# Modeling Animal Landscapes*

**W. P. Porter**[1,†]
**S. Ostrowski**[2]
**J. B. Williams**[3]
[1]Department of Zoology, University of Wisconsin, 250 North Mills Street, Madison, Wisconsin 53706; [2]National Wildlife Research Center, P.O. Box 1086, Taif, Saudi Arabia; [3]Department of Evolution, Ecology, and Organismal Biology, Ohio State University, 318 West 12th Avenue, Columbus, Ohio 43210

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## ABSTRACT

There is an increasing need to assess the effects of climate and land-use change on habitat quality, ideally from a mechanistic basis. The symposium "Molecules to Migration: Pressures of Life" at the Fourth International Conference in Africa for Comparative Physiology and Biochemistry, Maasai Mara National Reserve, Kenya, 2008, illustrated how the principles of biophysical ecology can capture the mechanistic links between organisms, climate, and other habitat features. These principles provide spatially explicit assessments of habitat quality from a physiological perspective (i.e., "animal landscapes") that can be validated independently of the data used to derive and parameterize them. The contents of this symposium showcased how the modeling of animal landscapes can be used to assess key issues in applied and theoretical ecology. The presentations included applications to amphibians, reptiles, birds, and mammals. The rare Arabian oryx on the Arabian Peninsula is used as an example for energetic calculations and their implications for behavior on the landscape.

## Introduction

### Introduction to the Field

A fundamental issue in ecology is to understand the patterns of distribution and abundance and how these patterns are tied to habitat features at different spatial scales (Andrewartha and Birch 1954). The urgent need to predict the effects of human-induced changes in climate and land use on biodiversity also makes this a critical issue in applied ecology (Thomas et al. 2004; Helmuth et al. 2005; Rosenzweig et al. 2008; Williams et al. 2008). To respond effectively to the challenges ahead in adapting to climate change, we need robust predictions of how threatened species, diseases, and pests will respond. Increasingly, there is an interest in explicitly incorporating physiological knowledge about the interactions between organisms and their environments into spatially explicit assessments of habitat quality under different scenarios (Chown and Gaston 2008; Pörtner and Farrell 2008). The spatial scale of these assessments ranges from the entire distribution of a species to finer-scale studies of habitat use by individuals, depending on the questions being asked. For example, how do continentally and seasonally varying climate and landscape properties affect developmental rates and movement rates of ectotherms and hence influence their present distribution versus how do local climates and vegetation on the landscape influence toad body temperatures, food requirements, water loss, movement patterns, and habitat utilization?

The development of geographic information systems (GIS) and high-resolution spatial data sets for climate, terrain, vegetation, soil, and other variables has revolutionized the way we tackle these questions. However, such studies are often done in a correlation manner without explicit consideration of known physiological links between the GIS data and the organism (Pearson and Dawson 2003). The symposium "Molecules to Migration: Pressures of Life" at the Fourth International Conference in Africa for Comparative Physiology and Biochemistry, Maasai Mara National Reserve, Kenya, 2008, illustrated how the principles of biophysical ecology can be used to make the links between morphological, physiological, and behavioral knowledge and spatial environmental data to understand and predict key ecological processes affecting distribution and abundance in different habitats (Gilman et al. 2006; Kearney and Porter 2009; Kearney et al. 2009*a*, 2009*b*).

Here we provide a general overview of the approach, using examples from the symposium to illustrate key points. The focus is on a steady state heat and mass transfer analysis of landscape/climate effects on amphibians, reptiles, birds, and mammals. The Arabian oryx is a specific example of how using generic microclimate and endotherm models in Niche Mapper allows one to compute environmental effects on energetics and behavior seasonally. This example shows previously unpublished data and calculations by W. P. Porter. The other studies in this symposium have been or will be published separately in other journals.

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[†] Corresponding author; e-mail: wpporter@wisc.edu.

