

MAPPING THE FUNDAMENTAL NICHE: PHYSIOLOGY, CLIMATE, AND THE DISTRIBUTION OF A NOCTURNAL LIZARD

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Abstract. The fundamental niche can be viewed as the set of conditions and resources that allow a given organism to survive and reproduce in the absence of biotic interactions. Quantitative descriptions of the environmental variables with which organisms are associated are becoming common with the advent of geographic information systems (GIS). Although such descriptive approaches to the niche are useful for interpolating species distributions, they implicitly incorporate biotic interactions and therefore do not represent the fundamental niche. A mechanistic understanding of the fundamental niche, when combined with GIS data, can provide us with greater insight into the causes of distribution and abundance, a solid foundation for exploring the role of biotic interactions, and greater confidence in extrapolating to novel circumstances such as climate change and species introductions. We apply such a mechanistic approach to study the climatic component of the fundamental niche of a nocturnal lizard, *Heteronotia binoei*, across an entire continent. We combine physiological measurements of this species (thermal requirements for egg development, thermal preferences and tolerances, metabolic and evaporative water loss rates), and high-resolution climatic data for the Australian continent (air temperature, cloud cover, wind speed, humidity, and radiation), with biophysical models to calculate the climatic component of the fundamental niche of this lizard and map it onto the Australian landscape at high resolution. We also use this approach to predict the effects of a mild global warming on the degree-days in the soil for egg development and the potential for aboveground activity of the study organism.

Key words: *Australia; biophysical modeling; climate; distribution; fundamental niche; generalist lizard; GIS; global warming; Heteronotia binoei; mechanistic; nocturnal ectotherm; physiology.*

INTRODUCTION

A basic aim of ecology is to understand the distribution and abundance of organisms. As emphasized by Andrewartha and Birch (1954), distribution and abundance are different aspects of the same problem and may be governed by the same laws and phenomena. The concept of the niche is useful in approaching the problem, but it has been defined in a variety of ways and for a variety of purposes (e.g., Whittaker et al. 1973, Schoener 1989, Colwell 1992, Griesemer 1992, Leibold 1995). To explain the distribution and abundance of a given kind of organism, we find it most useful to view the niche as a property of an organism, or of a population of organisms, rather than as a property of an environment. Following Hutchinson (1957, 1978), we see the niche as a multivariate space whose axes comprise those parts of an organism's environment that influence its potential to survive, develop, and successfully reproduce, i.e., its fitness. The fundamental niche, a term originally conceived by Mac-

Arthur, is the region of environmental space where fitness is greater than or equal to one in the absence of competitors or predators (Hutchinson 1957). The realized niche is usually a more restricted region of environmental space obtained after accounting for biotic interactions. In theory, if we can determine the set of conditions comprising an organism's niche and then map their spatial and temporal occurrence onto a landscape, we should be able to make predictions about the organism's distribution and abundance.

With the advent of geographic information systems (GIS) technology, a common approach to the study of the geographic distributions of organisms has been to quantitatively describe a number of physical conditions at known distribution points of a species, such as climate, elevation, or soil type (Green 1971, Caughley et al. 1987, Austin et al. 1990). These combinations of conditions are variously referred to as the organism's "environmental," "physiological," or "fundamental" niche. Such information can be used to derive statistical models, or empirical estimates, of probability of occurrence that can be interpolated to other parts of the landscape (e.g., Lindenmayer et al. 1991, Sykes et al. 1996, Peterson et al. 1999, Peterson 2001, Kearney and Moussalli 2003, Kearney et al. 2003). In many cases, this correlative approach successfully predicts species occurrences elsewhere on a landscape and can be a

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powerful tool for such applications. Although the correlative approach may provide some insight into the fundamental niche of a species (Peterson et al. 1999, Peterson 2001, Peterson and Holt 2003), it cannot provide a complete picture because it represents both the direct influences of the physical environment as well as climate-dependent biotic interactions. This makes inference of causation difficult, particularly with respect to the relative contributions of biotic and abiotic factors. Difficulty may also arise when one wishes to extrapolate such correlative analyses to novel situations, e.g., under scenarios of climatic change or species introductions. Ideally, such extrapolations should be based on a *mechanistic* understanding of the processes involved if we are to be confident of their predictions. That is to say, we need a mechanistic, rather than a descriptive, understanding of the niche if it is to have maximal predictive power.

*The "climate-space" component of the
fundamental niche*

If we are to determine the fundamental niche of a species in a predictive sense, we must begin with the organism itself and identify and measure key properties that influence its capacity to survive and to acquire energy and resources for growth and reproduction in different environments. We then need to develop a mechanistic understanding of how these properties of the organism interact with its physical environment throughout its life cycle to influence fitness. The difficulty lies in deciding which parts of an organism's environment influence its fitness, and therefore comprise its niche dimensions. This is because the properties of the organism determine how it "perceives" a given set of physical conditions and how those conditions influence its fitness (Lewontin 2000). The nature and relative importance of these axes will thus vary from organism to organism.

All organisms require a net input of energy and mass for successful growth and reproduction, and must maintain steady state or steady periodic thermodynamic interaction with their environment if they are to function efficiently and avoid excessively high or low body temperatures (Porter and Gates 1969). Important axes of any organism's fundamental niche will therefore include those environmental variables that influence energy and mass balance. In the case of a terrestrial environment, these include radiation, wind, air temperature, and humidity. Survival of any organism will be possible only in a subregion of this multidimensional "climate-space," and successful reproduction will be possible in a restricted part of this subregion. However, the exact nature of this region will depend on the relevant properties of the organism such as its size, shape, solar reflectance, insulation, thermal physiological optima, metabolic rate, permeability of skin to water, developmental requirements, etc. Considerable progress has been made over the past 30 years in our under-

standing of the mechanistic links between climatic conditions and the behavior, morphology, and physiology of terrestrial ectotherms and endotherms; it is now possible to calculate climatic influences on key fitness components such as potential activity time, development time, and energy and water balance, from first principles, given the properties of the organism and its physical environment (for overviews, see Porter et al. 2000, 2002). When spatiotemporal data are available for climatic conditions, a landscape view of components of the fundamental niche can be obtained. Such a perspective may explain much about an organism's distribution and also provides a solid foundation from which to consider the effects of other important determinants such as biotic interactions.

We illustrate the utility of this mechanistic approach to the fundamental niche by applying it to the problem of the distributional limits of a nocturnal ectotherm from Australia, the gecko *Heteronotia binoei*. We obtained measurements of a number of phenotypic traits of *H. binoei*, including thermal sensitivity of development, thermal tolerances and preferences, metabolic rates, and water loss rates. We then applied a mechanistic model of how these key organismal properties interact with the climate-space niche dimensions and map the effects onto the Australian landscape under current and predicted climatic conditions.

