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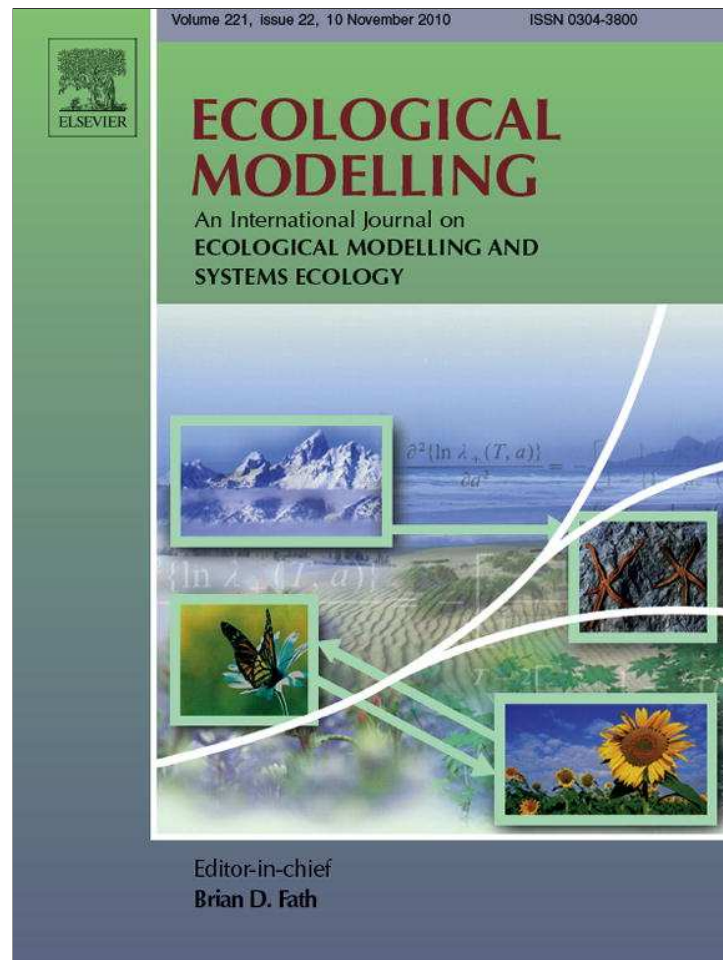
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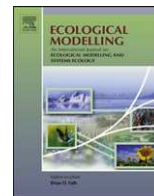
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Modeling amphibian energetics, habitat suitability, and movements of western toads, *Anaxyrus* (= *Bufo*) *boreas*, across present and future landscapes

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ABSTRACT

Effective conservation of amphibian populations requires the prediction of how amphibians use and move through a landscape. Amphibians are closely coupled to their physical environment. Thus an approach that uses the physiological attributes of amphibians, together with knowledge of their natural history, should be helpful. We used Niche Mapper™ to model the known movements and habitat use patterns of a population of Western toads (*Anaxyrus* (= *Bufo*) *boreas*) occupying forested habitats in southeastern Idaho. Niche Mapper uses first principles of environmental biophysics to combine features of topography, climate, land cover, and animal features to model microclimates and animal physiology and behavior across landscapes. Niche Mapper reproduced core body temperatures (T_c) and evaporation rates of live toads with average errors of 1.6 ± 0.4 °C and 0.8 ± 0.2 g/h, respectively. For four different habitat types, it reproduced similar mid-summer daily temperature patterns as those measured in the field and calculated evaporation rates (g/h) with an average error rate of $7.2 \pm 5.5\%$. Sensitivity analyses indicate these errors do not significantly affect estimates of food consumption or activity. Using Niche Mapper we predicted the daily habitats used by free-ranging toads; our accuracy for female toads was greater than for male toads ($74.2 \pm 6.8\%$ and $53.6 \pm 15.8\%$, respectively), reflecting the stronger patterns of habitat selection among females. Using these changing to construct a cost surface, we also reconstructed movement paths that were consistent with field observations. The effect of climate warming on toads depends on the interaction of temperature and atmospheric moisture. If climate change occurs as predicted, results from Niche Mapper suggests that climate warming will increase the physiological cost of landscapes thereby limiting the activity for toads in different habitats.

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1. Introduction

Amphibians are high-profile elements of the sixth mass extinction (Wake and Vrendenburg, 2008; Rohr et al., 2008), and loss, alteration, or fragmentation of both breeding and terrestrial habitat are leading causes of declines (Green, 1997; Stuart et al., 2004; Lannoo, 2005; Funk et al., 2005; Muths et al., 2006; Harper et al., 2008). Long-term historical climate change has facilitated genetic divergence of amphibian species through range alteration or population isolation (e.g., Goebel et al., 2009; Shepard and Burbrin, 2009). In contrast, rapid environmental change could contribute to amphibian population declines.

