Po’ouli landscape bioinformatics models predict energetics, behavior, diets, and distribution on Maui

W. P. Porter1,*, N. Vakharia,*, W. D. Klousie,* and D. Duffy†

*Department of Zoology, University of Wisconsin, Madison, 250 N. Mills Street, Madison, Wisconsin 53706, USA; and †Department of Botany, University of Hawai‘i Manoa 3190 Maile Way Honolulu, HI 96822-2279, USA

Synopsis This study uses a spatially explicit microclimate/biophysical approach to examine the potential distribution of the Po’ouli on Maui to find either new habitats to search for existence or refine search efforts in previously occupied areas. We used specific physiological and behavioral ecology bird data, and Po’ouli morphological and spectral data obtained from museum specimens to address ecological and conservation-related questions about the Po’ouli that are otherwise very difficult to quantify. Laboratory and field tested microclimate and biophysical—behavioral animal computer models were integrated with remote sensing technologies. To show that the generic microclimate and endotherm models can predict metabolic and water loss requirements of Hawaiian Honeycreepers, we used the 2 species with known physiological properties, the Hawaiian Amakihi, Hemignathus virens, and the Hawaiian Anianiau, Hemignathus parvus. Predictions were within experimental measurement error of the laboratory measurements. Then using field rather than laboratory conditions as input data, we predict the field distribution of the Amakihi on Maui as the first spatial test of the models applied to birds. Results are consistent with Amakihi field distribution data. Fossils show that the Po’ouli once lived on Maui at low elevations in dry/mesic habitats on a likely diet of native tree snails and insects. The arrival of lethal mosquito-borne avian malaria in Hawaii exterminated low elevation Po’ouli forcing a population shift to mountain rainforests and possibly a snail diet instead of insects. To explore the maximum consequences of such a diet shift we assumed exclusive diets of snails versus insects at both low and high elevations. Snail diets require ~4 times higher foraging rates than do insect diets, making a predominantly snail diet an unlikely prospect for the Po’ouli. Landscape scale simulations suggest that a snail diet would force a Po’ouli distribution inconsistent with observations. A predominantly insect diet is consistent with distribution observations. We show that as local environmental conditions change across the landscape in space and diurnal/seasonal time it is possible to quantify animal physiological and behavioral consequences of those variations in their local environment. This enables quantification of the requisite spatial and temporal distribution and amount or availability of resources that may affect species’ potential for survival, growth, reproduction and distribution.

Introduction

In 1973, a new species of bird, the Po’ouli (Melamprosops pheosoma), was discovered on the northeast slopes of Haleakala Volcano on the island of Maui, Hawaii (Casey and Jacobi 1974). A little over 3 decades later, in November 2004, the last known male Po’ouli died in captivity, leading to statements that the species might be extinct, as the other 2 known birds had not been seen in the wild for almost a year (Song 2004).

Scott and colleagues (1986) suggested that, when discovered, the Po’ouli had a range of ~13 km² ha in wet forest at altitudes between 1400 and 2100 m elevation and that this was only 1% of its original range, as fossils has been found down into dry forest as low as 300 m on the southwest slope of Haleakala (James and Olson 1991). Habitat destruction by humans at lower elevations and by pigs at higher elevations, avian diseases such as mosquito-borne avian malaria and avian poxvirus, competition with introduced predatory garlic snails (Oxychilus alliarius) for the species’ land snail food base, and direct preda-

Downloaded from https://academic.oup.com/icb/article-abstract/46/6/1143/716786 by guest on 21 January 2019
above 1000 m or above the avian malaria belt" (Reynolds and Snetsinger 2001). Po‘ouli were only seen in Hanawai Natural Area Reserve, 1 of the 4 sites sampled on Maui. In 523 h of observation over 4 visits totaling 34 days, a maximum of 5 birds were seen, with a detection rate of 0.013 birds/h. An additional effort between December 1995 and June 1997 focused on surveying “all suitable habitat within the historical distribution of the Po‘ouli and some adjacent areas” except for 1 area with degraded habitat and 2 areas being surveyed by others (Baker 2001). Teams of 2 spent 318 person days lasting 8–11 h searching 700 ha. Five birds were detected, but by mid-1997, only 3 birds remained (Baker 2001). The detection rate of roughly 0.0045 birds/h was an order of magnitude less than the previous study, but this may have been the result of different methods or personnel or more thorough coverage of marginal habitats.

In 2004, what may have been the last Po‘ouli died in captivity (Song 2004); however, it is possible that some birds continue to exist. Given the difficult habitat that this species occupies, “in or near small gulches with heavy vegetation” (Englis 1990) and the difficulty of observing individuals even when present (for example, Reynolds and Snetsinger 2001), it would require massive additional resources to discover additional individuals, given the existing vague search criteria. If birds still persist, they need to be found to implement the existing management plan (USFWS and Hawai‘i DLNR 1999).

This paper illustrates how we (1) use limited existing data as an input to the microclimate and endotherm models, (2) use state of the art modeling that integrates first biophysical principles with remote sensing technologies to predict likely diet, distribution and levels of environmental resources necessary for survival, growth and reproduction, in the absence of extensive field data. This modeling proves to be useful in situations that are important to ecological and conservation-related questions about an unmeasured species that otherwise are difficult or impossible to quantify.