METHODS

Study system

Heteronotia binoei is a small (to 130 mm total length; 5 g) lizard that is widespread throughout mainland Australia but is absent from the southeastern and southwestern parts of the continent (Cogger 2000) (Fig. 1a). It is an extreme generalist, occurring in a diversity of habitats and consuming a wide range of invertebrate prey (Pianka and Pianka 1976, Pianka 1986, Henle 1990). Detailed genetic study has revealed that this "species" is, in fact, a complex consisting of a number of genetically distinct sexual races with little or no distributional overlap, as well as numerous parthenogenetic lineages derived via hybridization (Moritz 1993 and references therein). In this study we focus on male individuals of the EA6 sexual race, which occurs in the most southerly parts of the range of *H. binoei* (Fig. 1b) (Moritz et al. 1990). We collected geckos from three sites in the vicinity of the townships of Woomera and Marla in South Australia in late August 2000. Details of collecting localities are summarized in Table 1. Maintenance of the lizards is described elsewhere (Kearney and Shine 2004).

Measurement of physiological traits

We measured the mass of each individual as well as the following physiological traits: voluntary thermal minimum (VT_{\min}), voluntary thermal maximum (VT_{\max}), selected body temperature (T_{sel}), evaporative

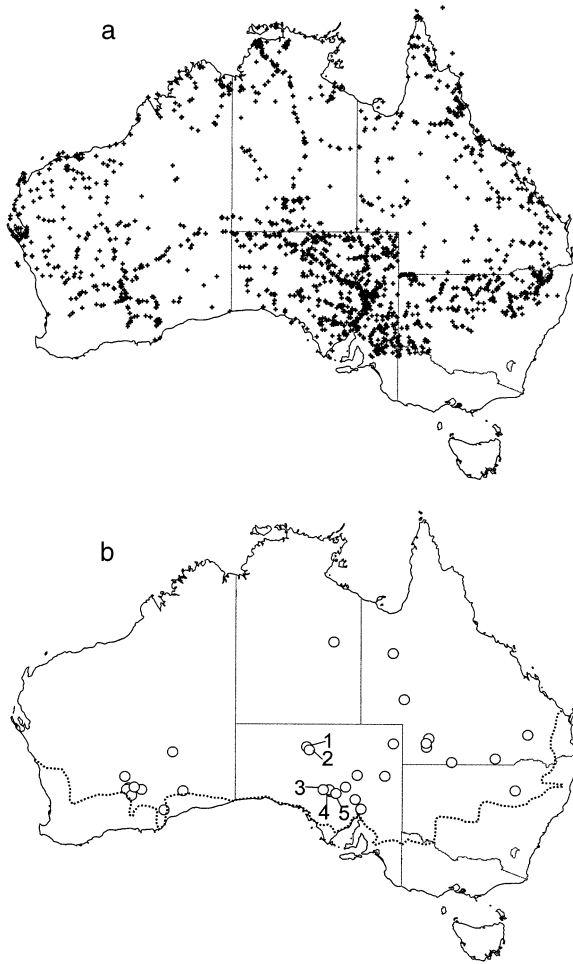


FIG. 1. The maps show (a) the known distribution of the *Heteronotia binoei* gecko complex based on museum records and (b) the distribution of the EA6 race of *H. binoei*. In the latter map, numbered sites are those where animals were collected for physiological measurements (see Table 1 for more details), and the dotted line indicates the southern limit of the *H. binoei* complex.

water loss rate, and resting metabolic rate. We measured the three traits relating to thermal behavior (VT_{max} , VT_{min} , and T_{sel}) using the laboratory thermal gradient described in Kearney and Predavec (2000). Body temperatures of lizards in the thermal gradient were recorded automatically every 30 s for 24 h using extremely fine type-T thermocouples (40-gauge) in conjunction with a Campbell CR10 Data Logger (Campbell Scientific, Logan, Utah, USA).

We determined water loss rates at 30°C by measuring the change in body mass of lizards placed in sealed 2-L jars at 5% relative humidity for 24 h. We measured resting metabolic rates of fasted lizards at 30°C using flow-through respirometry and a multiplexer. During measurement of metabolic rates, room air was drawn through a given chamber by an Ametek R-2 Flow Control Meter at a flow rate of 6.25 mL/min, after passing through a filter of Drierite and Ascarite (to remove H_2O and CO_2 , respectively). The oxygen concentration in the animal chamber was sampled every 2 s with an Ametek N-37M oxygen sensor and a S-3A/II oxygen analyzer (precision 0.001%; Ametek, Paoli, Pennsylvania, USA). Oxygen consumption measurements were made for 1.5 h for each animal chamber while simultaneously measuring oxygen concentrations in a reference chamber. A data acquisition program (Datacan V5.0, Sable Systems, Los Angeles, California, USA) recorded output from the oxygen analyzer and also controlled the multiplexer. We recorded resting metabolic rate in milliliters of oxygen per gram per hour as the mean of the most level 30-min section, after baselining the data and adjusting for barometric pressure, flow rate, and body mass.

Data on the number of degree-days required for development are derived from Kearney and Shine (2004) and M. Kearney (*unpublished data*). Incubations at 24°C, 27°C, and 30°C of a variety of sexual and parthenogenetic forms of *H. binoei*, including the EA6 race, indicate a developmental threshold of ~20°C and that ~600 degree-days above this threshold are required for successful egg development.

Biophysical modeling

We used a general model of heat and mass transfer for ectotherms (Porter et al. 1973, Porter 1989), in con-

TABLE 1. Collecting localities of the various races of *Heteronotia binoei*, as well as the number of individuals collected and used in this study.

Locality†	Latitude	Longitude	Sample size‡
1) Wintinna	27.711° S	134.115° E	4
2) Copper Hills	27.950° S	134.313° E	3
3) Kingoonya	30.911° S	135.315° E	3
4) Coondambo	31.060° S	135.865° E	4
5) Wirraminna	31.190° S	136.228° E	3
Total samples			17

† Locality numbers refer to those marked on Fig. 1b.

‡ Not all traits were measured for all individuals so sample sizes per analysis vary slightly from these maximum values.

junction with a microclimate model (Porter et al. 1973, Mitchell et al. 1975), to determine the biophysical effects on the amount of thermally suitable time for development and activity, temperature-dependent metabolic costs, and water loss, under realistic climatic conditions.