Amphibians are wet-skinned ectotherms that are closely coupled to their physical environment; factors that contribute to their core body temperature include dynamic, complex interactions of

heat energy fluxes and evaporation (Tracy, 1976). The amount of energy absorbed by a terrestrial amphibian depends on physical features of the animal (e.g., shape, color, and behavior) and weather conditions as modified by habitat structure (Fig. 1). The potential physiological states (e.g., core temperature) experienced by the animal then reflect the net energy absorbed, plus the cooling effect of evaporation. The animal's actual physiological states will be subsets of the potential states and influenced by factors such as food availability, predator avoidance, and the animal's hydration state (i.e., the more water it is storing, the more evaporation it can tolerate). Finally, the actual physiological state of the animal directly affects its behavior, growth, and other functions. Hence, habitats selected by an amphibian can have direct physiological and functional consequences (Huey, 1991), and the rapid climate change we are experiencing could exacerbate effects of habitat loss (Pilliod et al., 2002; Semlitsch and Bodie, 2003; Bartelt et al., 2004). We want to know how climate change might affect the microenvironments of amphibian terrestrial habitats. Predicting the movement corridors and distribution of amphibians across a landscape and how habitat changes might affect them is critical for developing

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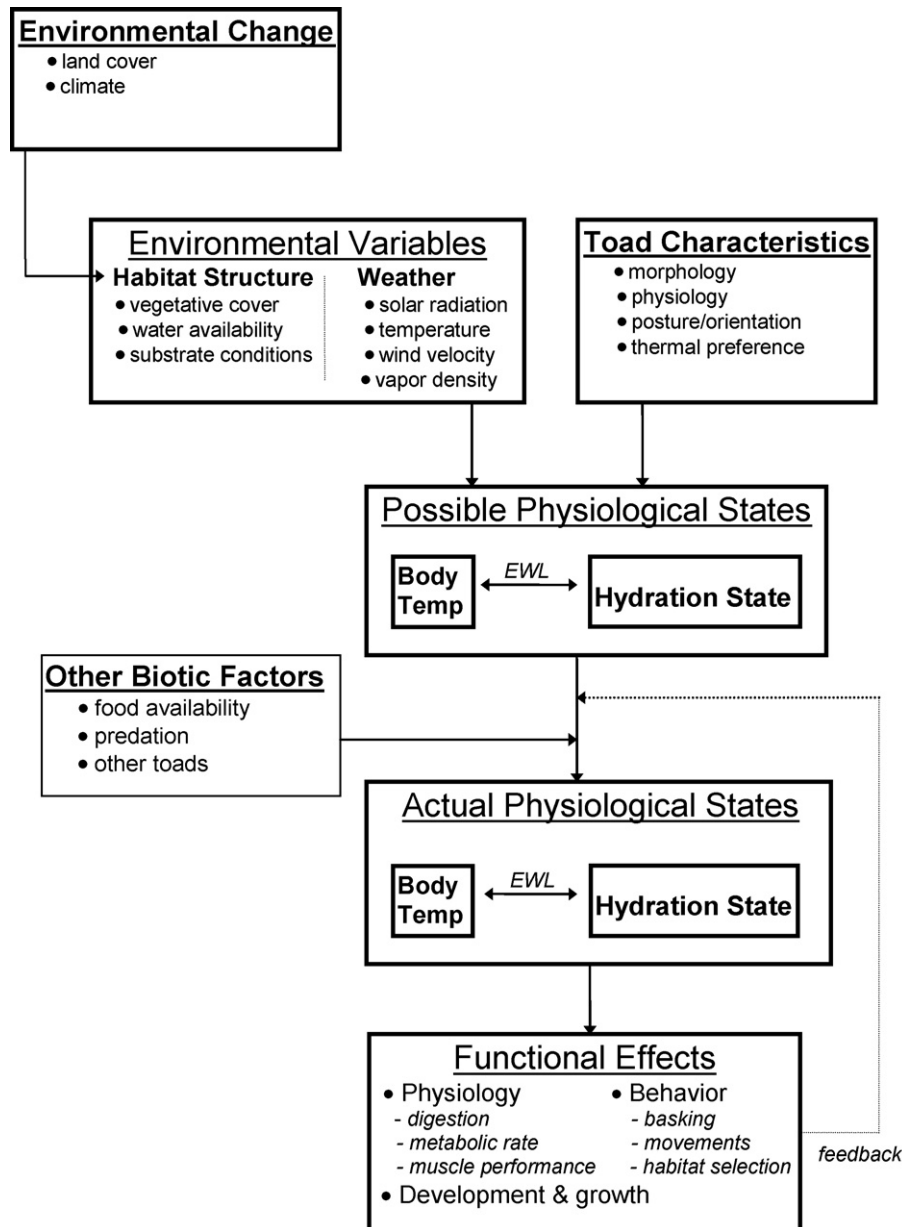


Fig. 1. Factors that affect amphibian body temperatures and physiology, and that are modeled by Niche Mapper. Environmental variables interact with intrinsic characteristics of amphibians to create a mosaic of microsite conditions for them. The microsite chosen by an amphibian will determine its body temperature and hydration state, and this can affect its physiology, growth, and behavior. Environmental change that alters either habitat structure or weather conditions also can affect amphibian body temperatures.

effective conservation strategies, especially in light of a changing environment.

Recent advances in computer technology, the development of remote sensing to create landscape datasets, and efficient Geographic Information Systems (GIS) make possible the ability to model animal energetics and behavior across entire landscapes. For example, Ray et al. (2002) used landscape data layers of estimated amphibian suitability within a GIS to estimate the ease of amphibians to move through landscapes. Boone et al. (2006) used diffusion models with remotely sensed data to test factors affecting movements of wood frogs (*Rana sylvatica*) among ponds in Minnesota, and Kearney et al. (2008) calculated present and future distribution limits of the cane toad in Australia. We used Niche Mapper, a process-driven mechanistic model (Porter and Mitchell, 2006), to model energetics and behavior in the context of detailed knowledge

of four highly divergent vegetation types (closed canopy forest, open canopy forest, dense shrub, and clearcut forest). To model toad energetics and movements and evaluate effects of climate change on these predictions we used three approaches. First, to test the accuracy of our approach, we made direct comparisons between field and laboratory measurements of toads and physical models (Bartelt and Peterson, 2005) against results calculated by Niche Mapper using identical environmental data. Second, we applied the results of Niche Mapper to a landscape where habitat use and movement and patterns of Western toads (*Anaxyrus (=Bufo) boreas*) were previously measured (Bartelt, 2000; Bartelt et al., 2004) and tested its ability to map these patterns. Third, we ran Niche Mapper on this landscape under different weather conditions to test the effects of a warming climate on altering the habitat conditions on this landscape and its potential effects on toads.