**Materials and methods**

We used the Micro2005 version of our microclimate model, and the Endo2005 version of our endotherm model (Porter and others 1973, 1994, 2000, 2002; Kearney and Porter 2004). These models are used serially for each pixel on the landscape to calculate first the local microclimates available from 2 m or more above the ground to 2 m or more below ground. Maximum and minimum shade conditions for each pixel based on local vegetation type are used to compute local coolest and hottest available micro-habitats for each hour of a day. These conditions are then used by the endotherm model to calculate energetic requirements and habitat choices that maximize activity time for the local choices available.

**The spatial–temporal data for the microclimate model**

Digital elevation maps and land-use data were obtained from the web site http://data.geocomm.com. We used USGS Digital Elevation Models (SDTS) to determine elevation, slope, aspect and vegetation/land-use type of individual pixels on the landscape at 30 m resolution as an input for microclimate modeling.

High resolution temporal 2 m air temperatures and other climate data were obtained from 4 weather stations on the island of Maui. Air temperatures are measured in the shade. The 4 weather stations are as follows: (1) Lahaina HA, 156° 41’ 17” W, 20° 53’, 4° N, (2) Kahakuloa HA 156° 28’ 47” W, 20° 53’ 33’’ N, (3) Haleakkala National Park, Visitors Station HA 156° 16’ 16” W, 20° 42’ 47” N and (4) Hana Airport HA 155° 59’ 19’’ W, 20° 4’ 36” N.

We used the digital elevation map of Maui and the monthly maximum/minimum temperatures from the 4 weather stations listed above to estimate spatially explicit 2 m shade maximum and minimum air temperature variation over Maui for the average day of each month of the year. This was done with thin plate spline fitting algorithms (Wahba 1979, 1990; Hutchinson 1989, 1993), program ANUSPLIN, to interpolate landscape temperatures and humidities. The solar radiation calculations for each pixel for clear sky conditions were computed from SOLRAD, a first principles solar radiation model (McCullough and Porter 1971) embedded in Micro2005. Wind speeds for each pixel were estimated to vary linearly from 0.1 m/s at sunrise to 2.0 m/s at 1 h after solar noon at 2 m height above the ground. Humidity for each pixel was assumed to be 100% at sunrise and to decline from there until air temperature reaches a maximum 1 h after solar noon. We assumed a constant mass of water vapor in the air and used equations describing the properties of air (Tracy and others 1980) derived primarily from the Smithsonian Meteorological Tables (1966).

**The microclimate model**

The microclimate model solves the daily 24 h heat balance problem,

\[ Q_{in} = Q_{out} + Q_{st} \]

by numerical integration for the surface of the ground, at least 10 user defined depths below ground and at
least 3 above ground locations. Heat in, $Q_{in}$, to the ground surface comes from solar and infrared radiation from the sky and vegetation. Heat out, $Q_{out}$, from the ground surface is the infrared radiation from the ground surface, convective heat loss and evaporative heat loss. The ground surface exchanges heat with the soil below it by conduction. Stored heat, $Q_{st}$, below the soil surface either elevates or depresses soil temperatures below the ground surface depending on heat flow direction. Input variables include geographic coordinates and day of year to determine solar radiation amount, soil reflectivity and thermal properties, variables that affect atmospheric airflow, such as roughness height, maximum and minimum air temperatures, humidities and wind speeds at 2 m, cloud cover and timing of maximum and minimum for each day’s time-dependent properties.

Table 1 in Appendix 1 provides a sample dataset used for all microclimate calculations. The microclimate model creates 4 output files. METOUT and SOIL contain hourly maximum sunlight microenvironments for each pixel above and below ground, respectively. SHADMET and SHADSOIL contain microclimate conditions for the minimum hourly sunlight for each pixel above and below ground, respectively.

Percent of the ground surface covered in shade is a function of the pixel vegetation type. Each vegetation type is assumed to have a maximum and minimum value associated with it for the shade it projects on the ground. Table 2, Appendix 1 defines the types of shade used for each of the land-use types on Maui.

The endotherm model

The endotherm model, Endo2005, is a new version of our early animal models (Porter and Gates 1969) with added integrated porous insulation model, coupled heat and mass balance models, distributed heat generation and distributed respiratory heat loss, with additional properties described in detail in Porter and colleagues (1994, 2000, 2002). Briefly, coupled heat and mass balance equations are solved using a numerical guessing routine, Zbrent, as described in Numerical Recipes (2006). The nonlinear equations containing infrared radiation and evaporation terms have no analytical solution. Numerical methods are necessary for maximally accurate solutions. The equations that are solved are simply

Heat Balance (W):

$$Q_{in} + Q_{gen} = Q_{out} + Q_{st}$$

Mass Balance (g/d)

$$m_{in} = m_{out} + m_{st}$$

Figure 1 illustrates the animal heat fluxes and the key environmental variables that are in the heat balance equation. Figure 1 could be a cross-section through a cylindrical, spherical or ellipsoidal geometry. The first heat balance equation term above is heat input, $Q_{in}$. It is the sum of absorbed incoming solar and infrared radiation from the sky, ground and vegetation that reaches the skin (Porter and others 1999). $Q_{gen}$ is the total distributed (not point source) heat produced by all the tissues of the body. $Q_{out}$ is the heat loss by convection to the air, respiratory (heating incoming air plus evaporation) heat loss and infrared radiation emitted through the porous feather insulation to the environment. $Q_{st}$ is the stored heat (positive or negative) due to body temperature rising or falling.