The microclimate model is a one-dimensional finite difference model that simultaneously solves heat and mass balance equations for the ground surface and below. It includes a subroutine for computing clear-sky solar radiation given a specific time, latitude, longitude, slope, and aspect (McCullough and Porter 1971). Wind speed and temperature profiles from the ground surface to 2 m, and daily variation in relative humidity, are generated from meteorological data on monthly maximum and minimum air temperature (2 m shade), wind speed, and relative humidity. We used sunshine duration data in combination with data on day length to account for the effect of cloud on incoming solar radiation, according to the Angstrom formula (Linacre 1992:176), and to obtain estimates of percent cloud cover for calculations of sky temperature. An example data input file for the microclimate simulations performed in this study is included in Appendix B. We obtained monthly estimates of maximum and minimum air temperature, wind speed, and humidity from continent-wide surfaces for these variables, interpolated from weather station data (>30 years) with the programs ANUSPLIN and ANUCLIM (Hutchinson 1991, 2000) using a 0.05°-resolution digital elevation model DEM (Hutchinson and Dowling 1991). Wind speeds and relative humidity were taken from 09:00 and 15:00 readings because maximum and minimum readings were not available. The relative humidity at 09:00 was taken as the maximum and the 15:00 value as the minimum. For wind speed, the greater of the two was taken as the maximum and the lower as the minimum. Cloud cover was assumed to remain constant throughout the day. Our calculations assumed flat ground and a dry, sandy substrate. At night the animal was allowed to seek shady microenvironments to minimize radiant heat loss.

The microclimate model outputs hourly estimates of long- and short-wave radiation, relative humidity, wind and temperature profiles above the surface, surface temperature, and soil temperature profiles at various depths down to 60 cm. These values are then used as inputs for the ectotherm model, in addition to various properties of the animal relating to morphology, physiology, and behavior. Briefly, the ectotherm model determines, on the hour, whether the physical environment above ground is suitable for activity. It assumes that the animal is always active (and exposed to local wind and humidity) when thermal conditions permit, and that it maintains its optimal core temperature, if possible. If conditions are too hot or too cold for activity, the animal retreats underground to a temperature as close to its optimal body temperature as possible

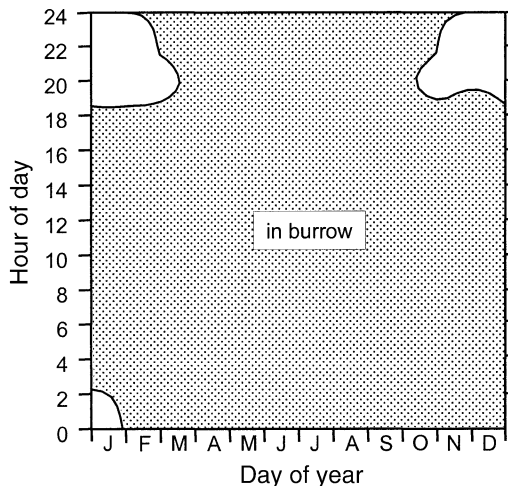


FIG. 2. Calculated seasonal and daily activity times for a male EA6 *H. binoei* at Alice Springs, Central Australia. The shaded region is where activity is not possible and the animal has retreated to its burrow.

(see Fig. 2 for an example of model output for daily and seasonal potential activity time). Humidity below ground is assumed to be 99% because it rarely goes below this value even in very dry soils (Brown and Van Havern 1972). The evaporative water loss rate is estimated on the hour from a molar flux balance model modified from Porter et al. (2000). The metabolic rate is also determined each hour from an empirical relationship with body temperature and body size. In this way, annual estimates of potential hours of activity as well as metabolic and water expenditures are obtained.

Our simulations of *H. binoei* calculated the effects of developmental rates, body size, selected body temperature (T_{sel}), voluntary thermal limits (VT_{min} and VT_{max}), metabolic rate, and water loss rate in interaction with "real" climates. (See Appendix C for an example of an input file for the ectotherm model.) Our calculations of degree-days in the soil for egg development assume a nest located 10 cm deep in the soil. We chose this depth based on our own observations of natural nests of this species. Shallower nests, although they have higher mean temperatures, also experience a greater diurnal range and therefore may experience lethally high temperatures. Metabolic rates were allowed to vary with body temperature and mass according to the equation described in Bennett and Dawson (1976), but these values were then multiplied by 0.8 to represent the proportional difference between that predicted by the equation and that observed for *H. binoei* in this study (see *Results*). We used our data on water-loss and metabolic rates at constant temperature, humidity, and wind speed in conjunction with the Colburn analogy, which calculates mass transfer coefficients from the heat transfer coefficients as a function of object size and environmental conditions (Bird et al. 2002), to determine the percentage of the skin that

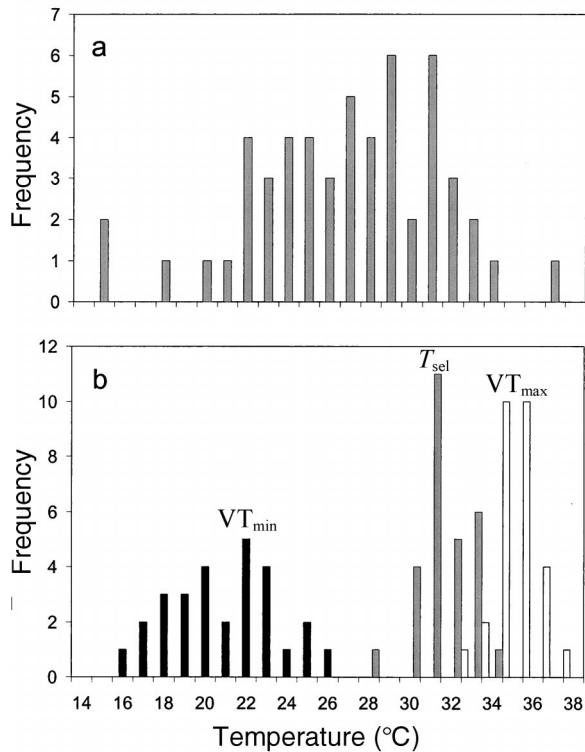


FIG. 3. (a) Frequency distribution of body temperatures of field-active *Heteronotia binoei* from a population within the range of the EA6 race (K. Henle, unpublished data), compared with (b) frequency distributions of voluntary thermal minimum (VT_{min}), voluntary thermal maximum (VT_{max}), and median selected body temperatures (T_{sel}) of EA6 *H. binoei* in a thermal gradient.

represents a free-water surface (Appendix D). These calculations of “percentage of skin wet” were made separately for each individual lizard and the average value was then used in the calculations (Table A1). To provide a more intuitive scale for comparing maintenance energy requirements and to provide estimates of discretionary water, we calculated the amount of food required to meet maintenance costs assuming a diet of “crickets” (see Appendix C for values used for dietary composition in terms of proteins, lipids, carbohydrates, and water, as well as the general input file for the ectotherm model).

