (-), σ is the Stefan-Boltzmann constant (5.67×10^{-8} Watts m^{-2} K^{-4}), and T_{ave} is the average of the organism's surface temperature T_s and radiant environmental temperature T_{rad} (K). The one lump model assumes that $T_s = T_c$. In a constant environment, Eq. 2 can be solved analytically for any time *t*, specifically $T_c = (T_{c,i} - T_{c,f})e^{-\frac{t}{\tau}} + T_{c,f}$ (see Appendix S1) where the time constant $\tau = \frac{C}{A(h_{conv} + h_{rad})}$, $T_{c,i}$ is the initial temperature, and $T_{c,f} = \frac{Q_{sol} + A(h_{conv}T_a + h_{rad}T_{rad})}{A(h_{conv} + h_{rad})}$ is the final temperature, with $T_s = T_c$ for the infrared radiation calculations.

Implementation in the NicheMapR package

The analytical function for the 'one lump' model described above is implemented as function `onelump` in the NicheMapR package, for example:

```
library(deSolve)# load the deSolve package
library(NicheMapR) # load the NicheMapR package
t <- seq(1, 3600 * 2, 60) # times (in seconds) to report back values
Ww_g <- 10 # body wet weight, g
Tc_init <- 27.4 # initial body temperature, °C
geom <- 2 # shape (2 = ellipsoid)
Tair <- 38.4 # air temperature, °C
Trad <- Tair # radiant temperature, °C
vel <- 0.57 # wind speed, m/s
Qsol <- 811 # horizontal plane solar radiation, W/m2
Zen <- 51 # zenith angle of sun, degrees
alpha <- 0.85 # solar absorptivity, -
Tb <- onelump(t = t, alpha = alpha, Tc_init = Tc_init, Ww_g = Ww_g, geom = geom, Tair = Tair, Trad = Trad, vel = vel, Qsol = Qsol, Zen = Zen)
```

Results from the code above are included in Figure 2, which shows computed heating rates and steady-state T_bs of 10 g and 1000 g ectotherms over 2 hours starting at midday in mid-September at Newhaven Wildlife Sanctuary in central Australia. Figure 2a assumes a Newtonian perspective, with both animals suspended in air at 7.5 cm, which is the natural height of the large ectotherm. The T_b of the 10 g ectotherm equilibrates faster (~ 10 vs. ~ 100+ minutes) but at a lower temperature than that of the 1000 g ectotherm (~ 41° vs. ~ 45°C), as expected (Stevenson, 1985). Figure 2b assumes a Geigerian perspective, with the small and large ectotherms positioned at their natural heights (1 vs. 7.5 cm, respectively). Here the T_b of the small ectotherm still equilibrates relatively quickly (~ 15 min) but now at a higher T_b than that of the large ectotherm (~ 47° vs. 45°C). This happens because the small ectotherm is lower in the boundary layer of the ground and thus exposed to lower wind speeds and higher air temperatures (i.e., Geiger counts!).

For the 'one lump' model under changing environmental conditions, and for the 'two lump' model in general, solutions must be obtained numerically using an ordinary differential equation solver. The functions `onelump_var` and `twolump` of the NicheMapR package

use the R package 'deSolve' (Soetaert, Petzoldt, & Setzer, 2010), with the forcing variables being interpolated between time steps by using the base R function `approxfun`.

The required forcing data can be obtained either from empirical microclimate measurements or from outputs of the microclimate model of NicheMapR (Michael R. Kearney & Porter, 2017). Applications using the microclimate model are illustrated in the help documents for the `onelump_var` and `twolump` functions. The one lump algorithm is incorporated into the `ectotherm` function of NicheMapR (Michael R. Kearney & Porter, 2019) and the transient case can be invoked by setting the option 'transient' to value 1. The algorithm is then solved using the DOPRI5 numerical integrator (Hairer, Norsett, & Wanner, 1993) (note, the `ectotherm` model implementation of the transient equations does not yet incorporate thermoregulatory behaviour).

Model tests

We tested the ability of the `onelump` and `twolump` functions to capture observed daily temperature variation in two sets of inanimate objects; (1) hollow copper and water-filled PVC pipes of different lengths, diameters and solar absorptivities, and (2) fruits of various sizes and colors (peaches, cantaloupe and watermelon). Full details of the methods and test outcomes are provided in Supporting Information (Appendices S2 & S3). Also, we compared model predictions against observations of two lizards, a military dragon *Ctenophorus isolepis* (~10 g) and a sand goanna *Varanus gouldi* (~1 kg) [see Supporting Information for methods and results].

Behavioural thermoregulatory algorithm

We considered a diurnally-active animal that spends the full 24-h day on the ground surface (i.e., does not climb or burrow; however, burrowing could be simulated by making radiant and air temperatures equal to soil temperature at a specified depth). We then developed a modelling scheme that incorporates transient heat budget functions and captures key thermoregulatory behaviours, including postural adjustments and shuttling between sun and shade through the course of a day. Behavioural shifts are initiated when T_b crosses a specified temperature threshold and triggers an exit from the ODE solver so that particular behaviours can be invoked. These user-adjustable thresholds are collected in the function `trans_behav` of NicheMapR (which could be modified for other motivations to move such as hunger, moisture). The function takes as input forcing data the 'metout', 'shadmet',

'soil' and 'shadsoil' outputs of the NicheMapR microclimate model, and then estimates hourly local air temperature and wind speed, surface and sky temperature, solar radiation and zenith angle, for sun and shade.

Specifically, the animal starts in maximum 'shade' at hour 0 (nighttime). After sunrise, the animal remains in shade; and its T_b gradually warms as ambient temperature rises. Once T_b in shade reaches the animal's minimum basking temperature (T_{b,min_bask}), the animal moves into sun ("emerge" event) and begins basking (body oriented perpendicular to the sun's rays). It remains basking until its T_b reaches the minimum activity temperature ($T_{b,min\_activity}$), when it begins foraging in the open ("forage" event) in a posture averaged between perpendicular and parallel to the sun's rays. It continues foraging in the sun until its T_b reaches the animal's maximum acceptable body temperature $T_{b,max\_activity}$, whereupon the animal retreats to shade ("shuttle" event). Once its T_b cools to at or near $T_{b,min\_activity}$, or to the shaded air temperature (if this is above $T_{b,min\_activity}$), the animal moves back to the sun and resumes foraging (new "forage" event); and so on throughout the morning. If T_b in the shade rises above $T_{b,max\_activity}$ the animal simply remains in the shade and tolerates the conditions. Once temperatures cool in the afternoon, it resumes shuttling until T_b drops below T_{b,min_bask} or until the sun is down: in either case, the animal then ceases activity and retreats to full shade ("retreat" event) for the night.