The mass balance equation terms refer to the gut and the respiratory system. The mass input, $m_{in}$ is
food entering the gut (or) air entering the respiratory system. Mass stored or absorbed, \( m_{\text{st}} \), is the food mass that must be absorbed by the gut given the food type and properties that meet the day’s energetic needs. It also represents the day’s oxygen that must be absorbed by the respiratory system to oxidize the particular diet type and amount of food that must be absorbed to meet those energetic needs. The second term in the generic mass balance equation, \( m_{\text{out}} \), is simply the feces from the gut (or) the exhaled air. It is computed by difference from the input less the stored or absorbed term. The determination of daily mass requirements for the digestive and the respiratory systems is based on integration of each hour’s heat and water balance solutions to maintain specified core temperature for that hour’s local climate conditions.

For the heat balance calculations the mass of the birds is so small, we assumed steady-state because of the short time constant they have (Porter and James 1979). Thus, \( Q_{\text{st}} = 0 \). The relative proportions of the dorsal and ventral diffuse radiant heat fluxes are determined by configuration factors (Siegel and Howell 2001) that are \( \sim 50\% \) of the total surface area exchanging radiant energy with the sky and \( 40\% \) exchanging radiant energy with the ground and the balance exchanging radiant energy with itself. In contrast, a sphere would have \( 50\% \) “seeing” the sky and \( 50\% \) “seeing” the ground.

The distributed heat generation term, \( Q_{\text{gen}} \) (Porter and others 1994) links the heat and mass balances as illustrated in Figure 2. The “chemical fire” of the body requires both fuel and oxygen. The daily integration of calculated hourly heat energy required to maintain core temperature requires that a specified mass of fuel and oxygen be available. The fuel (diet) contains proportions of protein, fat, and carbohydrate that determine the mass of food that must be absorbed to meet daily energy requirements.

The digestive system mass balance calculates daily mass that must be absorbed from the gut, \( m_{\text{abs}} \), if energy requirements are calculated independently. Required daily food intake is computed by knowing the digestive efficiency of a particular diet composition. These data are available in the literature for a wide variety of diets (Bjorndal and others 1990; McWhorter and Del Rio 2000; Whalen and Brown 2005). Thus, required daily intake of mass can be calculated to maintain body weight. The daily mass balance of the gut can be determined from basic principles since calculating the required intake and the absorbed mass allows by difference the mass out of the animal’s gut. This is important because if there are contaminants or pathogens in the food or water consumed, daily dosages can also be computed on a landscape scale.

The respiratory system oxygen and water mass balances are dependent on both energetic requirements and diet type. Instead of digestive efficiency, oxygen extraction efficiency needs to be known. This is well established for mammals (\( \sim 24\% \)), birds (\( \sim 31\% \)) (Hainsworth 1981). Bird oxygen extraction efficiency may vary diurnally and seasonally from 10\% to more than 40\% (Arens and Cooper 2005). Reptiles can vary between \( \sim 6 \) and 12\% (Klein and others 2003), depending on breathing rate and exercise level. We assumed 34\% oxygen extraction efficiency, since high elevation sites are typically cold with high moisture levels and low oxygen partial pressure. Each diet type requires a different amount of oxygen depending on its composition, which determines daily oxygen to meet the demands of the “chemical fire.” Oxygen demand specifies respiratory air flow and water loss.

Water lost from the respiratory system is calculated knowing that air will be saturated with water vapor in the lungs. Thus, local humidity, air temperature, and lung temperature (average body temperature integrated from core to skin), required total daily respiratory air flow and exit temperature make
up the water mass balance equation variables. Exit temperature can be estimated based on environmental conditions and the animal’s exit respiratory surface properties (Welch 1980). For cutaneous water loss we assumed that 0.2% of the skin functioned as a free water surface to account for the eyes and thin skin.

Daily food requirements are computed from the total heat energy requirements of the bird for resting and activity (J/d) divided by the caloric value of the diet (J/g of dry food). Water content of the food is assumed to be absorbed by the animal. Metabolic water production is added to the food water intake. The difference between mass of water intake and total water lost for the day determines the drinking water required for the day.

Average hourly foraging rates are calculated based on the calculated food requirements for the day divided by the number of hours of activity in a day. The Po’ouli is diurnal, not crepuscular, so hours of activity were from sunrise to sunset, unless heat stress during midday forces cessation of activity, which reduces total daily activity hours. We assume the Honeycreepers’ effective percent wet skin can rise up to 5% at 40°C heat stress.

Discretionary energy is the difference between a user-defined level of field activity and resting metabolism needed to maintain body temperature. Based on extensive doubly labeled water data from Nagy (1987, 1994) these field metabolic rates are 2.5–3.2 times greater than resting metabolism. This information is important because it allows us to estimate total mass and energy requirements, food requirements and therefore food densities/availability in different habitats. Different habitats and microclimates impose different resting energetic demands on their species. As we discuss below, habitats that impose greater energy demands for survival and/or growth and reproduction must provide (1) increased foraging time for the same resource base or (2) a greater resource base either in quality, quantity or both for a species to survive and reproduce. We can compute time available for foraging, we can determine whether resource base must change, in what direction and the relative amount of change over space and time.