We ran two continent-wide simulations at 0.05° resolution using the physiology of the EA6 males of *H. binoei* (278 289 separate locality runs of the model per continent-wide simulation, each continent-wide simulation taking approximately three days to calculate on an 850-MHz laptop computer). The first simulation used the interpolated long-term climatic averages, whereas the second simulation incorporated the monthly maximum and minimum air temperatures predicted by the year 2100 under a conservative scenario of global warming, SRES Marker Scenario B1 (Mid) (1.7°C rise in global mean surface temperature). We obtained

the delta values for this scenario at 25-km resolution for Australia with the software package OzClim Version 2.0.1 (CSIRO, Aspendale, Victoria, Australia), using the DARLAM climate change pattern.

Finally, we compared the predictions of the mechanistic, biophysical approach with the correlative, statistical approach under current conditions and under the scenario of global warming just described. We used a previously published logistic regression model for the EA6 sexual race derived using the Akaike’s information criterion, AIC (Kearney et al. 2003). The AIC is an information-theoretic approach to model selection detailed by Burnham and Anderson (1998). The original model in Kearney et al. (2003) included mean annual temperature, mean annual rainfall, mean annual humidity, temperature seasonality, rainfall seasonality, and rainfall variability as predictor variables. For the climate change scenario case, we recalculated the probability of observation surface using the projected values for mean annual temperature and mean annual precipitation.

RESULTS

Physiological measurements of Heteronotia binoei

The mean mass of males of the EA6 sexual race of *Heteronotia binoei* was 2.23 ± 0.100 g ($n = 17$ lizards). The mean voluntary thermal minimum (VT_{min}) and voluntary thermal maximum (VT_{max}) recorded in the thermal gradient were $21.1^\circ \pm 0.68^\circ\text{C}$ and $34.9^\circ \pm 0.27^\circ\text{C}$, respectively ($n = 14$). The VT_{min} ranged from 15.6° to 25.4°C , whereas the VT_{max} ranged from 33° to 37.5°C . The distribution of the VT_{min} and VT_{max} values measured in this study corresponds closely to the distribution of body temperatures measured in field-active individuals from Kinchega National Park (K. Henle, unpublished data), which are within the distributional range of the EA6 race (Fig. 3). We used the lowest VT_{min} and the highest VT_{max} values as activity thresholds in our simulations to fully bound the limits to activity. The mean selected body temperature in the thermal gradient was $30.8^\circ \pm 0.22^\circ\text{C}$ ($n = 14$), which was similar to those previously reported in the literature (30.0°C in Licht et al. 1966, based on thermal gradient data, 31.3°C in Henle [1990] based on field data; see also Fig. 3). The resting metabolic rate was 0.20 mL $\text{O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1} \pm 0.021$ ($n = 15$), $\sim 20\%$ lower than the expected value for a lizard of its size (0.25 mL $\text{O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$) based on the empirical equation of Bennett and Dawson (1976). Our calculated water loss rate of 0.77 mg $\cdot \text{g}^{-1} \cdot \text{h}^{-1}$ was similar to that previously reported for *H. binoei* (0.95 mg $\cdot \text{g}^{-1} \cdot \text{h}^{-1}$ at 30°C over 24 h; Warburg 1966). Based on our estimates of metabolic rate and evaporative water loss rate, we calculated the percentage of the skin area that is “wet” in *H. binoei* to be 0.44% (see Appendix D).

Biophysical simulations

The mean number of degree-days above 20°C at 10 cm depth in the soil decreased with latitude and ranged

from 0 at the southernmost tip of the island state of Tasmania, to >4000 near the townships of Wyndham and Jabiru in the far north of the Northern Territory (Fig. 4a). Some parts of the southern border of *H. binoei* were very close to the 600 degree-day contour, which is the lower threshold for development.

Potential annual activity estimates were entirely driven by the VT_{\min} (rather than VT_{\max}), because these nocturnal lizards are rarely exposed to high temperatures during their active period. A typical example of daily/seasonal activity patterns is provided in Fig. 2. Estimated potential activity decreased with latitude (Fig. 4b), with a large region of zero potential activity in southeastern Australia. In the far north of Australia, at a latitude of $\sim 12\text{--}13^\circ$ N, potential activity reached an upper limit of ~ 3950 h/yr, which represents all potential nighttime hours (Fig. 4b). The southern limit to the distribution of *H. binoei* was very close to the 400-h potential activity contour in some regions (Fig. 4b), and this activity contour was in a similar position to the 600 degree-day threshold contour (Fig. 4a).

Estimated absolute annual maintenance metabolic costs decreased with latitude, ranging from 13.9 kJ in the south to 52.8 kJ in the north (Fig. 4c). Assuming a diet of crickets, this equates to annual maintenance food requirements ranging from 2.2 to 8.5 g. As the zero-hours of potential activity contour is approached, an individual *H. binoei* would have to encounter prey at a rate of ~ 0.17 g/h if it were to meet its maintenance energy costs (Fig. 4d). At the southern border of *H. binoei*, a maximum encounter rate of ~ 0.03 g/h would be required.

Estimates of absolute annual water loss rates ranged from 0.28 g to >25 g (Fig. 4e). Because we assumed that the retreat sites of the lizards had high humidity (99%), our estimates of evaporative water loss rates were strongly influenced by potential activity time. Overall, water loss rate estimates increased toward the interior of the continent, reflecting both reduced humidity and increased potential activity times in this region, with the maximum water loss rates occurring in the northern half of the arid zone at a latitude of $\sim 20^\circ$. Decreases in water loss rate estimates in the far north of Australia occur because of an increase in relative humidity, despite a continuing increase in potential activity time (Fig. 4e).

Estimates of discretionary water comprise the water intake from food minus evaporative water loss, assuming a diet of crickets and that sufficient food is consumed to meet maintenance costs. Therefore, in our calculations discretionary water depends on both the

maintenance metabolic rate (because this determines food intake) and the evaporative water loss rate. A positive value of discretionary water occurs when sufficient water is obtained through food to maintain water balance without the need to drink. Estimates of absolute annual discretionary water ranged from net losses of >19 g to net gains of up to 3.3 g (Fig. 4f). The pattern of change in discretionary water across the Australian landscape was roughly the inverse of the pattern for evaporative water loss, with high discretionary water in the southern, eastern, and northern parts of Australia and low discretionary water in the northern part of the arid zone (Fig. 4f).