These four events – "emerge", "forage", "shuttle" and "retreat" – are passed to the ODE solver and conditionally impose a value of zero on the solution to trigger an exit from the solver so that new environmental conditions can be selected. The "forage" event required special care in how it referred to shaded air temperature, $T_{air,shd}$. In the case of an animal cooling in an environment where $T_{air,shd}$ was greater than $T_{b,min\_activity}$ (as might occur in midday heat), the threshold value to emerge needed to be set somewhat warmer than $T_{air,shd}$: otherwise, the lag-effect of large body mass during afternoon cooling prevented re-emergence in some cases. For our analyses, a 1°C offset sufficed. In addition, when $T_{air,shd}$ was approaching $T_{b,max\_activity}$ (as might occur on hot days), animals would emerge but engage in unrealistically short foraging bouts. Thus, a value somewhat less than $T_{b,max\_activity}$ was used to trigger foraging in this circumstance (for our analyses, a 2 °C offset sufficed). On very hot days, even T_b in shade at midday may exceed $T_{b,max\_activity}$; in this case the animal remains in shade and potentially may even be forced to experience temperatures above CT_{max}. [Note: the trans_behav code can be adapted to allow retreat to a burrow or to an elevated perch, if appropriate.]

Ecological Indices

The above heat-transfer and behavioural models produce a time series of potential T_b of animals moving about an open habitat and shuttling to shade. We converted these to ecological indices that include times or distances, which are interconvertible [assuming movement speed is independent of T_b within the range of activity T_b]:

(1) *Cumulative hours (or total distance covered) of foraging* (i.e., time when T_b is within the foraging range in the open) during a given day indexes a temporal (or spatial) aspect of a habitat's thermal suitability.

(2) *Number of shuttling bouts per day* indexes how frequently the organism is forced to retreat to shade and gives an indication of the costs of thermoregulatory behaviours such as locomotion costs and time potentially lost from other activities (foraging, courtship), and increased conspicuousness to predators (Huey & Slatkin, 1976).

(3) *Duration (distance) of the longest foraging bout* during the day measures the duration (distance) of a single best foraging opportunity as well as the maximum safety factor (time to forage and to return to shade without T_b exceeding $T_{b,max\_foraging}$). The maximum duration (distance) is ½ that of the maximal time (distance) time of a single foraging bout.

(4) *Cumulative hours of restriction to shade* estimates the total time per day when T_b in open is too hot for foraging (i.e., above $T_{b,max\_activity}$), and thus indexes environmental restrictions on foraging in the open (Sinervo et al., 2010).

In addition, we show how foraging radii can be mapped onto shade configurations in different habitats to determine spatial and temporal patterns of connectivity (Sears et al., 2016).

Simulation studies

We simulated a small (10 g) and large (1000 g) lizard at a hot site in central Australia (Newhaven Wildlife Sanctuary, 131.170° longitude, -22.724° latitude, 559 m). The mid-point of the body of the small and the large lizard was assumed to be 1 cm or 7.5 cm above the ground, respectively. In the absence of scaling data on field foraging speeds in nature, we assumed that the small and large lizards forage at speeds of 0.3 and 0.75 km/h, respectively, to demonstrate the approach. We used the `micro_global` function of NicheMapR to compute hourly microclimates for an average day in spring (September) and in summer (January). We assumed that both lizards would initiate basking at a T_b of 18 °C and forage between 33 °C and 43 °C (Pianka, 1971; King, 1980).

Results

The hourly simulation outputs for the two lizards at their natural and reciprocal heights in two seasons are presented in Figure 3. We begin by looking at the Newtonian effect on small and then on large animals in September (Austral spring) and again in January (Austral summer) at a site in central Australia. Then we compare Geigerian effects of size of lizards at their natural heights. The specific results are, of course, contingent on the explicit assumptions (e.g., sizes, event thresholds), but nonetheless serve as heuristic examples of why size-specific microclimates matter. Finally, we compare the model's predictions to the behaviours of small and large lizards foraging contemporaneously at the study site in October.

Cumulative hours of foraging and number of shuttling bouts

September (spring): If small and large lizards experience identical microclimates, the small animal should warm faster and thus have an earlier onset of foraging (Stevenson, 1985). Indeed, when both lizards are compared at a height of 7.5 cm (Newtonian comparison), the small lizard does heat faster and begins foraging earlier (~ 0945 vs. ~ 1020 h, Figures 2b & 2c). Nevertheless, the large lizard has a longer (cumulative) activity period in sun than does the small lizard (5.9 vs. 5.1 h, Figure 4a). Greater activity of the large lizard in this cool season reflects in part its hotter maximum potential T_b in the open, $T_{b,open}$, at midday (44.0 vs. 40.7 °C), which elevates its heating rate (Figures 2b & 2c). At this height in this cool month, neither lizard needs to shuttle to shade.

When the small lizard is at its natural height (1 cm), it still has the earlier onset of activity (0914 vs 0941 h, Figure 2a & d) but now has a longer activity period than would the large lizard lowered to that same height (6.2 vs. 5.1 h, Figure 4a). At this low height both sizes need to shuttle, but the large lizard's higher maximum $T_{b,open}$ (50.1 vs. 46.6 °C, Figures 2a & d) forces it to shuttle over a longer time window and to lose more time in the shade attempting to cool. When both lizards are at their natural heights, neither must shuttle; and both lizards have similar activity times (6.0 vs. 5.9 h, Figures 2a & 2b).

January (summer). When compared at 7.5 cm, the large lizard has a slightly shorter activity period than does the small lizard (5.5 vs 5.9 h, Figure 4a) but shuttles many fewer times (10 vs 50/day, Figure 4b & Figures 2f vs. 2g). Overheating is a risk for both the small and the large lizard, as their maximum T_e (50.3 vs. 53.6 °C, respectively) are higher than their shared CT_{max} (48 °C). When compared at 1 cm, the small lizard has the longer activity period

(4.9 vs. 4.6 h, Fig. 4a) but again must shuttle to shade much more frequently than does the large lizard (52 vs. 10/day, Figure 4b & Figures 2e vs. 2h). When both are at their natural height, the larger lizard has the longer activity time (5.5 vs. 4.9 h, Figure 4a), and the small lizard still shuttles much more frequently (52 vs. 10/day, Figure 4b & Figures 2e vs. 2f).

Distance (and duration) of the single longest foraging bout

September. When compared at 7.5 cm, the large lizard has a slightly longer maximum foraging bout (5.9 vs. 5.1 h, Figure S1; identical to the total foraging time reported above because no shuttling occurs). The small lizard is unable to move nearly as far from shade as can the large lizard (0.7 km vs. 2.2 km, Figure 4c), reflecting its lower speed and reduced thermal inertia. When the small lizard is at 1 cm, its natural height, it has a slightly longer maximal foraging bout than a large lizard at that height (2.5 h vs. 2.5 h, Figure S1). However, if the large lizard is at its natural height, its maximum foraging bout has increased substantially and has become much longer than that of the small lizard at its natural height (5.9 vs. 2.5 h, Figure S1), simply because the small lizard must shuttle frequently whereas the large lizard need not. Furthermore, the large lizard can always move substantially further from shade due to its greater assumed movement speed and thermal inertia (Fig. 4c).