Activity hours are calculated based upon the diurnal/crepuscular/nocturnal habits specified by the user, the hours of skylight when the sun is below the horizon and hours of sun above the horizon calculated in SOLRAD, and the number of hours of activity that might be lost due to heat stress. Additional details of program operations can be found elsewhere (Porter and Mitchell 2003).
year for the Po’ouli for both snail and insect diets (McWhorter and Del Rio 2000). A 95% digestive efficiency was used for nectar feeding months for the Amakihi. Elevation of metabolic rate above basal was assumed to be 1.5 times basal for all months except for April through September. Months of April through September were assumed to have activity levels 2.0 times above basal to allow for higher activity levels. Reproduction was assumed to occur during April–June for the Amakihi and Anianiau; April–May for the Po’ouli. Basal metabolic rates were computed based on the heat generation needed to maintain the user defined core temperature and subject to the bird’s morphological properties, the available environments and its behavioral choices at each pixel on the landscape.

Behavior was assumed to be diurnal, not nocturnal or crepuscular. It was assumed able to seek ground shade, seek vegetative shade at night to stay warmer, to be active in the shade in the daytime unless in heat stress and not to rest in a nest at night. Default behavior for each pixel habitat choice is minimum shade habitat unless heat stress would occur in a given hour, then it chooses maximum shade habitat for that hour for the local vegetation type.

Diet preference of the Po’ouli may consist of snails (Pratt and others 1997). Gomot (1998) determined that snails contain ~57.6% protein, 13.8% carbohydrate, 9.7% fat on a dry matter basis and 87.4% water. We used these values to compute grams of snail meat to meet the day’s metabolic demands. Although the input data format allows diet change in any given time interval from average monthly to average weekly, we used a constant Po’ouli diet exclusively of insects or snails to compute the extremes.

We assumed that the birds met their metabolic demands and calculated the average foraging rate per hour by dividing total food required by total activity hours. The current analysis describes best possible circumstances for Po’ouli eating snails, since we assume no impact of low density or prey encounter rate on their ability to find food to meet their needs.

### Single site (metabolic chamber) endotherm model tests

All models contain assumptions and must be tested against known data to assess how well they function. We tested our model against known laboratory determined physiological data from 2 species of Hawaiian Honeycreepers: the Amakihi and the Anianiau (MacMillen 1974). The Amakihi body weight varies from 13 to 17 g. Anianiau body weights vary from 7.9 to 8.0 g. The Amakihi diet consists of ~60% nectar, 30% insects and 10% seeds and fruits (Hawaii Department Land Nat. Res. 2005a). The Anianiau consumes nectar, spiders and Lepidoptera larvae (Hawaii Department Land Nat. Res. 2005b). Sample input data for the Amakihi and for the Po’ouli are listed in Tables 3 and 4 in Appendix 1.

Tests of the endotherm model used metabolic chamber simulations that assumed no sunlight. The chamber walls were made of glass or other non-reflecting materials in the long infrared wavelengths (Porter 1969). Relative humidity varied from 6 to 16% with temperature as defined by MacMillen (1974). We estimated a low wind speed in his metabolic chamber (0.04 m/s), and used the same 10–40°C air temperatures as in MacMillen’s Amakihi and Anianiau experiments.

Calculations for metabolic heat production and respiratory water loss assumed a uniform heat production and respiratory heat loss per unit volume (a distributed, not point source of heat generated and lost, which affects the accuracy of solutions; Porter and others 2000). It was assumed that the birds begin to respond to heat stress when the difference between core and skin gets smaller than a critical difference of 0.2°C to assure sufficient radial transport of heat generated by metabolism. In heat stress, water loss from the skin increases by increasing the percent of the skin that functions as a free water surface until the heat balance equation is solved (error tolerance is met) with a minimum 0.2°C core–skin gradient.

Cutaneous water loss is determined by (1) the current skin temperature, which determines saturation vapor density for the effective wet skin area to function as a free water surface, (2) free stream (outside the boundary layer) air temperature, (3) relative humidity, (4) wind speed, (5) body diameter, (6) plumage depth and (7) body geometry, which determine boundary layer thickness and moisture transport to the free stream air. It was assumed that 0.2% of the skin functions effectively as a free water surface under resting, nonheat stress conditions.

### Landscape scale calculations

Land-use on Maui can be found online at http://kumu.icsd.hawaii.gov/dbedt/gis/maps/alum_mau.pdf. MySQL database tables for maximum and minimum temperatures for Maui can be obtained from the senior author. We used the thin plate spline fitting program, ANUSPLIN (Hutchinson 1989), to derive spatially explicit monthly temperature variation for maximum and minimum temperatures. Briefly, maximum 2 m shade air temperatures vary with elevation from ~9–27°C in January to ~13.5–36°C in August. Minimum 2 m shade air temperatures can
vary from ~0–18°C with elevation in January to ~1–22.5°C in August. Maximum air temperatures are assumed to occur 1 h after solar noon. Minimum air temperatures and 100% humidity are assumed to occur at sunrise. Intermediate hourly temperatures are calculated using a linear interpolation.

User supplied Perl code controls the input topographic and climate data read from MySQL database tables for each pixel, overwrites the input data file for the microclimate program, reads the hourly, monthly and annual output files from the endotherm model and writes the output data with the appropriate pixel geographic coordinates to MySQL output database tables. We use ArcGIS 9 to process and image the output tables.

Results
Metabolic chamber comparisons

Metabolic rate calculations and measurements for the Amakihi and the Anianiau in a simulated metabolic chamber are in Figure 3. Mean regression lines from MacMillen’s measurements and the upper and lower bounds of his measurements establish the frame of reference for Endo2005 calculations. Calculated metabolic rates from 10 to 40°C lie within McMillan’s (1974) observed range of values for each species measured. Complete results are in Tables 1 and 2 in Appendix 2.