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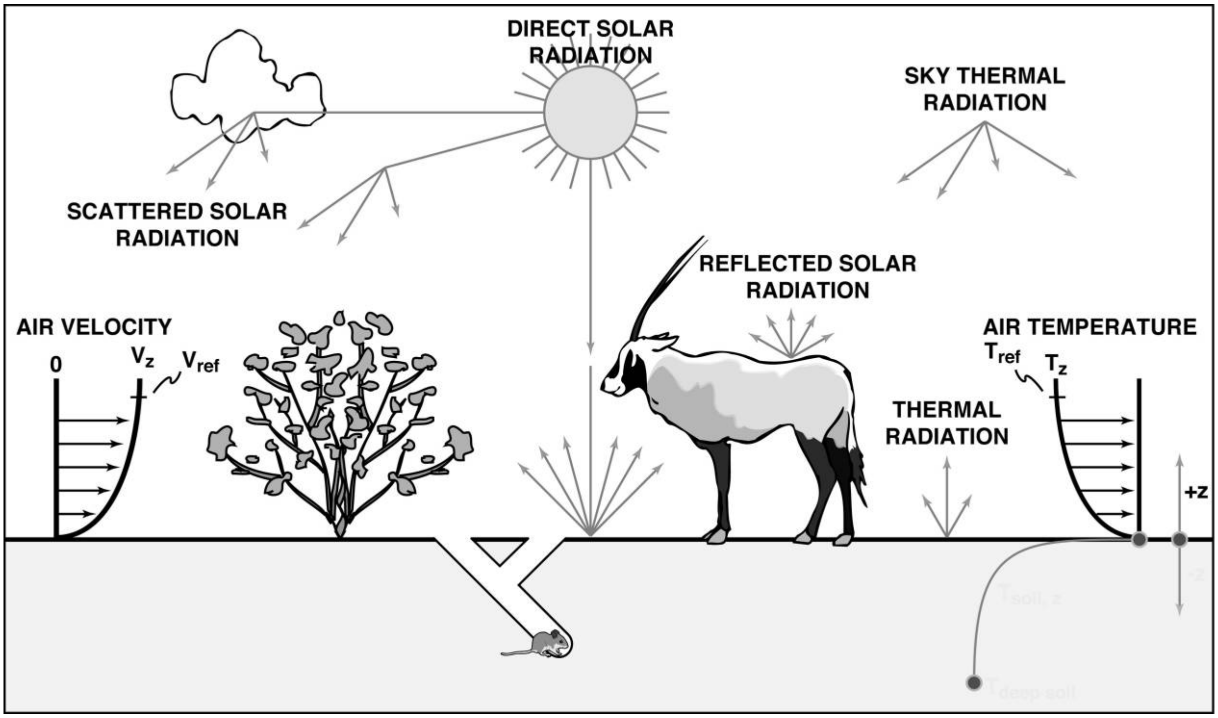

Figure 1. System diagram of environmental data needed for calculating animal heat and mass balances.

### *An Organism's View of the Environment*

There is an increasingly detailed range of climatic data sets at fine spatial resolution available for different parts of the world, including data for the entire globe (Hijmans et al. 2005; Kozak et al. 2008). These data are based on interpolations of weather-station data that are deliberately collected far enough above the ground that local positional effects are unimportant. Most organisms, however, experience a very different climatic environment: the climate near the ground (Geiger et al. 2003). Estimates of available microclimates can be made by applying principles of energy and mass balance to the habitats of organisms (Porter et al. 1973; Campbell and Norman 1998; Kearney and Porter 2009).

### *Biophysical Ecology: Basic Principles*

Biophysical ecology may be defined as a discipline that utilizes heat and mass transfer principles from physics and engineering to calculate local available microenvironments and their heat and mass exchange with animals. As currently practiced it also encompasses physiological and behavioral responses to heat and mass fluxes and the consequences for food and water requirements for survival, growth, reproduction, and distributions. Behavioral responses may include changes in habitat utilization and movement patterns across heterogeneous landscapes. The landscapes may be terrestrial or aquatic, but this symposium focused on terrestrial organisms.

The aim of biophysical ecology is to determine parameter values and solve the energy-and-mass-balance equations for organisms in their habitats (Porter and Gates 1969; Gates 1980; Campbell and Norman 1998). Animals exchange heat energy with their environment through absorbing and emitting radiation; through the endogenous production of heat; and through the processes of convection, conduction, and evaporation (Fig. 1). Given the environmental conditions and the relevant morphological, physiological, and behavioral traits of the organism, one can solve the heat-energy-balance equation to determine the animal's temperature (if it is an ectotherm) or its metabolic/water-loss rate (if it is an endotherm). The water balance of an organism is coupled to the energy balance through the evaporation term. The food-mass balance and the respiratory system—mass balance is coupled to the energy-balance equation through the metabolism term. Thus, key organismal heat and mass balances—heat, dry matter, and water balance—can be calculated from first principles under a single mechanistic framework (Porter et al. 1973, 2002; Kearney and Porter 2004; Porter and Mitchell 2006).