January. When both are compared at 7.5 cm, the small lizard has a slightly shorter foraging bout than the large lizard (2.1 vs. 2.3 h, Figure S1) but, again, the small lizard cannot move nearly as far from shade as the large lizard (0.3 vs. 0.85 km, Fig. 4c) due to its lower movement speed and lower thermal inertia. Qualitatively similar patterns (1.7 vs. 1.7 h, 0.25 vs 0.65 km) hold if both are compared at 1 cm (Figures S2 and 4c, respectively). When compared at their natural heights, the small lizard has a shorter maximum foraging bout (1.7 vs 2.4 h, Fig. S1) and a much shorter maximum foraging radius away from shade (0.25 vs. 0.85 km, Figure 4c).

Cumulative hours of restriction to shade

September. When compared at 7.5 cm in this cool month, neither lizard needs to retreat to shade (Figures 2b & 2c, Figure 4d). At 1 cm, however, the small and large lizards need to cool in shade for 30 and 89 min per day, respectively (Figure 4d). When compared at their natural height, only the small lizard needs access to shade (30 vs. 0 min, Figure 4d).

January. When compared at 7.5 cm or at 1 cm, both lizards need access to shade for considerable periods (small = 224 vs. 288 min; large = 326 vs. 383 min, Figure 4d). When

compared at their natural height, the small lizard is restricted to shade for slightly longer than the large lizard (326 vs. 288 min, Figure 4d).

Translation to space access

By mapping the maximum foraging radii computed above onto particular habitat configurations, the degree of habitat connectivity can be assessed from a physiological perspective. Figure 5 illustrates this by plotting radii from 50 randomly distributed shade points (e.g. bushes, burrows) across a 10 x 10 km landscape, for each of season, size and microclimate scenarios considered in Figures 2-4. In spring, this arbitrary habitat configuration of highly dispersed shade (~ 2 or 3 km between shade patches) would enforce 'central-place' foraging for the small lizard at its natural height but would be almost fully connected for the large lizard at its natural height but less so at 1 cm (Figures 5a & 5b). The physiological connectivity of this habitat for the two lizards at their reciprocal heights in spring would be very similar and low (Figures 5c & 5d). The situation is more extreme in the summer (Figs. 5e-h) when even the large lizard at its natural height would have extremely restricted movement.

Discussion

Attempts to model behavioural thermoregulation have used a variety of approaches, from simplified steady-state analyses that can bound the physical possibilities (Porter et al., 1973; Michael R. Kearney et al., 2009), to detailed individual-based models that are explicit about environmental heterogeneity and movement patterns (Sears & Angilletta, 2015; Sears et al., 2016) and variants in between (Rubalcaba et al., 2019). As always, the appropriate tool depends on the question being asked. The tool we developed here provides a simple means to assess how body size, height above ground, and habitat quality interact from the perspective of a given thermal physiology. Our analysis is unique in considering jointly the biophysical and microclimatic consequences of body size, what we have called the 'Newtonian' and 'Geigerian' effects, respectively.

Ecologically relevant indices and the Geiger effect

The ecological indices we developed capture aspects of the costs and benefits of behavioural regulation regarding foraging time, shuttling frequency, foraging duration and radius, and the time spent inactive in the shade. Our analyses are designed and interpreted for a species that forages predominantly in open (sunny) environments, but the same indices and

analyses can developed for a species that bask in sun but forages in the shade inside a forest. (e.g., *Ameiva*, van Berkum, Huey, & Adams, 1986).

Most significantly, the interpretation of all our analyses changes – qualitatively or quantitatively – depending on whether different sized lizards are at their natural heights or at the same height (Figure 4). This height effect is most dramatic for total activity time (Figure 4a) where, in spring, we would have concluded that big lizards had the greater activity time if both were at 7.5 cm, whereas that small lizards would have had greater activity time if both were at 1 cm. But if both are at their natural heights, they have nearly identical activity times. For this index in summer, we would have concluded that smaller lizards had greater activity time at either height but in fact, at their natural heights, the larger lizard has greater activity time. For all other metrics there are significant qualitative or quantitative changes of interpretation if both the Geigerian and Newtonian consequences of body size are ignored (Fig. 4). Ultimately, a more general analysis is required to explore how size, microclimate, and thermoregulatory parameters interactively affect ecological consequences, but the simple cases here are sufficient to indicate that Geigerian effects are potent and must not be ignored when studying the thermal consequences of body size.

Translation to habitat quality

We use access to shade as an indicator of the connectedness of the landscape, at least in hot environments (Figure 5). For landscapes with limited shade, a longer foraging distance enhances connectivity from a lizard's perspective. Consequently, a given landscape is in effect more connected for a large than for a small lizard: large lizards can cover more ground because of their relatively faster walking speeds, greater thermal inertia, and cooler microenvironments. As a result, large ectotherms can exploit more of warm habitats than can a small ectotherm, which cannot venture far from shade. Very likely, this constraint will cause small ectotherms to deplete the food in the vicinity of its shade retreat (though of course its metabolic needs are less than that of a large ectotherm), and reduced food consumption will exacerbate sensitivity to high temperature (Brett, 1971; Huey & Kingsolver, 2019). On the other hand, the greater ranging capacity of a large ectotherm may increase its spatial overlap with other large individuals, leading to resource depletion (Jetz, Carbone, Fulford, & Brown, 2004). The typically positive scaling of territory (home-range) size with body size has traditionally been explained in energetic terms (McNab, 1963; Schoener, 1968). Our simulations suggest that in warm habitats, the scaling of home-range size may also reflect size-dependent thermal considerations.

Comparison with real lizards

Comparison of our model results with detailed observations of the behaviour of two field-active lizards (Supporting Information) provides a small-scale reality check as well as an example of the value in having a model of physical expectation when interpreting such data. The behaviour of the two lizards was consistent with the model in that the large lizard was able to forage during the period when the small lizard was confined to a shade patch (Figure S4). But having the model predictions led us to new ideas about the lizard's behaviour. For instance, during the periods where the model indicated that the military dragon could forage in the open only by frequent shuttling, the military dragon neither shuttled nor retreated to a burrow. Rather, it waited in the shade at as low a temperature as it could achieve and dashed out only to capture passing prey items. Starting from a low temperature on these foraging bouts of course acts to maximise the time available to chase down prey observed beyond their shade patch. The strategy is obvious in retrospect, but apparently only after comparing predicted and observed behaviour. Such behaviour is probably widespread; one of us (WPP) has observed similar behaviour in the desert iguana *Dipsosaurus dorsalis* under extremely hot conditions.

Model applications to environmental change

Habitat destruction, plant dieback from climate stress, storms, and fire all decrease the amount of shade in a habitat. In some cases, decreases are small and transient, but other cases (as in recent fires in Australia) shade is essentially eliminated for years or perhaps decades. Decreased shade will reduce habitat connectivity as well as 'social' connectivity for ectotherms, especially for small ones. The model we have presented can quantify how reductions in the size and number of shade patches – whatever the cause – can constrain movement options of ectotherms of different sizes.

The Shiny app we have created to run the simulations via a graphical user interface (Supporting Information Appendix S4, http://bioforecasts.science.unimelb.edu.au/ectotherm_transient/) includes tools for visualising the results in comparison with satellite imagery and will facilitate applied use of the approach in managing and accessing thermal aspects of habitat connectivity.