Water loss results for the Amakihi and the Anianiau in the same simulated metabolic chamber are in Figure 4a and b. Data based on the regression of Macmillan’s experimental data and the upper and lower 2 SE of experimental data at each temperature are plotted. Both measured and calculated data are based on a mass of 15.3 g for the Amakihi and a mass of 8.0 g for the Anianiau. The calculations from Endo2005 lie within the standard errors of the experimental data except at 35°C where the estimate is above 2 SE for the Amakihi and below 2 SE for the Anianiau.

Fig. 3 A comparison of calculated (ellipsoid model) versus measured metabolic rates of a 15.3 g Amakihi, *Hemignathus virens*, and the 8.0 g Hawaiian Anianiau, *Hemignathus parvus* in a metabolic chamber. Measured metabolic chamber conditions for *L. virens* were 8–16% relative humidity, 0.04 m/s wind and no sunlight, using morphological properties from museum specimens and physiological data from the literature. Measured metabolic chamber conditions for the Hawaiian Anianiau, *Hemignathus parvus*, were 6–9% relative humidity, 0.4 m/s wind and no sunlight. Experimental data are from MacMillen (1974). L. parvus middorsal and midventral feather lengths, plumage depths and solar reflectivities were measured on LSU Museum specimens #81450, #81754 from H. Douglas Pratt collected 4 July 1975, Hawaii: Kauai Co.; headwaters of Haleahaha.

Fig. 4 A comparison of calculated (ellipsoid model) versus measured evaporative water loss rates of the Hawaiian Amakihi, *Hemignathus virens*, and the Anianiau, *Hemignathus parvus*, in a metabolic chamber. Chamber environmental conditions were the same as for Fig. 3. Experimental data are from MacMillen (1974). Calculations were part of simultaneous heat and mass balance solutions for metabolic rate (Fig. 3) for each species.
Amakihi Maui distribution calculations

Before computing the distribution of the Po’ouli on Maui, we decided to test first the models’ distribution prediction with a more common bird species whose distribution is well established. We computed Amakihi energetics and behavior to explore the models’ ability to estimate the Maui Amakihi distribution. Figure 5a and b show discretionary energy levels and requisite hourly foraging rates for April that suggests the best distribution of these birds. Figure 5a and b are consistent with distribution data on the Amakihi, Figure 5c from the USGS Hawai‘i Forest Bird Interagency Database Project (Woodworth and Pratt 2005). The presence of avian malaria in mosquitoes in the lower elevations is a factor affecting Amakihi distribution, but they are apparently developing resistance to avian malaria (Atkinson and others 2000; Woodworth and others 2005). Assuming this is the case, we chose the Amakihi because it may occupy habitats more in line with its historic distribution. Seasonal variation in their diets is specified in Appendix 1, Table 3. We assumed that during reproductive periods the Amakihi focuses more on insects in its diets to provide protein for breeding adults and their young.

Po’ouli measurements and calculations

Plumage length, depth and reflectivity are important variables that affect animal energy balance. Po’ouli feather length was 2.1 mm middorsally and 2.3 mm midventrally. Plumage depth was 1 mm dorsally and ventrally. Reflectivities (Fig. 6) dorsally were 34% when averaged over the solar spectrum and averaged 47% ventrally. All input values are specified in Table 4, Appendix 1.

Po’ouli monthly single locations calculations

We computed the consequences of a range contraction from sea level up to 2100 m, which is the highest recorded elevation of Po’ouli habitat on Maui. We also computed the consequences on Po’ouli energetics and behavior of switching from an insect diet to a snail diet. The complete details of the results of these simulations are in Appendix 2, Table 3. Environmental shade conditions at sea level were set to the more dry habitats (0–100%) that the Po’ouli inhabited in ancient times (James and Olson 1991), whereas forest shade was assumed to vary from 60 to 90% shade, which results in calculations of cooler local substrate, air and radiant temperatures.

Foraging rates, Figure 7a, rise 4 times from 0.96 g per hour for insects along the coast to 4.50 g per hour for snails at 2100 m when averaged over all 12 months of the year. Foraging requirements are driven by diet, elevation and temperature-dependent daily activity hours, which are reduced along the coast due to heat starting in the third month of the year (Appendix 2, Table 3).

Discretionary energy, Figure 7b, is independent of diet at low or at high elevations with the exception of
a snail diet which reaches the maximum of 3 times the body weight per day at high elevations. The high elevation snail diet for 2 months in April and May cannot reach the energy levels of an insect diet at the same elevation because of the ingested mass constraint associated with the low energy content of a snail diet. Endo2005 calculates metabolic cost for maintenance. Food consumption needs for maintenance are increased to satisfy user-specified demands for activity, growth and/or reproduction. Animals may eat as much as they need, except for a food consumption limit of 3 times the animal body weight per day. However, food intake is assumed to be limited based on doubly labeled water measurements of animals under field conditions (Nagy 1987, 1994).

Mapping Po’ouli energetics, behavior, and distribution onto Maui

Maui data for the elevation, slope, aspect and a fossil location at 300 m elevation (James and Olson 1991) and current data on Po’ouli distributions up to 2100 m are presented in Figure 8. We did a sensitivity analysis comparing 2 different pixels at 1200 m in forest with different slope (4° versus 7°) and azimuth angles (164° versus 118°) and slightly different maximum and minimum temperatures for each month. The average variation in calculated metabolic rates was ~4% with a range of 2.6–5.0% depending on the month. Appendix 1, Table 5 contains detailed input data.