2. Methods

2.1. The Niche Mapper models

Niche Mapper is a patented collection of three mechanistic models that include a broadly applicable microclimate, ectotherm and endotherm model of heat and mass transfer and animal behavior. More details of these models can be found in Porter et al. (1973), Porter and Mitchell (2006), and at “<http://www.zoology.wisc.edu/faculty/Porter/Porter.html>.”

2.1.1. Microclimate model

The microclimate model translates coarse spatial data, such as Digital Elevation Models (DEMs), vegetation data, weather station data and spatially interpolated climate records, into microclimatic environmental variables relevant to the thermal and hydric ecology of organisms. It includes a one-dimensional finite difference algorithm that simultaneously solves heat and mass balance equations for the ground surface and specified depths below. It includes a subroutine for computing clear sky solar radiation given a specific time, latitude, longitude, elevation, slope and aspect (McCullough and Porter, 1971). The microclimate model requires climate (2 m shade air temperature, wind speed, humidity and cloud cover) maximum and minimum data for arbitrary time intervals, e.g., monthly, weekly or daily, and physical properties of the soil as major input variables.

2.1.2. Ectotherm model

We modeled hourly core body temperatures (T_c) of toads by iterative solving for T_c in a steady-state heat (Q) energy balance equation containing terms representing solar (Q_{solar}), incoming (Q_{IRin}) and outgoing (Q_{IRout}) thermal infrared radiation (IR), generated metabolic heat (Q_{gen}), respiratory (Q_{resp}) and cutaneous (Q_{cut}) evaporation, convective (Q_{conv}) and conductive (Q_{cond}) heat transfer:

$$Q_{solar} + Q_{IRin} + Q_{gen} = Q_{resp} + Q_{cut} + Q_{IRout} + Q_{conv} + Q_{cond} \quad (1)$$

Basic elements of the model have been described elsewhere (Porter, 1989; Porter and Gates, 1969; Porter et al., 1973, 1994, Appendix A; Porter and Mitchell, 2006). A critical aspect of the model in the context of a wet-skinned amphibian is heat exchange via cutaneous evaporation. Q_{cut} , is determined by the latent heat of vaporization, λ , of water together with the rate of mass transfer such that, $Q_{cut} = m \cdot \lambda$. The rate of mass transfer is defined as

$$m = h_D \cdot A \cdot (\rho_{w,skin} - rh \cdot \rho_{w,air}) \quad (2)$$

where m is the rate of mass transfer, h_D is the mass transfer coefficient, A is the area of the skin that acts as a free water surface across which mass exchange occurs, rh is the local relative humidity, and $\rho_{w,skin}$ and $\rho_{w,air}$ are the densities of water vapor at saturation at the temperature of the animal surface and air, respectively. See Porter and Mitchell (2006) and Tracy (1976) for further details on the calculation of mass transfer rates.

The distributed metabolic heat generation term, Q_{gen} , in Eq. (1) was taken from Lillywhite et al. (1973) data for *A. boreas*, regressed to yield O_2 in ml/(g/h) = $0.00861 \times T_c - 0.06128$; and converted to J/s assuming a protein diet (4.5 kcal/L O_2). Q_{gen} defines skin temperature, T_s for current environmental conditions, a (spherical) geometry and a given iterative guess of T_c , since $Q_{gen} = 6kV(T_c - T_s)/R^2$ (Porter et al., 1994; p. 156, Eq. (2)), where V and R are animal volume and radius and k is the effective flesh thermal conductivity (0.5 W/mC). Q_{gen} also determines the requisite mass that must be absorbed from the gut, m_{abs} in Eq. (3).

Mass (molar) balance (g/d)

$$m_{in} = m_{abs} + m_{out} \quad (3)$$

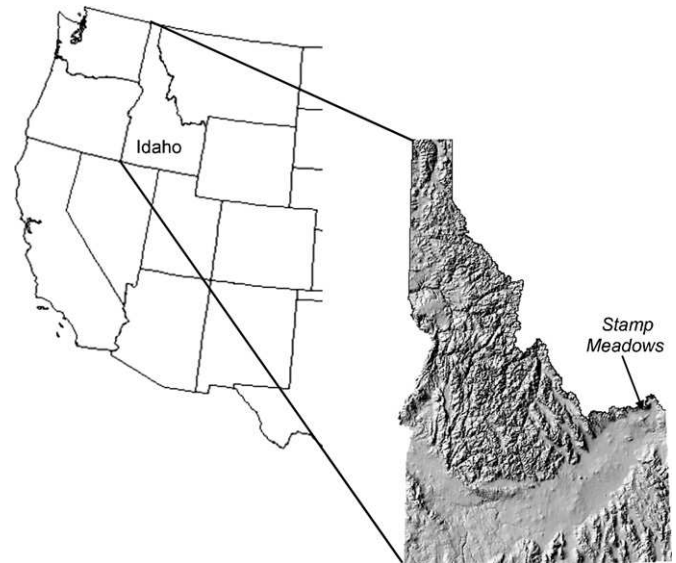


Fig. 2. Location of Stamp Meadows study area in southeastern Idaho, USA.