Simulated effects of a global-warming scenario

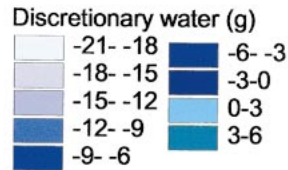
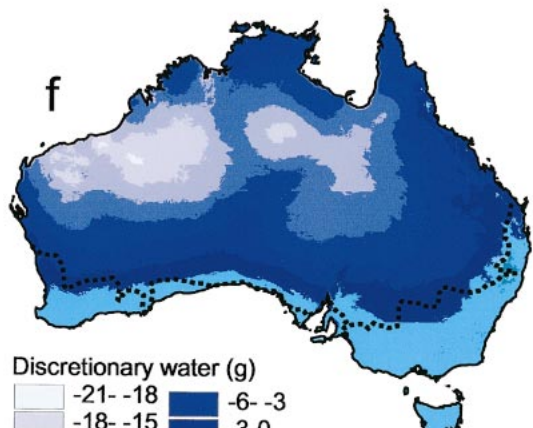
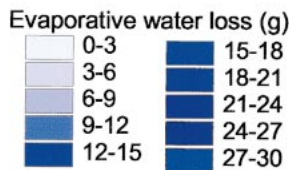
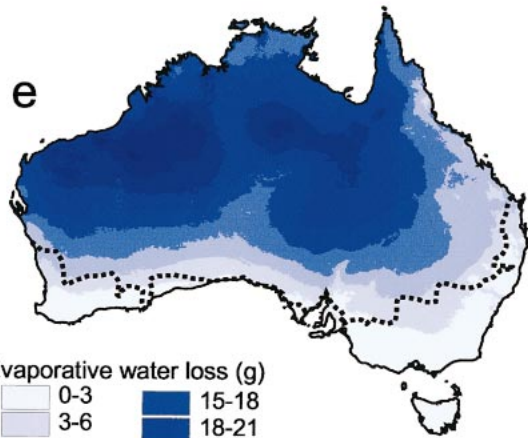
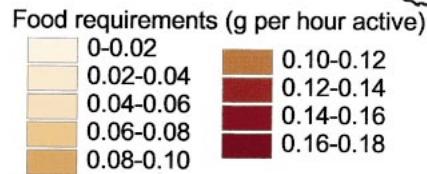
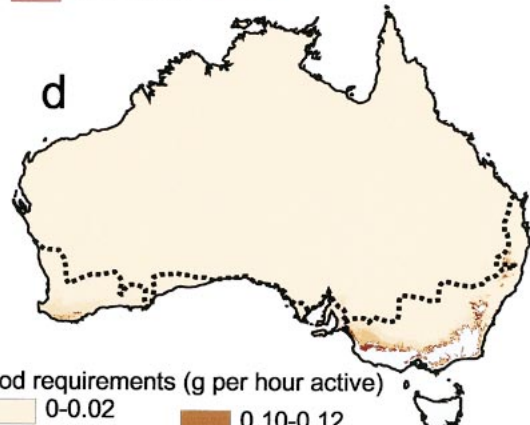
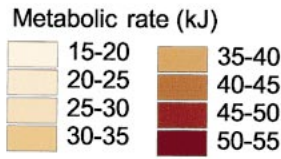
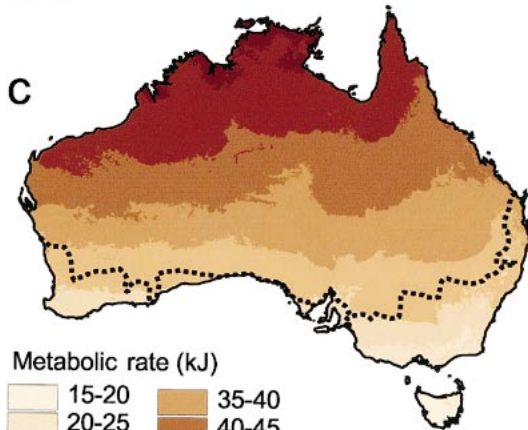
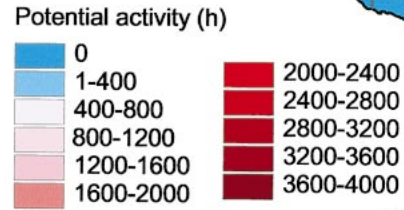
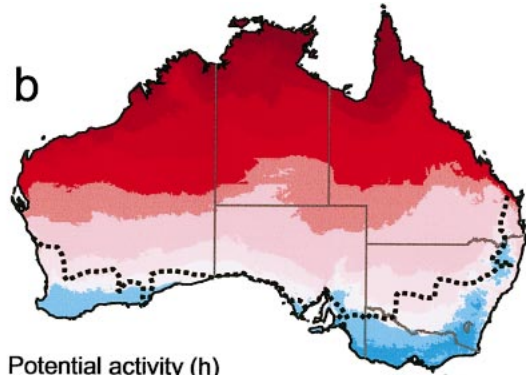
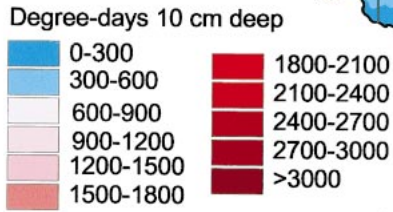
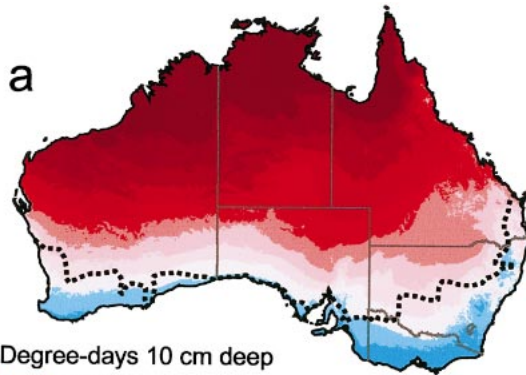
The degree-days for development and potential activity time were strongly affected under the global-warming scenario. The 600 degree-day threshold is predicted to shift south by as much as 170 km over 100 years under a 1.7°C global-warming scenario (Fig. 5a). Assuming a 15°C activity threshold, the zero hours of activity contour for a nocturnal ectotherm could shift by up to 100 km, whereas the 400 hours of activity contour could shift south by as much as 200 km (Fig. 5b). The magnitude of the change in potential hours of activity was greatest in the northern and southern parts of Australia (Fig. 5c).