Fig. 6 Reflectivities of dorsal and ventral plumage from paratype specimen (AMNH 810456) in the American Museum of Natural History in New York City. Ultraviolet = 350–400 nm, visible = 400–700 nm, near infrared = 700–2500 nm. The valleys in the curve in the near IR are due to water absorption peaks that deepen from left to right due to greater coupling of incident radiation with the quantum energy of water molecule electrons.

Fig. 7 (a) A comparison of the calculated required foraging rates of the Po’ouli on Maui in historical and modern times as a function of elevation, diet, seasonal temperature and reproductive status for single sites. April and May were assumed to be the months of reproduction. Low elevation open habitat generates warmer microclimates that reduce activity hours, elevate metabolic rates during heat stress. Foraging rates are elevated in part because of reduced hours at low elevation to find the necessary food to meet the day’s metabolic requirements. Reproductive foraging requirements also contribute to elevated costs. (b) Discretionary energy is a linear function of basic metabolism and independent of diet unless a maximum consumption limit is reached. Computed available energy as defined by user specified increases for activity levels and growth/reproduction based on well established physiological ecology data. Since the metabolic cost at sea level or at 2100 m is very similar, there should be only 2 lines here. The 0 m insect and 0 m snail diet calculations overlapped completely. However, the 2100 m snail diet does not reach the maximum of the insect diet at 2100 m because the model constrains food consumption to 3 times body weight per day. The low energy content of an exclusive snail diet forces a limit on food consumption per day in April and May, which reduces discretionary energy at high elevation.
Po'ouli discretionary energy calculations for the highest energy demand month, April, for an insect versus snail diet in Figure 9a and b. A diet of snails with its lower energy content and higher water content in April results in a prediction for best locations at low elevations where it is warmer and resting energy demands are lower. A maximum gut food limit reduces discretionary energy for growth or reproduction at higher elevations. The highest discretionary energy is where resting metabolic demands are lowest. In contrast, the insect diet does not exceed the day's gut capacity to process the biomass needed for full activity and reproductive demand at high elevations. This suggests that a snail diet might limit the existence of the Po'ouli at high elevations. Highest maximum discretionary energy per day is 126 kJ/day for an insect diet, but only 83.9 kJ/day for a snail diet because of a gut limitation.

Po'ouli discretionary energy calculations for the lowest energy demand month, December, for an insect versus snail diet are in Figure 10a and b. In this case neither diet demand exceeds the capacity of the digestive system to process a day's requirements. Highest maximum discretionary energy per day is 16 kJ/day for an insect diet and 14 kJ/day for a snail diet.

Po'ouli hourly foraging rates shown in Figure 11a and b map combined impacts of diet type and local climate differences for a breeding month, April. Results are due to diet effects and elevation, slope, aspect, vegetation, total hours of potential foraging activity and added activity level and reproductive energy requirements. The low quality snail diet forces a gut maximum limitation of 3 times the body mass per day that extends over most of Maui when energy demands are high during reproductive months. The gradients for the insect diet can be thought of as resource requirements for the animals that must be satisfied by increases in abundance and/or accessibility with increasing elevation to maintain the same function/activity levels across the island. Because of a maximum mass limitation on the gut, the gradients are largely obscured for a snail diet under high energetic demand conditions. This mass limitation causes the results of Figure 9b. Highest foraging rate is 2.38 g/h for an insect diet, but 5.8 g/h for a snail diet.

Figure 12 shows the predicted distributions of the Po'ouli with and without mosquitoes carrying lethal avian malaria on Maui. We compare the most energy intensive reproductive (April) and least energy intensive nonreproductive (December) months for
changes in optimal parts of the landscape for the Po‘ouli. Lowest foraging rates in the dark color show that in the absence of mosquitoes low elevation sites should be optimal for Po‘ouli. Avian malaria bearing mosquitoes were introduced in the 1800s to Hawaii. A fossil Po‘ouli site described by James and Olson (1991) (circle in the southwest corner of the large part of Maui) overlaps our predicted area of optimal habitat for Po‘ouli in pre-1800 Hawaii.

The extermination of Hawaiian Honeycreepers by the mosquitoes’ malaria at low elevation forced populations to elevations above 1000 m. Our calculations of maximum discretionary energy and water above 1000 m (light gray color) is composed of a triangular band of overlapped diet types and associated maximal discretionary energy and discretionary water. The last 3 known home ranges for the Po‘ouli lie within this band in the right corner of the hollow triangle. As a frame of reference, the 1000 m contour, the upper bound for mosquito distributions, and the 2100 m contour, the upper bound for Po‘ouli observations, largely bound our calculations of optimal locations for the Po‘ouli on Maui given the constraints that lethal mosquitoes occupy the region below 1000 m. The dimensions of the dark and light gray bands vary somewhat seasonally. We estimate that the cost to the Po‘ouli of having to move to high elevations is a 20–30% increase in foraging rate for insects (Figs 11 and 12).

Fig. 9 (a and b) Map of the calculated discretionary energy for the Po‘ouli on Maui for an exclusive insect or snail diet. The darkest area is the highest discretionary energy, representing maximum potential for growth and reproduction. A snail diet with its low food quality requires ~4 times more biomass for the same energy content. In months of high energy demand, a snail diet mass requirement on a daily basis exceeds an estimated upper bound of food consumption that is 3 times the body weight of the animal in a day. That means that the animal in effect is not getting sufficient energy for reproduction and only at the lower elevations where the maintenance costs are lowest is can their maximum discretionary energy achieved. These images can be thought of as probabilities of occurrence. A snail diet is not consistent with observed distributions, but an insect diet is consistent with the observed distribution.