defines molar balances for the respiratory and digestive system, where m_{in} is the rate of mass entering the imaginary surface across the entrance to the system, m_{out} is the rate of mass exiting through the imaginary surface across the exit of the system and m_{abs} is the mass crossing the internal surface of the system (the gut wall or the respiratory surface (lungs and skin)) (Fig. 2 in Porter et al., 2006). The metabolic processes of the body require that a specified mass of daily fuel and oxygen be available. Thus mass that must be absorbed daily, m_{abs} , from the gut can be calculated from Q_{gen} requirements. Daily food intake required to maintain body weight is computed using the digestive efficiency of a particular diet composition. The daily mass balance of the gut can be determined from basic principles of environmental biophysics, since calculating the required intake and the absorbed mass allows by difference the mass out of the animal's gut. Similarly, a molar balance on the respiratory system allows calculation of the mass of oxygen that must flow through the respiratory system on a daily basis to meet the demands of metabolism. Niche Mapper used an assumed oxygen extraction efficiency of 12% for amphibians. This was based on work by Withers and Hillman (1983) that reports an extraction efficiency for two species of forced exercised anurans as 18%. Kalliokoski et al. (2001) report oxygen extraction efficiency for exercising human muscle at 49% compared to resting efficiency of 29%. This suggests that resting oxygen consumption is approximately 59% of active efficiencies or for an 18% active anuran efficiency, a resting anuran efficiency of 11%. An additional 1% was added for cutaneous functions.

2.2. Testing the models

We tested the models at multiple scales. At the finest scale, we tested the ability of Niche Mapper to predict T_c and rates of evaporative water loss (EWL) of individual animals under controlled laboratory conditions. We then tested its ability to reproduce daily patterns of operative temperature, T_e (Bakken, 1989; Porter et al., 1973) and rates of EWL among four different habitats measured by physical models (Bartelt and Peterson, 2005). At the largest scale, we applied Niche Mapper to an 8 km² landscape to test its ability to predict known movements and habitat use patterns of Western toads in a forested area in southeastern Idaho, on the southern slopes of the Centennial Mountains (Fig. 2; Bartelt et al., 2004).

2.3. Predicting T_c and rates of EWL

Bartelt and Peterson (2005) used a wind tunnel under controlled laboratory conditions to compare rates of heating and cooling and rates of EWL of physical models to those of live toads. We entered weather values for these conditions into Niche Mapper to calculate expected T_c and EWL rates under the same controlled conditions and compared these results against the actual T_c and EWL rates.

2.4. Comparing patterns of T_e and EWL among habitats

Before applying Niche Mapper to a landscape, we modified the shade calculations to correct for solar zenith angle effects on vegetation specific shade patterns and effects of different foliage densities on daily variations of relative humidity.

2.4.1. Modifying Niche Mapper

To improve the ability of the microclimate model to predict variations in temperature and humidity in different habitats across the landscape we collected additional environmental information, including measures of solar absorptivity and the percent of the surface that is wet for different habitat types in nearby Yellowstone National Park (D. Anderson, USDA Forest Service, unpubl. data). We also used a sling psychrometer and sets of physical models in Yellowstone National Park to measure daily differences in vapor densities (≤ 20 cm above ground) among vegetation cover types during summer and used these data to adjust the vapor density inputs at 2 m height for corresponding habitats into the microclimate model.

We collected data on percent shade of different vegetation types at different solar altitudes in the Big Horn Crags of the Frank Church Wilderness with four separate MicroWeather Stations from Onset Computer Corp (Pocasset, MA). The canopy cover values were calculated with a GAP Light Analyzer (Simon Frazier University, REM Department, 1999) using image data collected with a fish-eye lens (Nikon Fisheye Converter FC-E8, 35 mm focal length equivalent, 183° angle) and camera (Nikon, 4500 Coolpix). The equation describing these results we used was:

% shade reduction from vertical sun values

$$= 0.0973122 - 0.9297X + 0.0286672X^2 - 0.00021071X^3 \\ + 334.216Y - 835.91Y^2 + 1072.99Y^3 - 468.996Y^4$$

where X is the zenith angle ($^\circ$) and Y is the % cover/100. The regression includes data over the range of 0.7–70.2% cover with an R^2 of 0.797.

2.4.2. Comparing Niche Mapper to field data

To test the ability of Niche Mapper to predict T_e and rates of EWL in particular habitats, we used field data collected on 25 July, 1995 with replicates of physical models placed within four different forested habitats (Bartelt, 2000). These habitats included mature forest (canopy cover = 67%), thinned forest (canopy cover = 25%), shrub (tree canopy cover = 5% and shrub canopy cover = 80%), and clearcut (canopy cover = 2%). By placing these stationary physical models in exposed and shaded microsites, we were able to bound the extremes of conditions available to free-ranging toads among these habitats. Using data from an on-site weather station, we ran Niche Mapper to calculate hourly values of operative temperature and EWL for these habitats.

2.5. Using Niche Mapper to map the landscape for toad suitability

We applied Niche Mapper to an 8 km² study site in southeastern Idaho (Stamp Meadows) to test its ability to accurately map daily

habitats for Western toads and estimate movement patterns. We compared these results to known patterns of toad movements and habitat use (Bartelt et al., 2004). Although Western toads are considered habitat generalists (Muths and Nanjappa, 2005), field data show that microenvironmental variation among habitats affect their activity and habitat selection (Bartelt, 2000; Bartelt et al., 2004).