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AUTHORS' CONTRIBUTIONS

M.R.K., R.B.H and W.P.P designed the study; W.P.P. and M.R.K. developed the models; M.R.K. collected the empirical data, M.R.K. and R.H.B. performed the simulations and analysed the data, M.R.K. and R.B.H, wrote the first draft of the paper with contributions from W.P.P. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABITY STATEMENT

All data used in the tests of the model provided in the Supporting Information are available via Zenodo (Kearney, 2020a). The NicheMapR release relevant to this paper (v3.0.0) is also available via Zenodo (Kearney, 2020b).

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606 FIGURES

607

608 **Figure 1.** Conceptual diagram of how body size (black filled circles) alters microclimates in
609 sun, with each animal's boundary layer (white) proportional to its body mass. (a) A
610 "Newtonian"-only perspective assumes that small and large individuals experience identical
611 air temperatures (grey), wind speeds (blue arrows), and radiation loads, as might be the case
612 if they were suspended in air at midday. (b) A "Geigerian" perspective assumes additionally
613 that the larger animal experiences relatively cooler air temperatures as well as higher wind
614 speeds, which reduce the thickness of its boundary layer. Thus, a large diurnal animal on the
615 ground experiences a cooler and more convective environment at midday than does a small
616 diurnal animal on the ground.

617

618 **Figure 2.** Computed heating rates of 10-g and 1000-g ellipsoid bodies under fixed conditions.
619 A) A 'Newtonian' perspective with both the small and large objects positioned at 7.5 cm
620 above ground (the natural height of the large ectotherm) with wind speed 1.36 m s^{-1} and air
621 temperature 34.2 °C. The small ectotherm heats relatively quickly but has a lower steady-
622 state T_b than does the large ectotherm, as expected due to boundary layer effects. B) A
623 'Geigerian' perspective has the small and large ectotherms positioned at their natural height
624 (1 vs. 7.5 cm, respectively). Here the small ectotherm, now experiencing a wind speed of
625 0.57 m s^{-1} and air temperature of 38.4 °C, still heats quickly but has the higher steady-state
626 T_b.

627

628 **Figure 3.** Body temperature trajectories of thermoregulating 10 g (dragon) and 1000 g
629 (goanna) lizards experiencing microclimates at either 1 cm or 7.5 cm above the ground on an
630 average spring (September) or summer (January) day in central Australia.

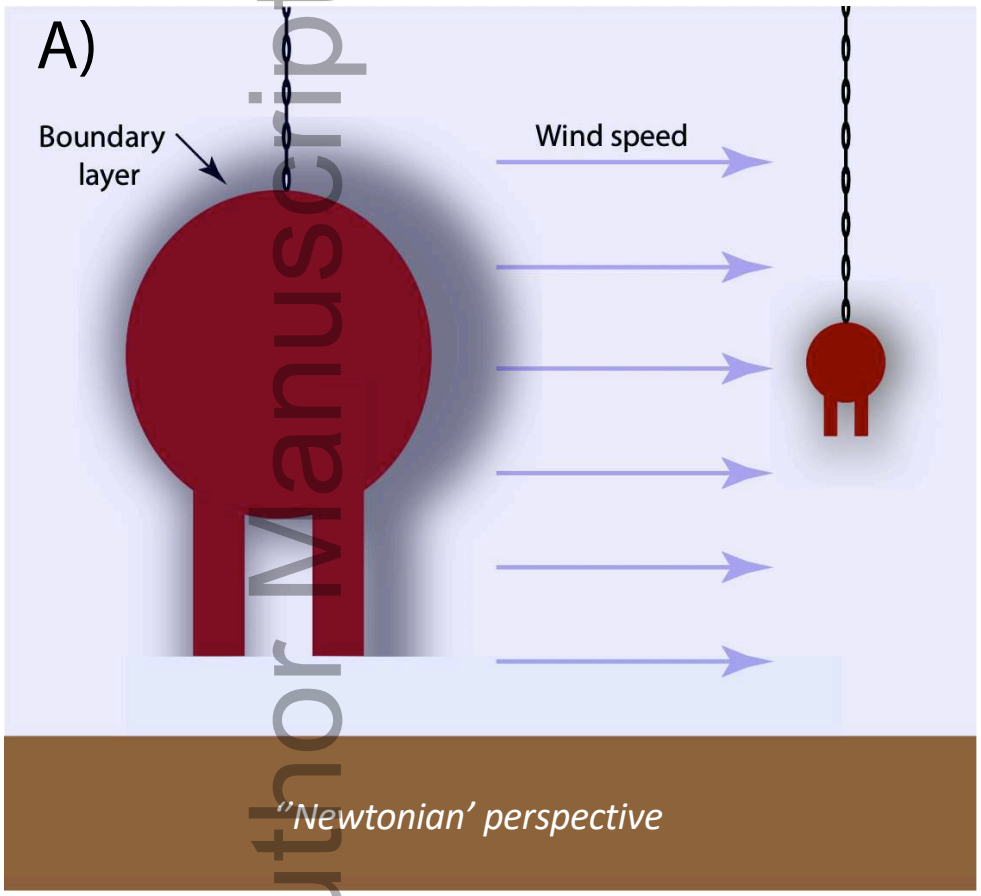
631

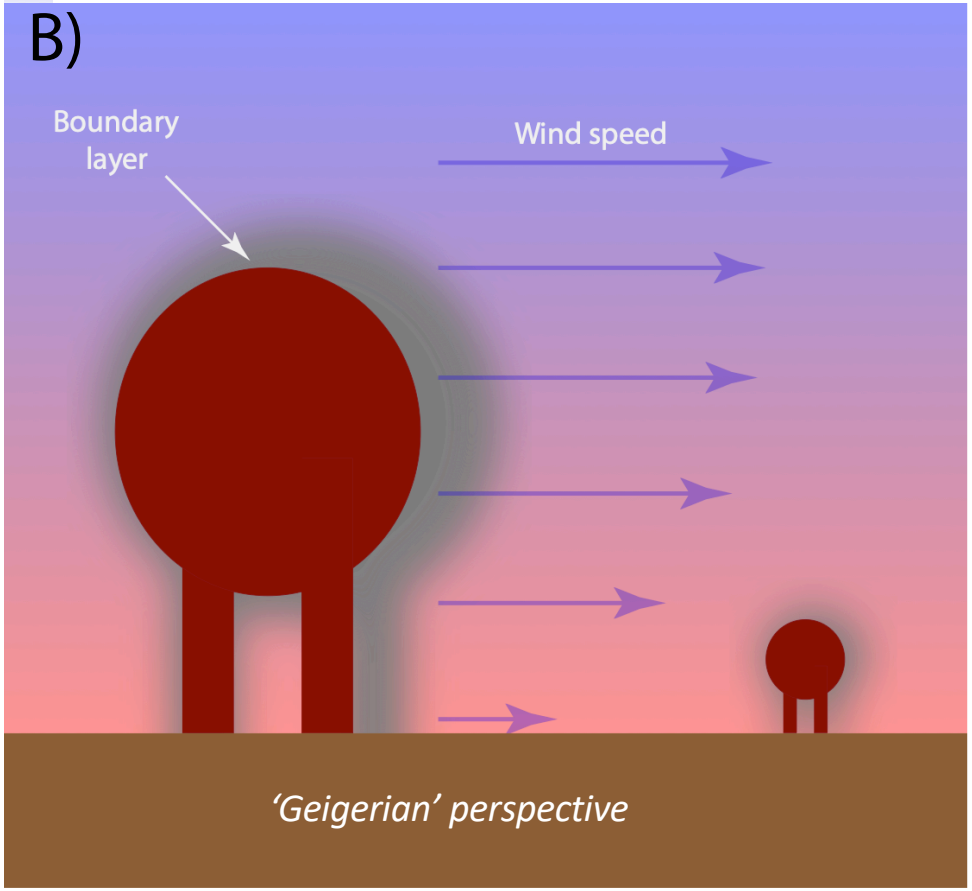
632 **Figure 4** Summary of ecological consequences of thermoregulating for a 10 g (dragon, small
633 dots, dashed line) and 1000 g (goanna, large dots, solid line) lizards experiencing
634 microclimates at either 1 cm or 7.5 cm above the ground on an average spring (September,
635 blue) or summer (January, red) day in central Australia.