Knowledge of the morphological properties of surface area, volume, reflectivity, and skin, fur or feather characteristics provide the basis for determining climatically imposed energy and water costs. If further details are available on the quality and availability of food and on the digestive system, one can also determine the dry matter, energy, and water income and thus the overall profits in these currencies. This was illustrated in the case of double-crested cormorants (Meadows et al. 2008) and the greater glider (Kearney et al. 2008). For ectotherms, such as the western toad (Bartelt et al. 2008), the approach is similar except that the energy-balance equation is solved for core body temperature instead of metabolic rate, given the core temperature to be maintained through behavioral adjustments. Empirically measured physiological constraints imposed by body temperature on activity, feeding and movement rates, and so forth, can then be determined. Ultimately, this approach provides a means to estimate how much energy, water, and nutrients an organism may have to invest in development, growth, reproduction, or storage. However, to estimate these currencies across real landscapes as functions of climate and terrain, one needs to estimate the range of available microclimates and incorporate the behavioral capacity of the organism to use them. This is the basis of Niche Mapper, an integrated suite of microclimate, ectotherm, and endotherm models (Porter and Mitchell 2006) that computes hourly warmest and coolest available microclimates for each pixel of landscape and animal heat, mass, and physiological and behavioral responses to those microclimates.

### *Symposium Overview*

This symposium illustrated the ability to predict landscape-scale consequences of animal heat and mass transfer for key biological processes, including movement patterns, habitat utilization, toxin accumulation, food and water requirements, survivorship, growth, development, reproduction potential, distribution limits, and optimal body sizes. The symposium showed that biophysical/behavioral approaches have enormous potential to integrate physiological knowledge into spatially explicit studies in ecology. Most of these calculations were done with Niche Mapper (Porter and Mitchell 2006) and hourly calculations for each simulation day (up to 366 d). Output files for hourly, daily, monthly, and annual results are loaded into MySQL database tables by Perl code for each landscape pixel. GIS programs can use the MySQL tables for creating temporal and spatially explicit maps and graphs: "animal landscapes."

The first paper of the symposium was "Modeling large mammals on real landscapes" (Porter et al. 2008). This paper showed that the percent shade available and the season of the year were critical variables for black rhino behavior and distributions on the Serengeti and for Arabian oryx energetics and behavior. The paper illustrated that climate influences on the Arabian oryx force a seasonal shift from diurnal to nocturnal activity with a consequent change in metabolic expenditures seasonally, which explained doubly labeled water data from field experiments. It also illustrated the relative predictive accuracy of two regression approaches: a stable isotope method and a metabolic theory approach. Neither regression approach correctly estimated the seasonal variation of experimental data.

The second paper, "Through a toad's eye: using cost-surface analysis to model amphibian movements through terrestrial habitats" (Bartelt et al. 2008), illustrated that it is possible to compute toad hourly body temperatures and water-loss rates that agree extremely well with experimental lab data and field experiments for a study site with four major vegetation types over daily cycles of climate. By combining these physiological results with a minimum cost algorithm for each pixel on the landscape, movement patterns across the landscape could be calculated that agreed within less than 5% deviation from perfect minimum cost of water loss and body temperature needed for movement, based on radiotelemetry tracking data from multiple toads. Important factors affecting heat and water balance and movements on the landscape were the degree of shade available from vegetation (partly determined by solar zenith angle), air temperature, wind speed, and humidity.