2.5.1. Study area

Stamp Meadows is located on the Targhee National Forest in southeastern Idaho. It is a grassy meadow surrounded by a mosaic of coniferous habitats (*Pinus*, *Picea*, and *Abies* spp.) that have been modified by logging. In spring of normal to wet years, water collects to form a large (10–15 ha) pond, bordered by willows (*Salix* spp.), aspen (*Populus tremuloides*), and lodgepole pine (*Pinus contorta*). Toads bred in this filled pond from late May through mid-June.

2.5.2. Input data

We compiled all geospatial information as raster data at 30-m cell size. We used a Digital Elevation Model (DEM; Gesch et al., 2002) to acquire topographic data (elevation, slope, and aspect) and DayMet weather model (Thornton et al., 1997; <http://www.daymet.org>) to acquire maximum and minimum temperatures and vapor densities. Because the weather data were compiled at 1-km resolution, we resampled the data to 30-m cell size and adiabatically adjusted temperature ($-5.5^\circ\text{C}/\text{km}$) for each cell according to changes in elevation relative to the elevation for the 1 km cell. Habitat data (cover types and percent canopy cover) were acquired from previous field measurements (Bartelt et al., 2004). Because these field measurements were collected for each of two years (1993 and 1995), we ran Niche Mapper twice, once for each year.

2.5.3. Derived variables for the suitability index

In addition to the standard output variables computed by Niche Mapper (e.g., daily evaporation, maximum core body temperature), we derived additional data related to the biology of Western toads. Lillywhite et al. (1973) found that 27.3°C was an optimal T_c for a number of physiological functions; hence, we counted the number of hours that $T_c \geq 27^\circ\text{C}$ (T_{c27}). We counted the number of hours that air temperature (T_a) $< 8^\circ\text{C}$ (T_{c8}), because toads generally moved least during cool night-time air temperatures ($T_a \leq 8^\circ\text{C}$ in Bartelt et al., 2004; $T_a < 5^\circ\text{C}$ in Sullivan et al., 2008). We also counted the number of hours that T_c ranged between 15 and 27°C (T_{c20}) to estimate the daytime hours available for toads to forage, etc. Basking toads shuttled between sunlight and the moist substrate of shade, apparently balancing their thermal and moisture needs. In drying habitats, hydroregulation can be costly to toads because lower body water content constrains their activity. The maximum water that toads would voluntarily lose before seeking shade was about 7.5 g ($\sim 14\%$ of body weight; Bartelt, 2000). In more humid habitats, this was not a problem; but in drier conditions toads showed reduced basking and/or foraging times and cooler T_c s. Cooler body temperatures can reduce growth rates (Lillywhite et al., 1973), sprint speeds (Tracy et al., 1993), and have cumulative physiological consequences (Huey, 1991). To estimate the cost of hydroregulation to toads (i.e., potential hours of basking and solar heating constrained by evaporation), we divided the calculated evaporation by 7.5 and reduced the values of T_{c27} by this proportion.

Finally, we wanted to create a single, composite and unitless measure that would capture the totality of a habitat's suitability for toads (similar to an approach used by Karr, 1981). We created a unitless overall "suitability index" through a linear combination of the derived variables described above. Toads were most active and

Table 1

The set of seven *a priori* models used to predict the daily habitats used by Western toads in the Stamp Meadows area, southeastern Idaho. For each of 13 toads, 80% of the field data were used to build logistic regression models and 20% reserve data to validate the best models.

Model #	Predictor variables
1	Suitability
2	Evaporation
3	T_c27
4	Evaporation + T_c27
5	Evaporation + suitability
6	Evaporation + T_c27 + T_c20 + suitability
7	(Evaporation $\times T_c27$) + T_c20 + suitability

made long-distance movements during the months of June, July, and August; hence, this “suitability index” used data calculated only for these months:

$$\text{Suitability} = T_c20 + \left(T_c27 - \left(\frac{\text{daytime evap}}{7.5} \right) \right) - T_c8 \quad (4)$$

2.6. Predicting habitat use and movements

At the Stamp Meadows site, toads selected daily retreat sites in habitats where they could hydroregulate and thermoregulate during daytime activities, such as foraging, basking (Bartelt, 2000), and making shorter (≤ 50 m) movements. We used Niche Mapper to test the hypothesis that toads selected sites that were less costly. To map the distribution of these sites (a measure of habitat selection), we used a Geographic Information System (GIS) and logistic regression models with data layers for each of several standard and derived Niche Mapper output variables. For each toad, we used the coordinates of its retreat sites, coordinates from an equal number of randomly selected sites, and sampled the data layer for each of the variables. We used Niche Mapper results from 1993 or 1995, depending which year the toad was studied. Eighty percent of the data were used to build the logit models, reserving the remaining 20% for validation. For each toad, we tested an *a priori* set of models (Table 1) and selected the best model with an information–theoretic approach (Burnham and Anderson, 2002), then validated its accuracy. For each toad, we tested an *a priori* set of models (Table 1) and selected