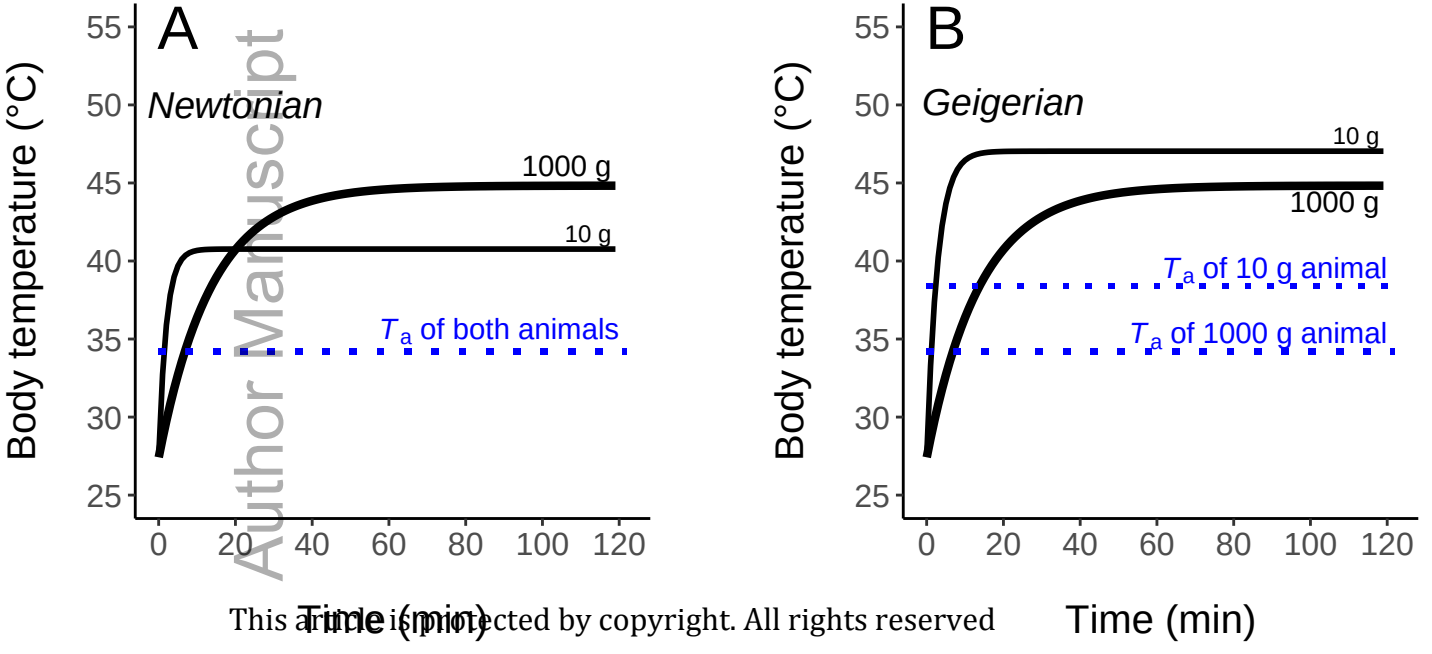
636

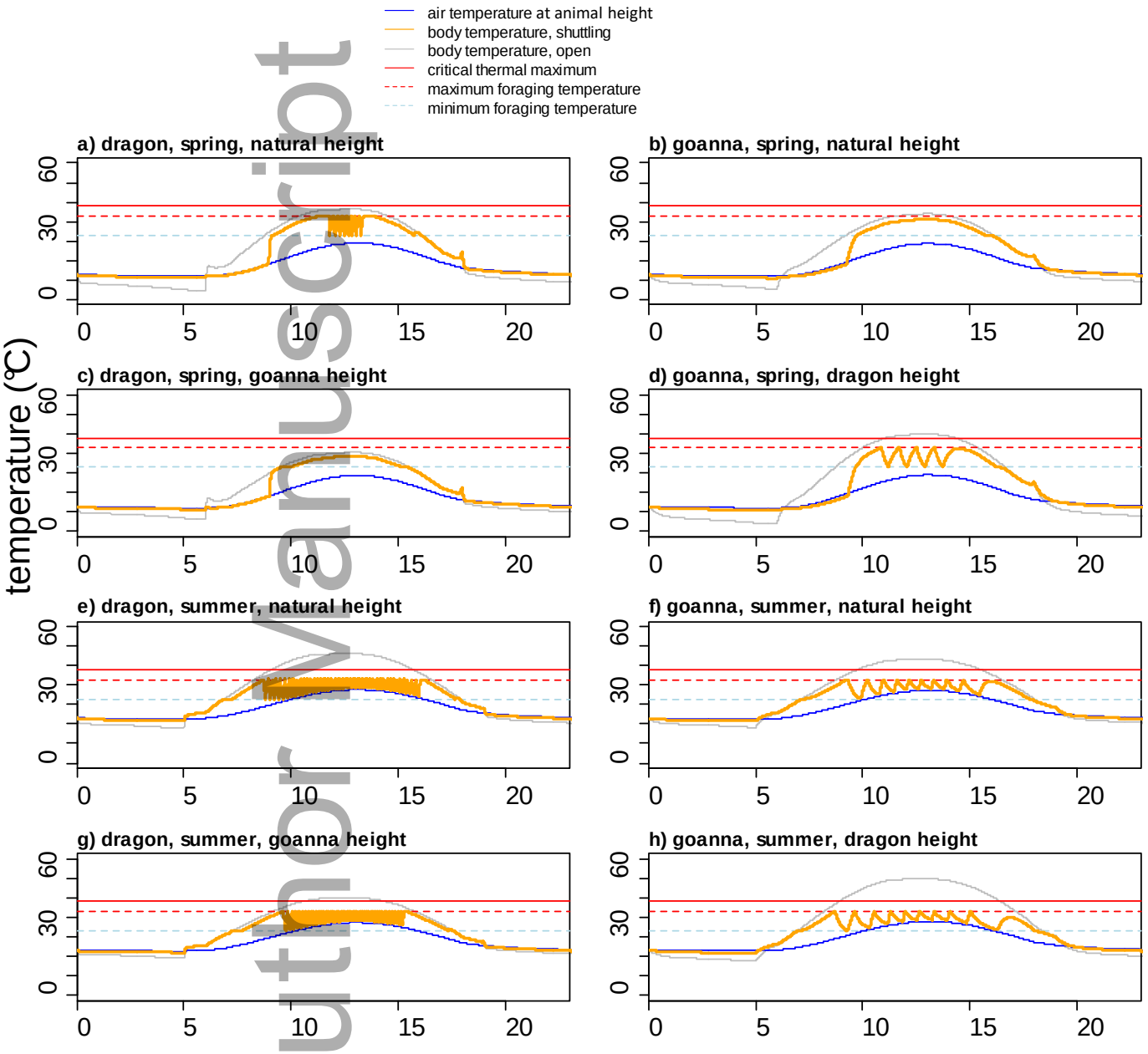
637 **Figure 5.** Maximum daily foraging radii from randomly arrayed patches of shade
638 thermoregulating 10 g (dragon) and 1000 g (goanna) lizards experiencing microclimates at