Fig. 10 (a and b) Map of the discretionary energy for the Po‘ouli in December on Maui. In December there is no reproductive demand and activity levels are also somewhat lower. There is not much difference for either diet in terms of discretionary energy. In December neither diet forces a consumption rate beyond the upper limit of food intake.
Discussion

Our unique MICRO2005 and ENDO2005 models allow us to map ecological landscape bioinformatics for species with limited available data such as endangered species. The advantage of the models is that it allows us to gain information about species’ function in the context of landscape and animal properties, present and future climate variation, diet availability, the presence of pathogens and environmental...
contaminants that may act as limiting factors influencing species’ distributions across a landscape.

Our computational models can predict the range or bounds of possible variation in metabolism, water intake and expenditure, growth and reproduction potential and activity hours for a species. These maps effectively form a probabilistic multidimensional surface for the greatest likelihood of successful survival, growth and reproduction. We have shown that mapping landscape scale discretionary energy and foraging rates and other variables requisite for reasonable levels of activity and reproduction for species is feasible. The comparison of an exclusive snail diet versus an insect diet on landscape maps illustrates how these kinds of approaches can provide insight into animal distributions and animal resource acquisition requirements. The models specify what must be present on the landscape for species persistence. The models specify how the resource base must change with variation in climate, elevation, slope, aspect and vegetation type to maintain a given level of activity, growth and reproduction.

In this paper, we provide evidence for a predominantly insect rather than snail diet at least while breeding and at higher elevations for the Po‘ouli and identify the most favorable areas for Po‘ouli on Maui with information from only a single specimen. This approach also proves very useful for other species that are not as rare as the Po‘ouli, where more data are available to test more detailed models not only of physiological performance in the laboratory, but distribution in the field. In the absence of abundant data, it is clear that a first principles model can provide substantial information about a rare or endangered species’ behavior, energetics and distribution and the resources it requires for survival, growth and reproduction. Habitat and population management can use these models and refine them based on available data to prevent total loss like the Po‘ouli’s and prevent last ditch efforts to find the last few survivors (Rosa and others 1998; USFWS and Hawaii LDNR 1999; Simon and others 2002).

Po‘oulis may prefer gulches with heavy vegetation. Available GIS spatial resolution for Maui is 30 m. Although we did not explicitly model gulches in detail, their microhabitat is relatively uniform from ground to high in the tree canopy because of nearly 100% shade present in such habitats. In the absence of direct sunlight, there is typically very little temperature gradient, since the ground cannot be heated by the sun to generate that gradient. Furthermore, evaporative water loss in such habitats promotes uniformity of temperature. In this case microclimate calculations for the rainforest are directly relevant to gulches and very close to the microclimates that exist in them. The pixel sensitivity analysis at high elevation suggests variation of 2.6–5.0% in Po‘ouli energetic requirements for different slopes and aspects.

Different habitats impose different resting energetic demands on their species. Habitats that impose greater energy demands for survival, growth and reproduction must provide (1) increased foraging time for the same resource base or (2) a greater resource base either in quality, quantity or both for a species to survive, grow and reproduce at the same rate across the landscape. Change in survival, growth and reproduction across the landscape may imply altered resources needed by the species. It may also suggest the presence of pathogens, contaminants or interactions with other species. For example, assuming an unlikely exclusive diet of snails for the Po‘ouli forces the bird into a circumstance where its gut cannot process sufficient biomass on a daily basis to maintain activity and reproductive demands, which reduces its discretionary energy as Figure 9b shows. A snail diet predicts an optimal occupied area on Maui for the Po‘ouli that is warmer and low in elevation where maintenance energetic demands are reduced. Lower maintenance costs mean more resources available for activity, growth and reproduction since daily gut capacity is limited on a snail diet. A predominantly insect diet has a completely different predicted discretionary energy pattern and predicted species distribution that is consistent with field distribution data.

It is clear that diet quality is very important for potential growth, reproduction, hours needed for foraging and amount of drinking water needed. Temperature variation driven by elevation, slope, aspect and vegetation type is also a very important variable. The shift in Po‘ouli habitat from a historically dry, mesic lowland habitat to a modern wet high elevation habitat had substantial effects on the ecology and survival of the species.

Regression approaches have substantial limitations when trying to address issues of animal energetics in the field. When physiological measurements are made or regressions are derived based on physiological data, the range of variation in these values needs to be considered. There are no regression data for climate (radiation, air temperature, humidity, wind speed) dependent metabolism in the literature for a broad range of animal sizes and properties. There are no regressions that take into account climatic, topographical and vegetation conditions that can substantially modify all aspects of animal physiology and behavior, which can alter how animals function. Animal dimensions, geometric shape and insulation layer depth and density also affect convective heat
transfer and water transfer from the skin because they alter boundary layer thickness which determines heat and mass flow.

Typically, metabolic measurements do not include observations of the posture of the animal. We have illustrated for the endangered orange-bellied parrot of Australia that piloerection and putting the head under the wing to closely approximate a sphere rather than an ellipsoid geometry can each introduce variation in the heat generation requirements of the bird, especially as experimental temperatures change (Porter and others 2000, Fig. 18).