The mechanistic and statistical approaches to distributional modeling make similar predictions with respect to the current southern distributional limit but different predictions with respect to changes induced by global warming in the southern border of the EA6 race of *H. binoei*. Under average climatic conditions, the southern 10% probability border of the AIC_c best model predicted distribution for the EA6 race corresponds closely with the 600 degree-days contour and the 400 hours of potential activity time contour (Fig. 5d). When predicted changes induced by global warming in mean annual temperature are used with the AIC_c best model, the southern border of the EA6 race shifts south a similar distance to that predicted for the 600 degree-days contour (and the 400 hours of potential activity time contour). However, the AIC_c eastern range limit contracts substantially inland (Fig. 5e). When predicted changes in mean annual temperature and rainfall are used with the AIC_c best model, the predicted distribution changes little in comparison with the AIC_c distribution under average climatic conditions (Fig. 5f).

DISCUSSION

Our goal in this study was to apply a mechanistic model of the fundamental niche of a nocturnal ecto-

FIG. 4. Results of continent-wide 0.05° -resolution biophysical simulations for the physiology of EA6 male *Heteronotia binoei* for (a) degree-days for egg development, (b) potential activity time, (c) maintenance metabolic costs, (d) food requirements per hour of activity, (e) water loss, and (f) discretionary water. All maps are of annual summations. The dotted line represents the known southern distributional limit of *H. binoei*.



therm, *Heteronotia binoei*, and to map this onto the Australian landscape to better understand the constraints on its distributional limits. We tested the microclimate and ectotherm models against our own microclimate measurements and against published data on another nocturnal lizard (*Oedura marmorata*) from the Australian arid zone, with favorable results (see Appendices). We then measured key organismal properties of *H. binoei* and analyzed how these properties interact with climatic variation across the Australian continent to influence potential for egg development, potential for activity, and energy and water balance. Our discussion begins by considering whether regions of the Australian continent can be considered to be outside the fundamental niche of *H. binoei*, based on our data and calculations. We then consider climatic effects on energy and water balance and how these data could be further incorporated into building a picture of the fundamental niche. Finally, we consider how a mild global-warming scenario is predicted to affect aspects of the fundamental niche of *H. binoei*, and we compare our approach and predictions with those of a non-mechanistic approach.

*Climatic limits to the fundamental niche
of Heteronotia binoei*

Imagine that the gecko *Heteronotia binoei* had no competitors or predators on the Australian continent. If this were true, the distribution and abundance of *H. binoei* would reflect its fundamental niche only. Potentially, there would be parts of the Australian landscape where abundance would be zero because the conditions and resources it requires to successfully complete its life cycle are absent. Our mechanistic approach to calculating and mapping the fundamental niche gives us a partial picture of this scenario with respect to climatic constraints, particularly in relation to development and aboveground activity.

Egg development in reptiles is frequently constrained by cold climatic conditions (Shine 1999). Given that *H. binoei* lays its eggs in the soil and requires 600 degree-days above 20°C to complete development, we can calculate where on the Australian landscape soil temperatures would be suitable for successful development. Clearly, any region that has insufficient degree-days available in the soil would be outside the fundamental niche of *H. binoei*. Moreover, for this species we can ignore the possibly important effects of soil water potential on egg development because *H. binoei* has a watertight calcareous-shelled egg akin to

that of birds, as do all geckos from the subfamily Gekkoninae (Dunson 1982). Our calculations demonstrate that a considerable portion of southern Australia is outside the fundamental niche of *H. binoei* in this respect (Fig. 4a). In some areas the southern border of *H. binoei* lies very close to this limit, suggesting that at least part of the distributional range of *H. binoei* is directly controlled by climatic constraints on egg development. In other areas, however, the southern border is a considerable distance north of the 600 degree-day contour, which suggests the action of other kinds of constraints.

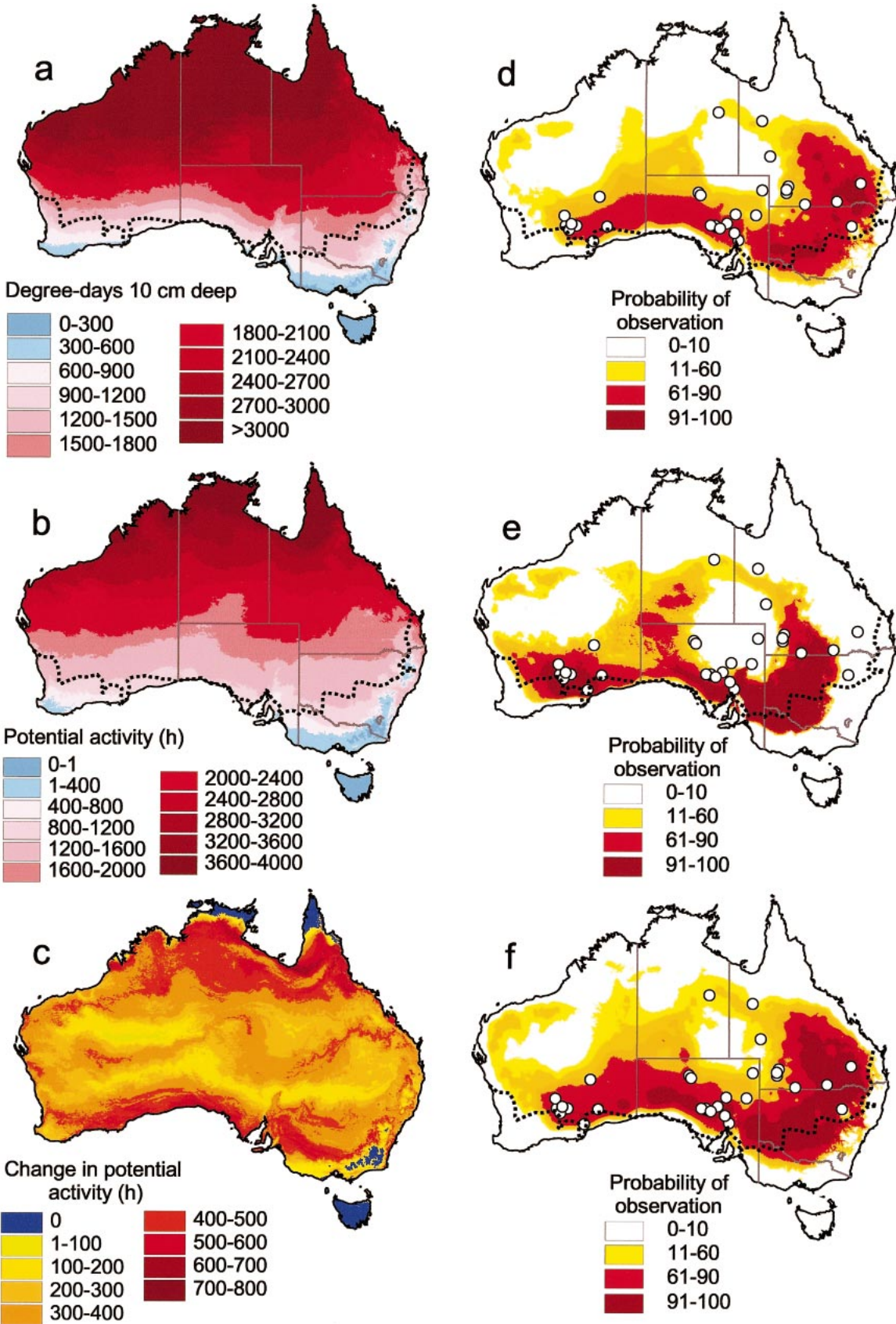
Another variable we have calculated that is to some degree assignable as either inside or outside of the fundamental niche of *H. binoei* is potential activity time. Given the thermal thresholds for activity that we have measured for this species (which correspond well with the body temperatures of field-active individuals; Fig. 3), a considerable portion of southeastern Australia, including all of the island state of Tasmania and mountainous parts of the mainland, would provide zero hours of potential activity and is therefore clearly outside the fundamental niche of *H. binoei* (Fig. 4b). If potential activity time did completely determine the southern distributional limit of *H. binoei*, however, we would not expect the distribution limit to coincide with the zero-activity threshold. Instead we would expect the limit to occur once insufficient time is available to gather the required amount of resources for successful reproduction. This point illustrates the multifarious nature of the problem of calculating the fundamental niche. To fully address this problem, we need to know the total energy and mass requirements of the organism, the availability of those resources across the landscape, and the capacity of the organism in question to acquire those resources.