The third paper, "Predicting the fate of a living fossil: how will global warming affect sex determination and hatching phenology in tuatara?" (Mitchell et al. 2008), addressed sex-dependent development and emergence times of hatchling tuataras on Brother Island near New Zealand. This paper provided evidence that soil properties and local microenvironments, including slope and aspect, were important variables affecting morphological and physiological responses of tuatara embryos. The microclimate model in Niche Mapper was used to reconstruct microclimates above and below ground from modern 2-m climate data at the weather station on the island. Field soil temperature data were used to verify the soil temperature predictions. Experimentally determined temperature-dependent development rates of tuatara hatchlings and sex-determination data were used with computer-derived hourly soil temperatures at nest depths to compute time to hatching and sex at nest locations where field data were available. Close agreement between model calculations and field data were obtained. Then future climate scenarios for the island were used to construct future soil temperatures and demonstrate changes in developmental rates for sex determination and time of emergence. It was found that hatching times would shift from spring to fall, when there would be little food to promote hatchling survival. Furthermore, there was a significant shift in emergence sex ratios to an all male population by the 2080s. Altered nesting behaviors were unlikely because of photoperiodic effects. The approach allows the assessment of the thermal suitability of current reserves and future translocation sites for tuatara and can be readily modified to predict climatic effects on any species with temperature-sensitive development.

The fourth paper, "Spatially explicit models estimate metabolic requirement and depredation of economically valuable and destructive fish species by double-crested cormorants (*Phalacrocorax auritus*) in southern Green Bay, Wisconsin, USA" (Meadows et al. 2008), made calculations of double-crested cormorant food requirements using the biophysical/behavioral programs of Niche Mapper, which indicated that air temperatures and percent composition of food protein, lipid, and carbohydrate were critical variables. Food quantities estimated both in terms of mass and energy were within 2 SE of detailed empirical data from the field. Calculations of dietary dichlorodiphenyldichloroethylene (p,p′-DDE), a DDT metabolite, and polychlorinated biphenyl (PCB) intake associated with food requirements indicated that there were insufficient concentrations to affect development or reproduction, which was consistent with field observations.

The endotherm model in Niche Mapper computed hourly adult cormorant energetics for the average day of each month.

It also calculated daily chick food requirements for resting metabolism based on their down properties and change in measured body weight over time. Adult energy/food requirement calculations were based on the observed percent of each hour that consisted of flight, diving, and resting/nesting on the island. Metabolic costs dictated fish consumption needed to meet energetic costs. Diet-composition data for each fish species consumed and observed percent consumption of each species were available from field observations. PCB and DDE contaminant concentrations in the fish were also available from field data. Thus, it was possible to calculate contaminant accumulation in chicks and adults feeding on fish from day of hatching. Estimated metabolic requirements and contaminant intake of adults and chicks were consistent with previous research measurements. This paper supported the cormorant's bioindicator role and proposed that the employed modeling approach might facilitate the continued use of the cormorant as a model to track remediation efforts and be expanded to calculate energy requirements and organochlorine contaminant intake by other species at different trophic levels in aquatic ecosystems.

The fifth paper, "Climate and social factors affect horn length in African antelope" (Fleming and Cameron 2008), explored the presence/absence of horns in African antelopes using regression approaches. In the investigation of the function of horns, Fleming and Cameron (2008) suggested multiple functions, for example, thermoregulation, defense, and mating. Their data suggest an important association of horn presence/absence with the climate/habitat that the animals occupy.

The sixth paper was "The metabolic capabilities and limitations of *Papio anubis* (olive)/*Papio cynocephalus* (yellow) baboons in the changing environment of Amboseli National Park, Kenya" (Klousie et al. 2008). The biophysical/behavior models presented by Klousie et al. revealed the complex interactions between climate, vegetation, and baboon properties. Air temperatures, amount of vegetation, percent shade available, fur properties, and body size were critical variables. Results of simulations from 1968 to 2000 indicated key effects of vegetation, land-use change, and climate interacting with each other to provide seasonal advantages to each of the two species of baboons.

The final paper was "Climate change and the distribution limits of folivorous possums from Australia: predictions from a biophysical model" (Kearney et al. 2008). Many organisms shelter in retreat sites such as tree hollows, and this paper on greater gliders illustrated how the interaction between the metabolic heat production of these possums and the external environment impinging on the tree hollow can be calculated to determine the ultimate thermal environment "seen" by the possums when inactive. This work showed climatic constraints on the greater glider's distribution varied from thermally imposed water limitations in the north to thermally imposed energy limitations in the south, with the availability of tall trees limiting penetration inland to the west and nitrogen availability likely controlling abundance within the predicted range. The mechanistic biophysical/behavioral models also correctly predicted body size variation with latitude.