either 1 cm or 7.5 cm above the ground on an average spring (September) or summer (January) day in central Australia.









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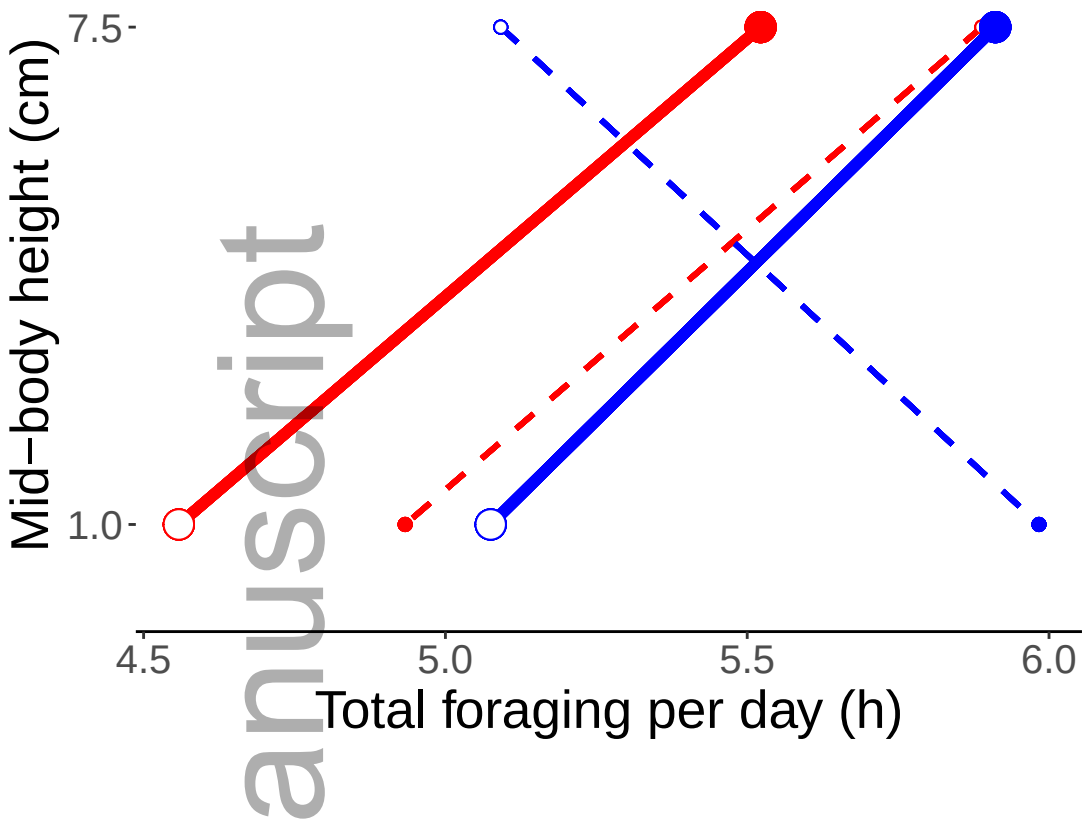

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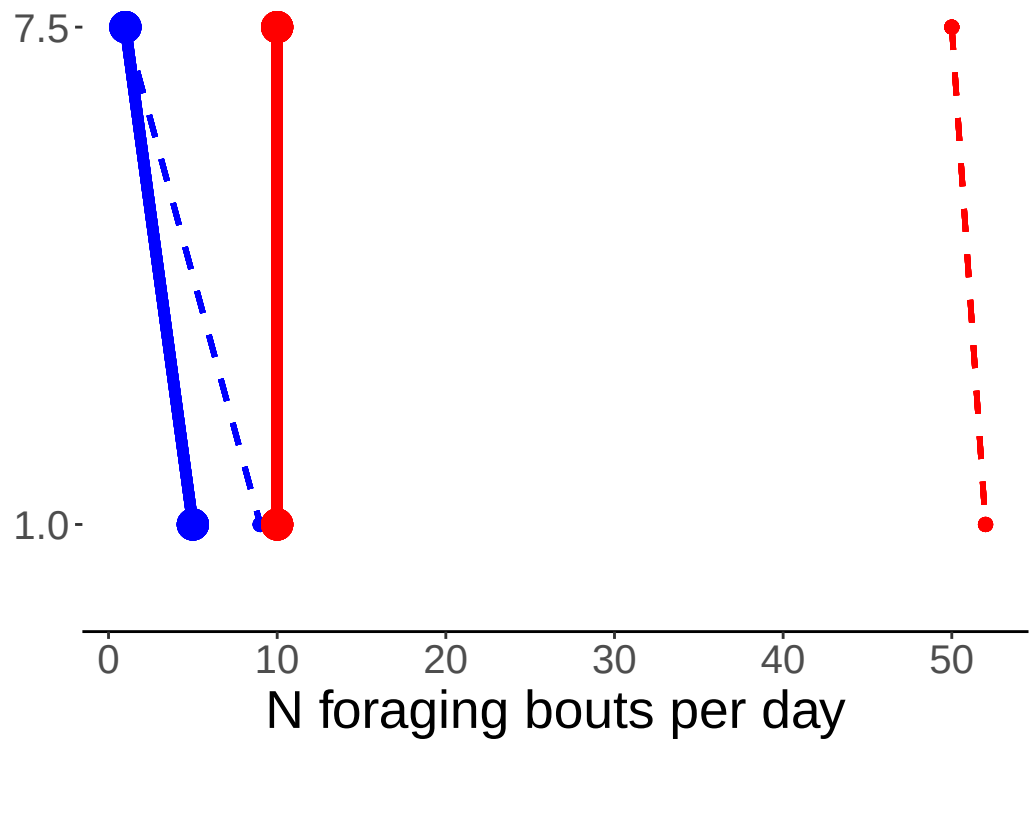