By restricting their long-distance (>100 m) dispersal movements primarily at night, these toads avoided the higher hydroregulatory costs of drier daytime conditions. By connecting the sequential coordinates of daily retreat sites, Bartelt et al. (2004) estimated the seasonal paths followed by toads. They found that female toads traveled longer distances from their breeding pond and selected daily habitats with warmer and more humid conditions. We used Niche Mapper and cost-surface analysis to calculate cumulative costs and replicate patterns of movement. Cost-surface (or friction surface) functions are fundamental operations of the GIS toolbox (Berry and Tomlin, 1982; Berry, 1987; Douglas, 1994). We used the GIS (ArcMap v. 9.2) function “COSTPATH” to calculate two sets of ideal least-cost paths for each of six toads that traveled the longest distances; one set was created using the “overall suitability index” and the second with calculated amounts of daily EWL. We

compared the cost of paths used by toads to those of straight lines connecting the beginning and ending points of travel (the shortest Euclidian distance), and some randomly generated paths for each toad. Cost-surface analysis uses two input maps: a map of habitat patches that function as sources and a map of the cost of moving among patches. The output mapped locations with the least accumulated cost (i.e., the summated cost of sequential cells) for a toad to reach it from the source habitat patches. The locations may be interpreted as a species-specific connectivity measure that is weighted by the intervening matrix. We used Niche Mapper results for 1993 for toads #25 and 31, and 1995 results for toads #4, 72, 73, and 78.

2.7. Testing scenarios of environmental change

We used Niche Mapper to estimate how a warming climate might affect conditions of the habitats used by toads in Stamp Meadows. We based this test on long-term (1937–2008) average weather conditions collected at the Island Park weather station (~10 km from Stamp Meadows and similar elevation), because these data show that monthly summer temperatures for 1993 were cooler than average (0.5–7.1 °C for maximum temperatures and 0.2–2.9 °C for minimum temperatures); because precipitation for the summer of 1993 was greater by only 0.5 cm, we used 1993 values for moisture. A number of climate scenarios predict a range of warmer temperatures, from a minimum of about 2 °C to a maximum of 6 °C (IPCC, 2007) and increased precipitation. Therefore, we tested three different warming scenarios (Table 2) with Niche Mapper.

3. Results

3.1. Predicting T_c and rates of EWL

Niche Mapper reproduced toad T_c with an average error of 1.6 ± 0.4 °C over the temperature range of 8–29 °C (Fig. 3A). It reproduced rates of EWL with an average error of 0.8 ± 0.2 g/h over a total EWL range of 0.2–6.7 g/h (Fig. 3B).

3.2. Comparing patterns of T_e and EWL among habitats

In some habitats, daily variations of T_e recorded by physical models included the effect of shading and sun flecks as they moved across the ground (Fig. 4). While Niche Mapper did not capture these short-term temporal variations, its general predictions of toad T_c showed similar maxima and minima as T_e for the different habitats and a similar number of hours that T_c and T_e occurs within certain temperature ranges (Table 3). The average error was 1.4 ± 0.2 h. This was expected given that the time step in the animal calculations was hourly and rounding error could account for most of these differences.

Under similar weather conditions, Niche Mapper calculated greater amounts of EWL for habitats with less cover (Fig. 5A). The average error in predicting amounts of EWL was 2.4 ± 1.7 g/d ($7.2 \pm 5.5\%$ of that measured by the physical models; Fig. 5A). Average daily T_a increased from May to July and then decreased to

Table 2

Three different scenarios of climate change for the Stamp Meadows area tested with Niche Mapper. Each scenario is described by a change in maximum temperature (T_{max}), minimum temperature (T_{min}), and relative humidity (RH; estimated from predicted changes in precipitation). These values were added to long-term (1937–2008) average temperatures.

Scenario #	ΔT_{max} (°C)			ΔT_{min} (°C)			ΔRH		
	June	July	Aug	June	July	Aug	June	July	Aug
1	+2	+2	+1	+0.5	+0.5	0	$\times 1.05$	$\times 1.05$	$\times 1.05$
2	+4	+4	+3	+2	+2	+1	$\times 1.1$	$\times 1.1$	$\times 1.1$
3	+6	+5	+5	+4	+4	+6	$\times 1.15$	$\times 1.15$	$\times 1.15$

Table 3
Number of hours within selected temperature ranges.

	Habitat	<8 °C	8–15 °C	15–27 °C	>27 °C
Physical models (T_c)	Closed Canopy	7	10	6	1
	Open canopy	9	7	5	3
	Shrub	9	4	5	6
	Clearcut	10	5	3	6
Niche Mapper (T_c)	Closed Canopy	6	11	5	2
	Open canopy	10	6	3	5
	Shrub	10	5	3	6
	Clearcut	7	8	2	7
Difference	Closed Canopy	1	-1	1	-1
	Open canopy	-1	1	2	-2
	Shrub	-1	-1	3	0
	Clearcut	3	-3	1	-1

September, and average daily RH varied inversely (Fig. 5B). As predicted by Niche Mapper, monthly rates of EWL generally increased from May to July, then decreased to September. However, the amount of change varied among the habitats, with less variation occurring in habitats with greater amounts of shade and foliage density.

3.3. Using Niche Mapper to reclassify a landscape

Results from Niche Mapper generated a patchy landscape where, for example, toads could maintain a T_c of $\geq 27^\circ\text{C}$ for different hours in a day (Fig. 6A), or the amount of water toads would lose

through evaporation during the day (Fig. 6B). The patterns of these maps reflect the patterns of vegetation and cover on this landscape (Fig. S1).