## Material and Methods

### *An Integration of Biophysical Principles to Compute Metabolic Rates and Activity Patterns Seasonally*

As an example of exploring climate effects on animal energetics and behavior, consider the Arabian oryx, a 75–90 kg antelope on the Arabian Peninsula. Unlike most endotherms, these oryxes can vary their body temperature from 36.5° to 41.5°C. They increase metabolic rate and lower core temperature under cool environmental conditions, and they reduce evaporative cooling requirements under warm environmental conditions by allowing their body temperature to rise (Ostrowski et al. 2003). During daytime activity, these animals are exposed to solar radiation and absorb a small fraction of this energy relative to most mammals. Measurements of solar reflectance across a spectral range from 290 to 2,600 nm (using a Beckman DK-2A spectroreflectometer) reveal that their white fur reflects 76% of the incident diffuse and direct solar radiation (Porter 2008). Their fur is also critical in affecting convective heat exchange and in determining the flow of heat generated from the core into the external environment. Key properties of the fur that affect overall heat exchange are the middorsal and midventral hair length and pelt depths (McClure and Porter 1983). The Arabian oryx has very short hairs and a thin pelt (see Table A1 in the online edition of *Physiological and Biochemical Zoology*). Convective and radiative heat exchange are strongly dependent on surface area, which can be estimated from photographic measurements of the front and side views of the animal. The ratios of measurements of the length, width, and height of the head, neck, torso, and legs were used in an allometry subroutine to compute independently the volume and surface areas and actual dimensions of the animals (Natori and Porter 2007). A shoulder height of 90 cm (Nowak 1999) was taken to provide an absolute reference measurement for the relative measurements from photographs.

From these relatively few basic morphometric data and knowledge of the body temperature response of the oryx under different heat loads, one can calculate the consequences for its energy and water balance of any combination of radiation load, wind speed, air temperature, and humidity. In the case of the Arabian oryx, a critically endangered species, it is noteworthy that these data were obtained without the need for invasive measurement procedures.

The Arabian oryx is far more efficient even than the camel in terms of its energetics and water balance. It utilizes both behavior (shade seeking, digging shallow pits in the ground underneath shade) and physiology (reducing metabolic and water-loss rate lowers body temperature at night and allows it to rise in the daytime in summer, and catabolizing internal organs when food is scarce) to minimize its food and water requirements (Williams et al. 2001; Ostrowski et al. 2002). More subtle heat-exchange processes than those described above can be important in heat exchange. For example, horns of antelope may play an important role in heat exchange (Wathen et al. 1971, 1974; Fleming and Cameron 2008).

Local weather-station data at the oryx reserve show that during a typical summer day in this habitat, air temperature at ~2 m varies from 26.5° to 41.2°C, and wind speed was assumed to vary from 1.4 to 2.0 m/s at a height of 24 cm. Solar radiation under clear skies in this location can be estimated from first principles (McCullough and Porter 1971) and ranges from 553 to 923 W/m$^2$ on a horizontal surface at solar noon in January and June (see Table B1 in the online edition of *Physiological and Biochemical Zoology*). The environment experienced by the oryx, however, is a function of its height above the ground, the level of shade it experiences, and the temperatures of the surfaces surrounding it, among other things. Temperatures at the soil surface and below can be determined by solving transient energy-balance equations numerically (Porter et al. 1973; Porter and Mitchell 2006), and this requires knowledge of soil properties such as thermal conductivity, density, specific heat, and reflectivity, whose values were 0.35 W/m °C (http://www.engineeringtoolbox.com/specific-heat-capacity-d_391.html), 1,600 kg/m$^3$, 830 J/kg K (values for density and specific heat are from http://www.hukseflux.com/thermalScience/thermalConductivity.html), and 26%, respectively (W. P. Porter, unpublished data).

### *Model Outputs and Validation Procedures*

Calculations of metabolic rate needed to maintain body temperature throughout a typical June day at the oryx reserve were made (Fig. 3) for two different body weights of oryxes, which represent the average weights for the groups measured in the spring versus the summer using doubly labeled water (Ostrowski et al. 2002). Microclimate differences were calculated (Fig. 2) between full sun and full shade over 24 h in the oryx reserve at 2 m, at the average height of the oryx lying down (24 cm), and at the ground surface in July. To capture the best approximate air temperature, wind speed, and humidity for convective heat transfer for the oryxes whether they are standing or lying down, a height of 24 cm above the ground was chosen for use in calculations reported here.