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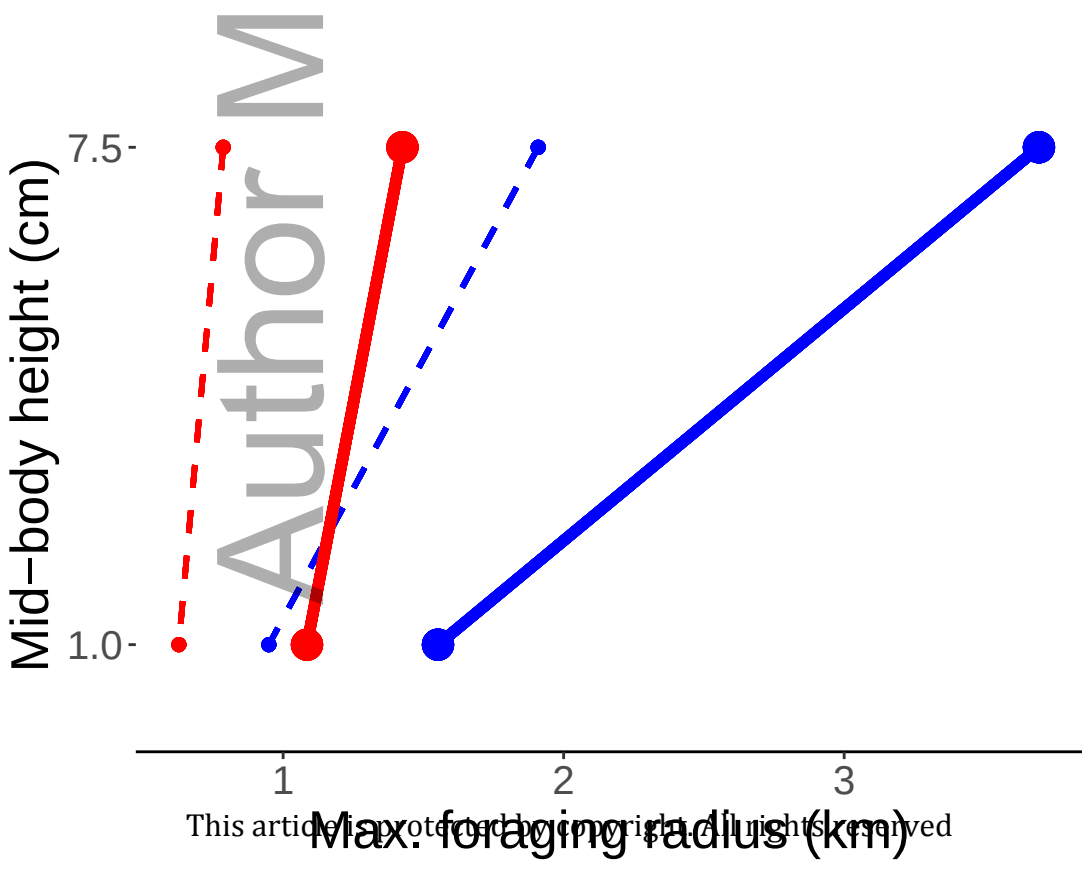
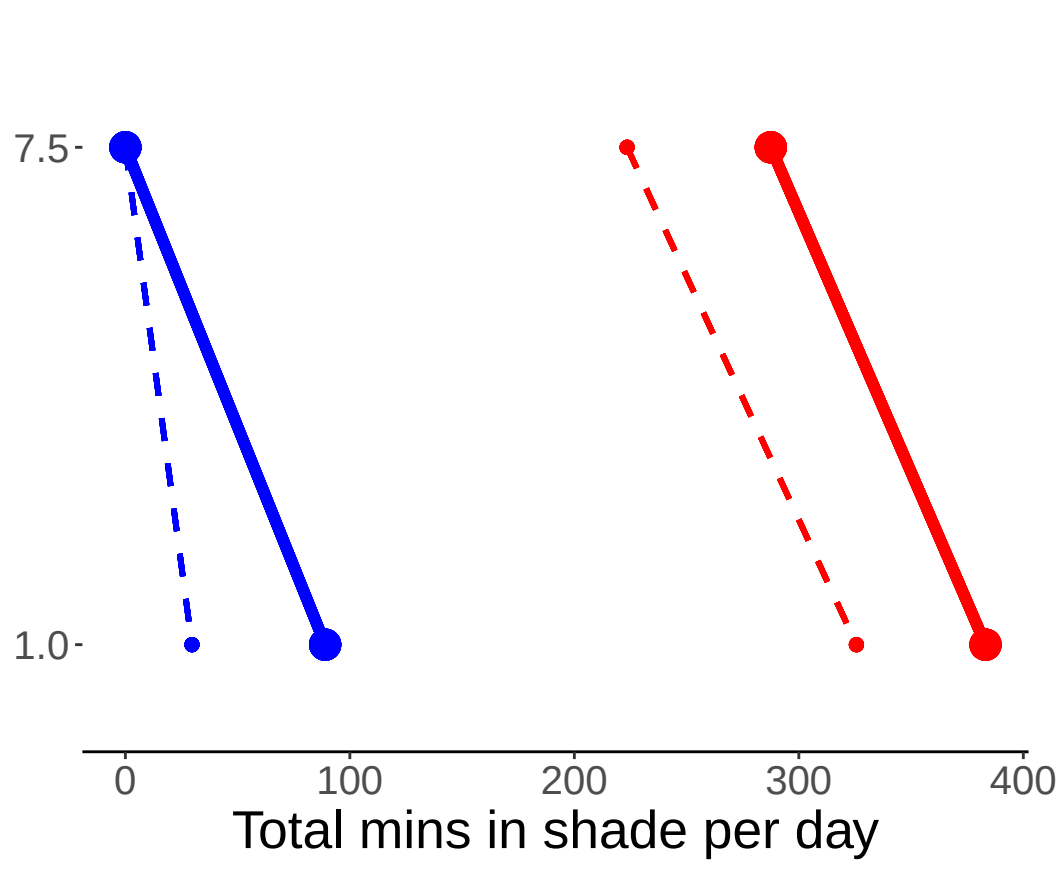
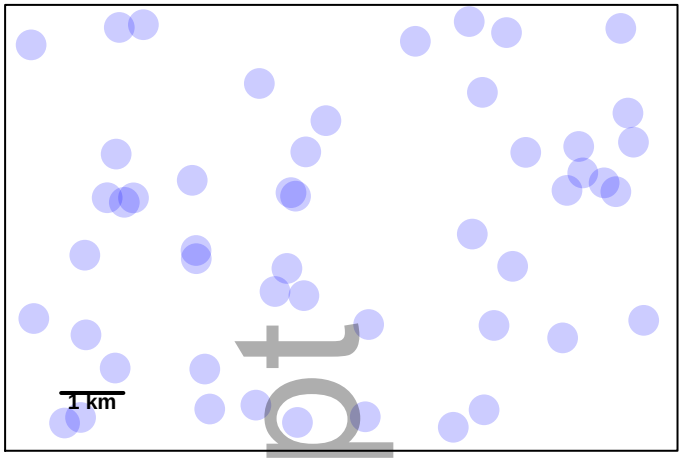