*Climatically imposed energy and water costs in
H. binoei*

Although it is very difficult to determine the composition and availability of suitable prey for an organism such as *H. binoei*, we are in a good position to make estimates of its food and water requirements that result from climatically imposed maintenance costs. Thus we can partially address the issue with respect to the required amount of potential activity time. The maintenance metabolic costs of ectotherms are dependent on body size, body temperature, and cellular machinery. Our measurements of resting metabolic rates indicate that the maintenance costs of the EA6 race are 20% lower at 30°C than predicted for a lizard of that

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FIG. 5. Calculated effects of SRES Marker Scenario B1 (Mid) global warming by year 2100 on (a) annual degree-days for egg development, (b) annual potential activity time, and (c) annual change in potential activity time, as well as statistically modeled distributions (AIC_c best model) under (d) "current" climatic conditions, (e) predicted changes in mean annual temperature, and (f) predicted changes in mean annual temperature and precipitation. The dotted line represents the known southern distributional limit of *H. binoei*. Distribution of the EA6 race (open circles) is shown in (d)–(f). Probabilities of observation are reported as percentages.



size. Other factors that influence maintenance metabolic rates are thermoregulatory behavior and thermal constraints imposed by the environment. Our biophysical calculations consider all of these influences on maintenance energy costs simultaneously, in a mechanistic framework. Thus they allow us to make quantitative estimates of maintenance energy requirements. We calculated that the absolute annual maintenance energy requirements would range from 13.9 to 52.8 kJ (Fig. 4c). If these are translated into food requirements, assuming a diet of crickets, the lizards would have to consume ~ 2.2 g in the south of Australia and ~ 8.5 g in the north to meet their maintenance costs.

We can combine our data on potential activity time to estimate the rates at which prey must be encountered to meet these maintenance costs (Fig. 4d). With an hourly time step, the required encounter rate reaches a maximum of 0.17 g/h just before the zero-hour activity contour, which equates to approximately one gecko-head-sized cricket captured per hour. A considerably higher encounter rate would be required to obtain sufficient resources for successful reproduction. The problem is exacerbated because a reptile's performance is strongly temperature dependent; thus, the efficiency with which it can acquire resources decreases with temperature (Huey 1982). This is particularly the case for active foragers such as *Heteronotia binoei* (Henle 1990) because of their high thermal sensitivity of locomotor performance (Autumn et al. 1999). The southern border of *H. binoei* shows an approximate association with the 400-h activity contour, suggesting that they cannot acquire resources at a sufficient rate to exist below this threshold (Fig. 4b). The encounter rate required at this threshold to meet maintenance costs is approximately one order of magnitude lower than that at the zero-activity contour, i.e., ~ 0.03 g/h.

Water loss rates depend on body size, metabolic (breathing) rate, and the permeability of the organism's skin to water, as well as the temperature, humidity, and wind speed of the environment surrounding the organism. Our biophysical calculation of the combined influence of these factors indicates that potential evaporative water loss rates vary considerably across the Australian landscape (Fig. 4e). We urge some caution in considering the absolute values of our calculations of water loss rates for two reasons. First, for our calculations of percentage of "skin wet," the key organismal property determining rates of cutaneous water loss, it was necessary for us to guess at the "wind speed" in the jar in which water loss rates were measured (which represents the combined effect of animal movement and free convection; see Appendix D). Second, the wind speed surfaces that we used were not based on maximum/minimum data but rather on 09:00/15:00 data; thus, we may have overestimated the wind speeds that the lizards encounter while active at night. Irrespective of their accuracy, however, these data illustrate the qualitative nature of patterns of water costs

across the Australian continent and show how such data can be used to calculate aspects of water balance.

The highest annual rates of water loss occur in the northern part of the Australian arid zone (Fig. 4e), reaching a maximum of ~ 12 g of water per year per gram of lizard. These high water loss rates are partly the result of the low relative humidity and high temperature in this region, but also result from the extensive amount of time available for activity in this part of Australia (in our calculations, animals are assumed to be active whenever thermal conditions permit). In this region there is a strong trade-off between the duration of time spent active and the amount of water lost by evaporation. Because so much time is potentially available for activity, lizards in this region may be more "choosy" about the times when they are active to conserve water (and reduce predation). For instance, they may restrict their activity to rainy nights when humidity is high, especially because the region that they occupy receives regular summer rainfall. The places in which geckos are active could also influence water loss. Our calculations assume that geckos are foraging on open ground, but they could significantly reduce their water loss by foraging in microhabitats with low wind, e.g., among boulders or dense vegetation. Arboreal geckos would be exposed to higher wind speeds than the terrestrial geckos that we consider here, leading to increased water loss rates. We have also assumed that no water loss occurs during periods of inactivity due to the high relative humidity and minimal wind in burrows. This would not be the case in all retreat sites used by geckos, such as rocky crevices and tree branches. These consequences of microhabitat selection may explain the tendency for saxicolous and arboreal geckos to have lower cutaneous water loss rates than terrestrial geckos (Withers et al. 2000).