Two sets of calculations were made: one assuming animals resting 24 h a day, and the other allowing them to be active when environmental temperatures were permissible; that is, there was no calculated requirement for evaporative water loss for cooling to maintain body temperature within the allowable range observed. When they were active their metabolic rates were estimated to be 2.1 times resting metabolism (Nagy 1987). Because it is impossible to estimate for an individual exactly what it does at any moment, the calculations are done to estimate the upper and lower limits (bounds) within which the animal is likely to function. All Niche Mapper calculations of field metabolic and water-loss rates were done without knowledge of the actual data collected from free-ranging oryxes using doubly labeled water (Williams et al. 2001).

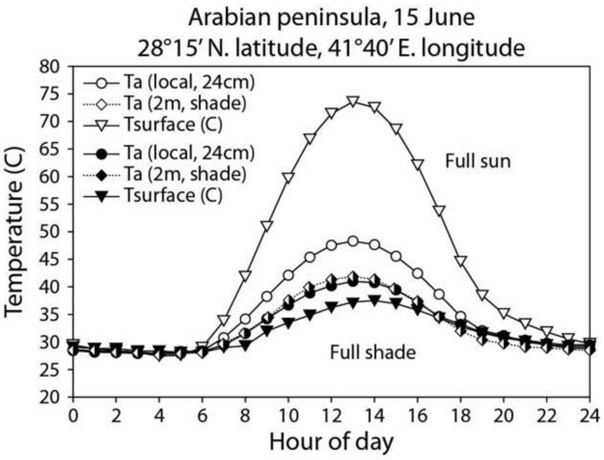

Figure 2. Sun and shade microclimates at 2 m, at the average oryx height (24 cm), and at the ground surface. Three different air temperatures, $T_a$, from 2 m above the ground to "local" air temperatures at average animal height, 24 cm, to the ground surface, $T_{\mathrm{surface}}$, in full sun and in full shade illustrate the air and ground temperature extremes at 1300 hours from approximately 35.6°C to nearly 72.1°C. Niche Mapper was used to calculate air temperature profiles and ground surface temperatures from 2-m shade air temperature and wind speed climate data and sand physical properties including reflectivity typical for this sand.

## Results

### *Arabian Oryx on the Arabian Peninsula*

The daytime air temperature at oryx height is 7°C warmer than the 2-m weather-station estimate, and because of soil thermal storage, air temperature at oryx height does not drop below 2-m air temperature until 1600–1700 hours. Soil surface temperatures, which affect conductive and infrared radiative exchange, vary dramatically from full sun to full shade. The maximum midday surface temperatures in the sun in June demonstrate the huge effect of solar radiation on ground surface temperature. Instead of a maximum of approximately 72.1°C in full sun, the soil surface temperature in full shade at 1300 hours would be approximately 35.6°C.

The metabolic rate calculations using these estimates of extremes of activity in Arabian oryx embrace the doubly labeled water metabolism estimates from experimental data, which suggests that levels of activity in spring are approximately twice those in summer (Fig. 3). The horizontal lines defined by three connected square boxes in Figure 3 are the doubly labeled water estimates of field metabolic rates for spring and summer. The calculated metabolic rates for the fourth month (April) were low because of an unusually warm month for the time of year. Similarly, the calculated metabolic rates for the fifth month (May) were higher because of an unusually cool month for that time of year.

Figure 3 also contains plots of estimates of metabolic rate using two different regression approaches. The thick lines using three connected diamonds are based on extrapolations of data using doubly labeled water estimates for other smaller animals