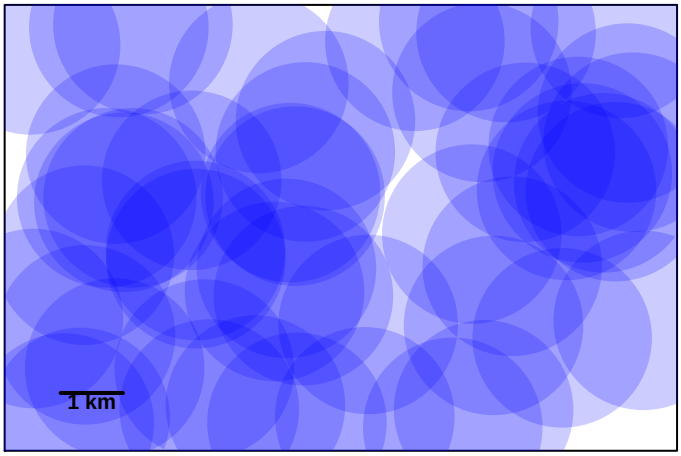
(d)



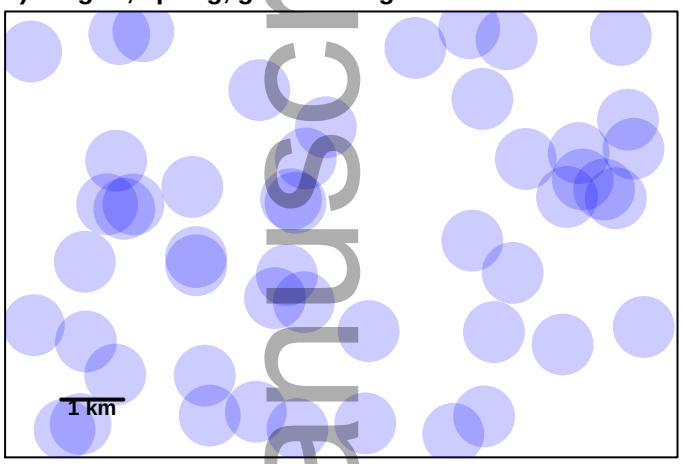
a) dragon, spring, natural height



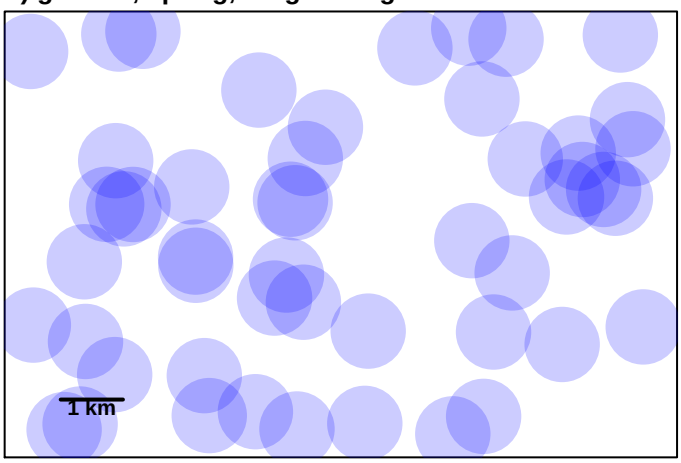
b) goanna, spring, natural height



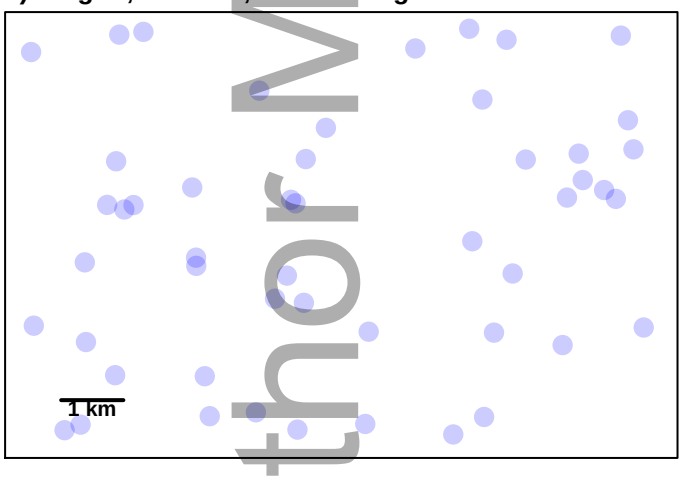
c) dragon, spring, goanna height



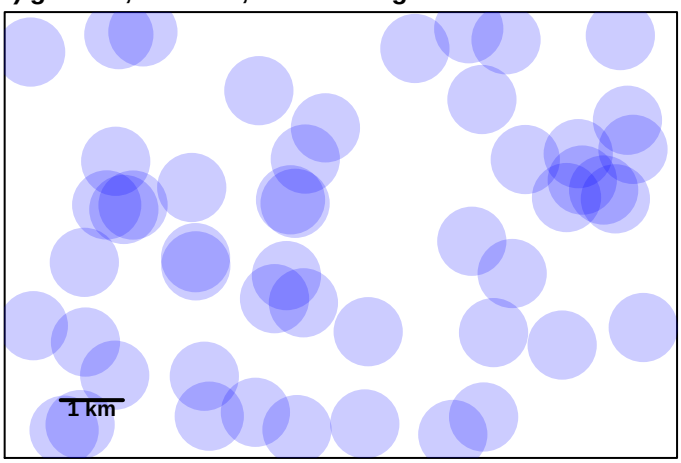
d) goanna, spring, dragon height



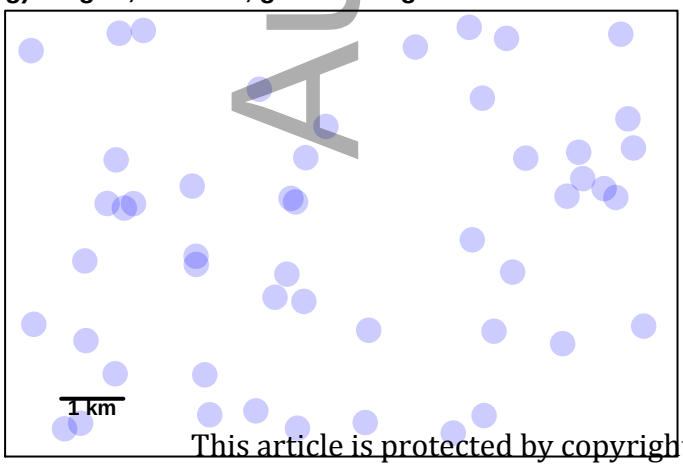
e) dragon, summer, natural height



f) goanna, summer, natural height



g) dragon, summer, goanna height



h) goanna, summer, dragon height