If we assume that the different races of *H. binoei* eat sufficient food (crickets) to meet their maintenance energy requirements, would they obtain enough water through their food to balance evaporative water loss, or would they be required to drink additional water? Our calculations of discretionary water suggest that, throughout almost the entire range of *H. binoei*, the lizards would be in negative water balance if they did not drink additional water (Fig. 4f). However, our calculations also suggest that geckos living in the far north of Australia would have relatively low water costs, despite very high potential activity times, due to the high humidity of this region. Thus water loss may not constrain activity in geckos from this area. Field metabolic rates of the gecko *Oedura marmorata* from this region were much higher than predicted based on thermal effects alone, despite congruence between field metabolic rates and predictions based on thermal effects in the same species from a temperate/arid site (Christian et al. 1998; see also Appendix A, Table A1). This pattern may be due to higher levels of activity in the tropical populations of *O. marmorata*.

*Potential effects of global warming
on the distribution of H. binoei*

An important application of climatic niche analysis is in the assessment of potential range shifts under predicted scenarios of global warming. Global warming may affect minimum temperatures more than maximum temperatures (Easterling et al. 1997); thus it may have particularly strong effects on the distributions of nocturnal ectotherms. We have explored the potential impact of a mild (1.7°C) global-warming scenario on the different races of *H. binoei* across Australia by the year 2100. Our calculations predict relatively minor effects with respect to maintenance metabolic costs (data not shown). This is mainly due to the buffering effect of the lizards' thermoregulatory behavior; the lizards in our simulations were able to regulate their body temperatures (and thus their metabolic rates) during the day by moving to suitable places in the soil profile, as nocturnal ectotherms have been shown to do in the field (Kearney and Predavec 2000). However, a mild global warming could substantially increase the number of degree-days for egg development and the potential time available for activity (with follow-on effects on evaporative water loss). For instance, if the distribution of *H. binoei* were limited in the south by thermal constraints on development, by year 2100 it could have increased its range by up to 170 km in some areas (Fig. 5a). However, we doubt that the dispersal capacity of *H. binoei* would allow it to track such a rapid expansion in its potential distributional range.

Mechanistic vs. correlative approaches

Mechanistic and correlative approaches to ecological niche modeling answer different questions and, in this sense, are complementary rather than alternative techniques. When studying a species' current distribution, correlative approaches provide an excellent means of identifying environmentally suitable regions on a landscape that are outside the species' known point distribution. For instance, a previously derived AIC_c best model of the study species based on mean annual temperature, humidity and rainfall, seasonality of temperature and rainfall, and rainfall variability (Kearney et al. 2003) accurately predicts the southern limit of *H. binoei* in the southern states of Victoria and South Australia (Fig. 5d). Although the power of the correlative approach lies in *prediction*, the mechanistic approach provides considerably more power in *explaining* patterns of distribution and abundance. Statements can be made regarding the relative importance of the independent variables used in a correlative modeling procedure; e.g., "temperature" was identified as a key variable in the statistical model for the EA6 race of *H. binoei* (Kearney et al. 2003). The mechanistic approach, however, allows us to derive more specific hypotheses regarding thermally related causal processes limiting distribution, i.e., constraints on the potential

for egg development and activity time. The mechanistic approach also provides a rigorous framework by which to identify the relevant environmental variables to include in the modeling procedure, in contrast to the more subjective procedure of independent variable selection under correlative approaches. One interesting possibility that is yet to be explored is the use of the geographically projected output from mechanistic models as independent variables in correlative models.

Correlative approaches are likely to be inappropriate when considering a species' *future* distribution under novel circumstances such as global warming, especially when strong climate-dependent biotic interactions are involved (Davis et al. 1998). In the present case, when we re-interpolated the AIC_c best model using the predicted change in mean annual temperature by year 2100, the southern 10% probability limit shifted south a comparable amount to the 600 degree-days contour (Fig. 5e). However, the eastern 10% probability limit retracted inland up to 400 km. In contrast, when predicted changes in mean annual temperature *and* precipitation were used for interpolation, there was very little change to the predicted distribution from that under current conditions (Fig. 5f). Without an understanding of the causal effects of the independent variables, it is difficult to assess whether such predictions are realistic or instead represent statistical artifacts resulting from extrapolation of the model outside the conditions with which it was derived. Our mechanistic approach, however, allowed us to make specific statements about the direct effect of climate change on the fundamental niche of the study species, particularly with respect to egg development and potential activity time. These statements will be true, irrespective of changes in biotic interactions, and indeed such changes would form part of the stage on which the biotic interactions are played out. Clearly, the detailed information required to fully address the niches of organisms from a mechanistic perspective will remain unavailable for the majority of species. However, we urge caution in extrapolation of statistical distributional models to novel situations and recommend a mechanistic approach where possible.

Extensions to the mechanistic approach

We have demonstrated that it is now feasible to calculate climatic components of the fundamental niches of organisms and map them onto real landscapes to predict potential egg development, activity time, and energy and water costs across an entire continent. Yet our analysis remains preliminary. First, although we do not have data on the rate of acquisition of resources (food and water) in *H. binoei*, incorporation of such information with the food and energy costs that we have calculated would allow the calculation of "discretionary" energy for growth, maintenance, or storage (Porter 1989, Grant and Porter 1992, Porter et al. 2000, 2002). Second, although our goal in this study was to

provide a mechanistic view of the fundamental niche, our approach can be extended to consider some kinds of biotic interactions and thus to a mechanistic understanding of the realized niche. For instance, it is possible to calculate the degree of daily and seasonal overlap in potential activity times between predators and competitors (Porter et al. 1973, 2002), and to determine the metabolic costs of fever resulting from infections (Porter et al. 2002). Finally, the niche of a "species" may vary across space if there is spatial variation in the relevant organismal traits (Peterson and Holt 2003); thus it may be necessary to incorporate such information when applying the mechanistic approach to avoid underestimating niche dimensions. We hope that our study will encourage further mechanistically based analyses of the distribution and abundance of organisms.

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APPENDIX A

A description of tests of biophysical models is available in ESA's Electronic Data Archive: *Ecological Archives* E085-102-A1.

APPENDIX B

An example data input file for the microclimate model is available in ESA's Electronic Data Archive: *Ecological Archives* E085-102-A2.

APPENDIX C

An example data input file for the ectotherm model is available in ESA's Electronic Data Archive: *Ecological Archives* E085-102-A3.

APPENDIX D

A description of the calculation of percentage of skin "wet" is available in ESA's Electronic Data Archive: *Ecological Archives* E085-102-A4.