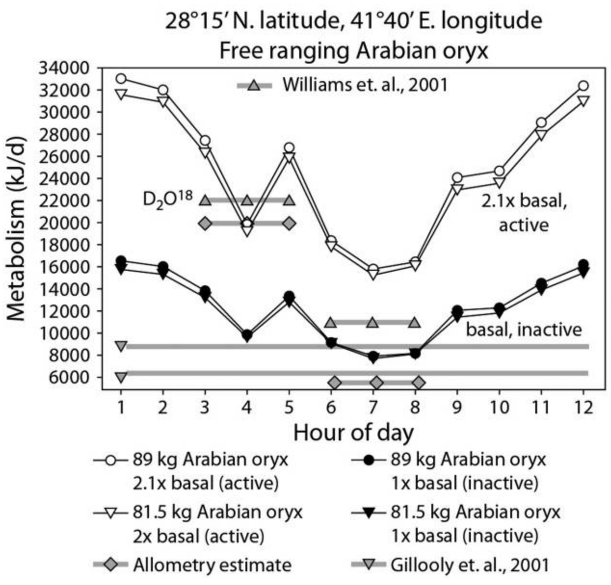

Figure 3. Comparison of biophysical versus regression approaches to calculate the range of metabolic costs throughout a year for the Arabian oryx on the Arabian Peninsula's oryx reserve.

but using the body weights of the oryxes. The other two line estimates at the bottom of the graph utilize the regression model presented by Gillooly et al. (2001), where the upper core temperature of 41.5°C and the lower oryx core temperature of 37°C are used to estimate metabolic rate. Those two lines are defined by downward-pointing triangles at the left end of each of the two lines.

## Discussion

A biophysical approach that incorporates morphology, physiology, behavior, genetics, and GIS-based technologies (Kearney and Porter 2009) including remote sensing opens up substantial new vistas for exploring how animals function on earth and how they may adapt to future changes. It also offers the opportunity of merging or combining this mechanistic approach with regression-based approaches to broaden our understanding of the relationships between species and the environments they inhabit.

For some applications, subtle effects of slope and aspect on soil temperatures can be extremely important. A good illustration of this was provided in the symposium paper on tuatara (Mitchell et al. 2008), where the effect of nest-site selection on offspring sex ratios was assessed across North Brother Island near the western coast of New Zealand.

For other applications, subtle differences such as solar altitude and azimuth can affect vegetation shade patterns on the ground and therefore modify local ground and air temperatures and humidities that affect small animals such as toads. Cost-surface analysis to model amphibian movements through terrestrial habitats (Bartelt et al. 2008) showed that including solar altitude effects on shade patterns yielded excellent agreements between measured and calculated toad body temperatures and water-loss rates.

Sensitivity analyses of variation in microclimate and animal properties typically indicated for all the studies in the symposium that there were relatively few critical variables driving the results. However, which variables were primary causative factors varied with the life stage of the animal, the class of animal, the season of the year, the geography, and the habitat type.

Models are always approximations of reality. They must be tested, examined, and revised as we continually learn more and as the tools we use become more sophisticated. This symposium demonstrated that the three fundamental balances—momentum, heat energy, and mass—can provide many new directions for exploration at multiple temporal and spatial scales of the constraints facing different species as they evolve in response to changes in local conditions. The balance equations for animals, microhabitats, and climates are the same form, but the values of the parameters change depending on circumstances.

For the Arabian oryx on the Arabian Peninsula, the summer infrared radiant heat load from sunny soil compared with shaded soil forces the oryxes to find shade and spend their daytime hours there to avoid extreme water loss. They rarely are able to drink water, and they get it from dew condensing on vegetation at night in midsummer (Ostrowski et al. 2002). Their activity pattern changes from diurnal to nocturnal depending on season. During the summer they are crepuscular and nocturnal. Postural changes, including lying down and positioning themselves on cool substrates, can strongly influence the microclimates they experience.

The observation that it is possible to define the range of potential variation for metabolic costs for a free-ranging animal such as the rare Arabian oryx across an annual cycle of climate variation using an amalgam of geographic, climatological, morphological, physiological, and behavioral data, much of which already exists in the literature or on the World Wide Web, is an exciting concept. The recognition that everything is interconnected through physical principles presents the opportunity to explore applications to individual and collective functions both within and across species and to be able to generate better estimates of constraints future changes may place on living systems. The papers in this symposium confirm the potential broad applications of mechanistic approaches to modeling dynamic systems that exhibit countless variations on the theme of living.

## Conclusions

This symposium provided a diverse range of examples of how the principles of biophysical ecology can be used to assess how climate and terrain can affect the distribution and abundance of animals. Biophysical principles have now been developed to an extent that they can be used in conjunction with increasingly detailed GIS data sets to model physiological and behavioral consequences at multiple landscape scales—that is, to model animal landscapes. These advances will provide physiologists with the means to make valuable contributions to our understanding of the effects of global change on biodiversity.

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