3.3.1. Predicting habitat use and movement paths

In predicting daily habitats, models that used a combination of warmer body temperatures and “suitability”, constrained by evaporation, scored highest (Table 4). Maps of daily habitats produced by these models (Fig. S2) were consistent with differences observed in patterns of habitat selection between male and female toads (Bartelt et al., 2004). That is, the models had weak or no predictive power for males and better predictive power for females, reflecting stronger patterns of habitat selection among females. Limiting tests of validation to toads with at least six observations in the reserve data, predictive accuracy for seven males averaged $53.6 \pm 15.8\%$, and that for six females averaged $74.2 \pm 6.8\%$.

Daily amounts of EWL provided the best results for cost-analysis and produced idealized least-cost paths that best replicated paths used by toads (Fig. 7). In all cases, accumulated costs for least-cost paths were substantially less than costs for either used or

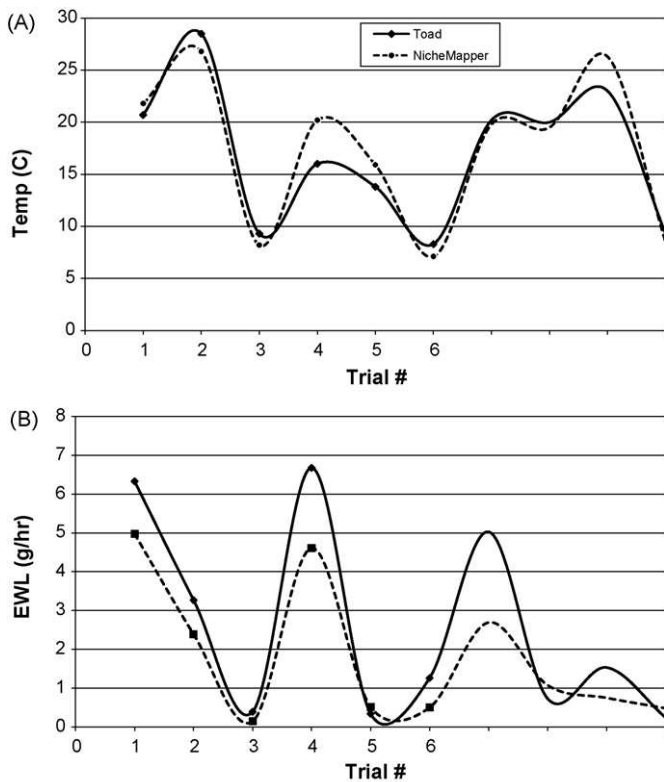


Fig. 3. Comparison of actual toad body temperatures and rates of evaporative water loss to those calculated by Niche Mapper. Bartelt and Peterson (2005) compared the behavior of physical models to live toads under 10 separate trials of controlled conditions. We entered these same experimental conditions into Niche Mapper to test its ability to reproduce the T_c and EWL rates of live toads. (A) Body temperatures. Except for two points, Niche Mapper temperatures were within 1.5°C of actual temperatures. The two points of larger differences may have resulted from measurement error. (B) Evaporative water loss (EWL). Niche Mapper tended to underestimate higher rates of EWL.

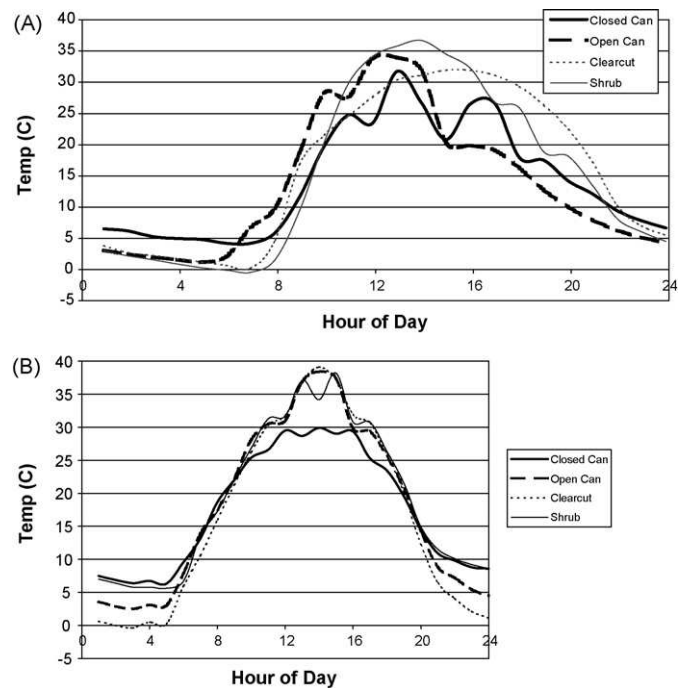


Fig. 4. (A) Daily variation of operative temperature (T_c) in the Stamp Meadows area (southeastern Idaho) recorded by physical models on 25 July 1995. (B) Variation in core body temperature (T_c) of Western toads as predicted by Niche Mapper using weather conditions recorded for the same area on the same day.