However, ecological landscape–endotherm bioinformatics models, such as the ones described here, can address the complications of living in the real world instead of a metabolic chamber. Simply changing air temperature from thermal neutral conditions of regression animal metabolism equations can exert substantial changes on energy and water requirements for an animal outdoors (Porter and others 2000).

Calculations of water loss for metabolic chamber conditions suggest that calculations are in very good agreement with experimental data until the birds reach temperatures that induce heat stress (temperatures \(\geq 35^\circ\text{C}\)). The model assumes that the birds are trying to maintain a minimum temperature difference between core and skin to be able to dissipate metabolic heat generation at higher temperatures. The typical core temperature of \(40^\circ\text{C}\), is elevated \(\sim 1^\circ\text{C}\) at these higher temperatures as shown by the data of MacMillen (1974). The core–skin temperature difference was assumed to be maintained exclusively through the mechanism of increased water permeability of the skin. However, it seems more likely that temperature induced breathing frequency (volume dependent) changes in oxygen extraction efficiency may be a better heat stress model based on recent work on variation in oxygen extraction efficiency in birds, for example, the work of Arens and Cooper (2005).

Although interactions of the Po‘ouli with other species, such as mosquito vectors for avian malaria in its various forms have not been considered in this paper, mosquito reproductive success and population dynamics are also subject to thermal and hydric constraints (Kingsolver 1979; Ahumada and others 2004). Containers for temperature dependent egg development can be simulated and temporal and spatial variation in reproductive success can be estimated using the same kinds of techniques presented in this paper. As previously illustrated (Porter and others 2002) multispecies food web interactions and the influence of climate, topography, vegetation and infection on those interactions can be estimated quantitatively and are a function of species’ morphological, physiological and behavioral responses to the temporal and spatial variation of their environments.

Finally, our predictions for the distribution of Po‘ouli before lethal avian malaria was introduced into Hawaii in the 1800s are consistent with the only fossil site for their remains. The projections for areas on Maui where they would have maximal discretionary energy and water for reproduction are consistent with the 3 home ranges identified in the 1900s. The presence of lethal avian malaria at elevations below 1000 feet imposes an added 20–30% cost in foraging above 1000 m elevation. There are slight seasonal changes in the areas that we calculate would be optimal at high elevation. However, those areas encompass the 3 known home ranges for the Po‘ouli defined in the 1900s. It seems that in the context of both paleo distributions and modern distributions, our calculations for optimal Po‘ouli habitat are consistent with the available data. These calculations allow us to estimate added costs of the presence of a lethal disease for the Po‘ouli. These calculations also suggest locations that might be explored in the hope of finding remnant individuals still on Maui if they exist.

Conclusions

Our findings suggest that (1) a diet of snails creates a pattern of maximum discretionary energy for the Po‘ouli that is inconsistent with its known distribution. (2) A diet consisting principally of insects creates a maximum discretionary energy pattern for the Po‘ouli that is consistent with its known distribution. (3) Average hourly foraging rates required for a diet of snails is 4 times higher than for insects. (4) It is possible to identify areas on the landscape that are the most seasonally most likely places for Po‘ouli to flourish. (5) Calculations of metabolic rates and water loss rates for metabolic chamber conditions are consistent with experimental data collected by MacMillen (1974). (6) Calculated Amakihi distributions based on calculated discretionary energy patterns of the Amakihi are consistent with their observed distribution on Maui. (7) Microclimate calculations allow for temporal and spatial estimates of local environments across the landscape. We showed that as local environmental conditions change across the landscape in space and diurnal/seasonal time it is possible to quantify animal physiological and behavioral consequences of those variations in their local environment and thereby quantify the requisite spatial and temporal distribution and amount or availability of resources that affect species’ potential for survival, growth, reproduction and distribution.
These models are a means for doing landscape ecological bioinformatics to understand system biology. This complex set of models uses generic variables that are readily obtained to gain sophisticated information about an ecosystem and its effect on the survival of species. It is now possible to ‘design’ an animal and ask how much energy and water it needs for normal activities or how much extra resources are needed for growth or reproduction. What are the consequences of behavioral changes like switching from diurnal to nocturnal activity or likely responses to changing land-use patterns by altering vegetation or in the longer term altering global climates.

A key factor in the extinction of species can be the impact of man’s changes in land-use and global climate change (Benning and others 2002; Hare 2003). The spatially explicit models used here can quantify the consequences to animal energetics and behavior on real landscapes of future climate scenarios and how those changes might play out in terms of interactions with other species and shifts in distribution limits (Porter and others 2002; Kearney and Porter 2004).

Acknowledgments
The authors wish to thank Paul R. Sweet, collections manager, and Peter Capainolo, scientific assistant, at the American Museum of Natural History in New York City, who allowed us to measure properties of the Po’ouli specimen there. Steve Cardiff, collections manager at the Louisiana State University Museum, generously loaned us specimens of the Amakihi, the Anianiau, and other Hawaiian bird species. We also wish to thank Richard Dwelle, who performed some of the reflectance measurements on Hawaiian birds. Dr. Helen James, National Museum of Natural History, provided data on past Po’ouli distributions. We thank the Hawaii Forest Bird Interagency Database Project—USGS Pacific Island Ecosystems Research Center for sharing their Amakihi data to create Figure 5c. We thank Dr. Fariba Assadi-Porter, Mark Jankowski, Rebecca Kirby, Dr. Michael Samuel, and 3 anonymous reviewers for comments and suggestions on earlier versions of this manuscript.

References


Song J. 2004. Bird may have been last of kind. Honolulu Advertiser 1 December 2004.