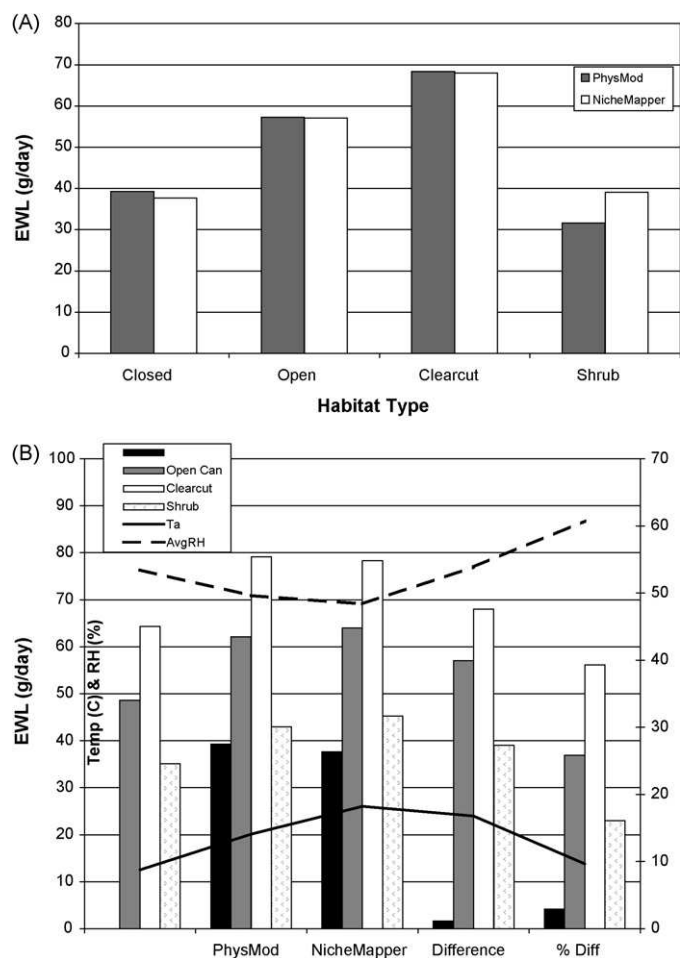


Fig. 5. (A) Total amounts of water lost for 25 July 1995 as recorded by physical models and predicted by Niche Mapper for the Stamp Meadows area (southeastern Idaho). (B) Monthly variation of EWL predicted by Niche Mapper, compared to variation in T_a and RH.

straight-line paths (Fig. 8). With one exception, the accumulated cost difference between used and straight-line paths diminished as the total distance traveled decreased.

3.3.2. Testing scenarios of environmental change

Ignoring the need for hydroregulation, toads could theoretically maintain a warmer body temperature ($T_c \geq 27^\circ\text{C}$) under the sce-

nario of a warmer climate (Fig. 9A). Evaporation rates, however, also increased over a large percentage of the landscape (Fig. 9B); thereby, constraining the number of hours a toad could maintain a warm body temperature by its need for hydroregulation. The effect of all three warming scenarios was similar: compared to average conditions, a smaller proportion of the landscape would provide toads the ability to maintain a warm body temperature without dehydrating (Fig. 10). Furthermore, this proportion decreased with increased warming.

4. Discussion

4.1. Predicting T_c and EWL

Niche Mapper was able to predict T_c of live toads under controlled conditions with an average error of $1.6 \pm 0.4^\circ\text{C}$. Among the total 10 trials, it overestimated T_c in trials #4 and 9 by 4.2 and 3.3°C , respectively; a difference up to 10 times greater than the error for other trials. Excluding these two data points reduced the average error to $1.1 \pm 0.2^\circ\text{C}$. Niche Mapper underestimated rates of EWL in four trials with peaks of evaporation rates. The overall error was 0.92 g/h ; excluding these four trials reduced the error to $0.44 \pm 0.1\text{ g/h}$.

Cause for these large errors is uncertain. It could have resulted from potential measurement error reported in Bartelt and Peterson (2005), or Niche Mapper may simply be under-calculating higher rates of EWL. The trials where T_c was overestimated were also two of the four where evaporation was underestimated. This pattern of error would be consistent with the physiology of amphibians where, within steady-state conditions, reduced rates of evaporation would translate into higher T_c (Tracy, 1976; Campbell and Norman, 1998). If so, this discrepancy can be adjusted: $\text{toad EWL} = (\text{Niche Mapper} \times 1.3925) + 0.0541$; $R^2 = 0.932$, $F_{1,9} = 124.6$, $p < 0.001$.

The practical effect of these errors would be to incorrectly estimate animal metabolism and activity, because physiological performance in amphibians is markedly temperature dependent (Carey, 1978). However, because their physiological performance lacks broad plateaus of thermal independence (Carey, 1978) and change in metabolic rate diminishes at warmer temperatures (Lillywhite et al., 1973; Carey, 1978) when toads are more active, the amount of error will change with T_c and may be relatively small. For example, using calculations of hourly CO_2 consumption (mol/h) and wet food requirements (g/d) from Niche Mapper (fitted to linear regression models), at temperatures of $T_c \geq 20^\circ\text{C}$ the

Table 4

Summary of ability of logit models to predict daily habitat use by Western toads in the Stamp Meadows area, southeastern Idaho. Only toads with reserve data sets of ≥ 6 were used for this analysis.

Toad #	<i>n</i>	Best model	AIC _w	ROC	Prediction accuracy (%)
Male toads					
5	6	7	0.310	0.708	50
50	6	6	0.898	0.878	100
61	6	7	0.854	0.844	100
63	8	4	0.208	0.647	0
65	8	6	0.754	0.694	50
67	12	6	0.305	0.593	0
71	8	6	0.530	0.781	75
Average = $53.6 \pm 15.8\%$					
Female toads					
4	12	4	0.537	0.715	70
22	6	4	0.594	0.728	67
31	8	6	0.501	0.750	50
46	6	7	0.648	0.853	100
72	8	6	0.953	0.901	75
78	12	6	0.646	0.814	83
Average = $74.2 \pm 6.8\%$					

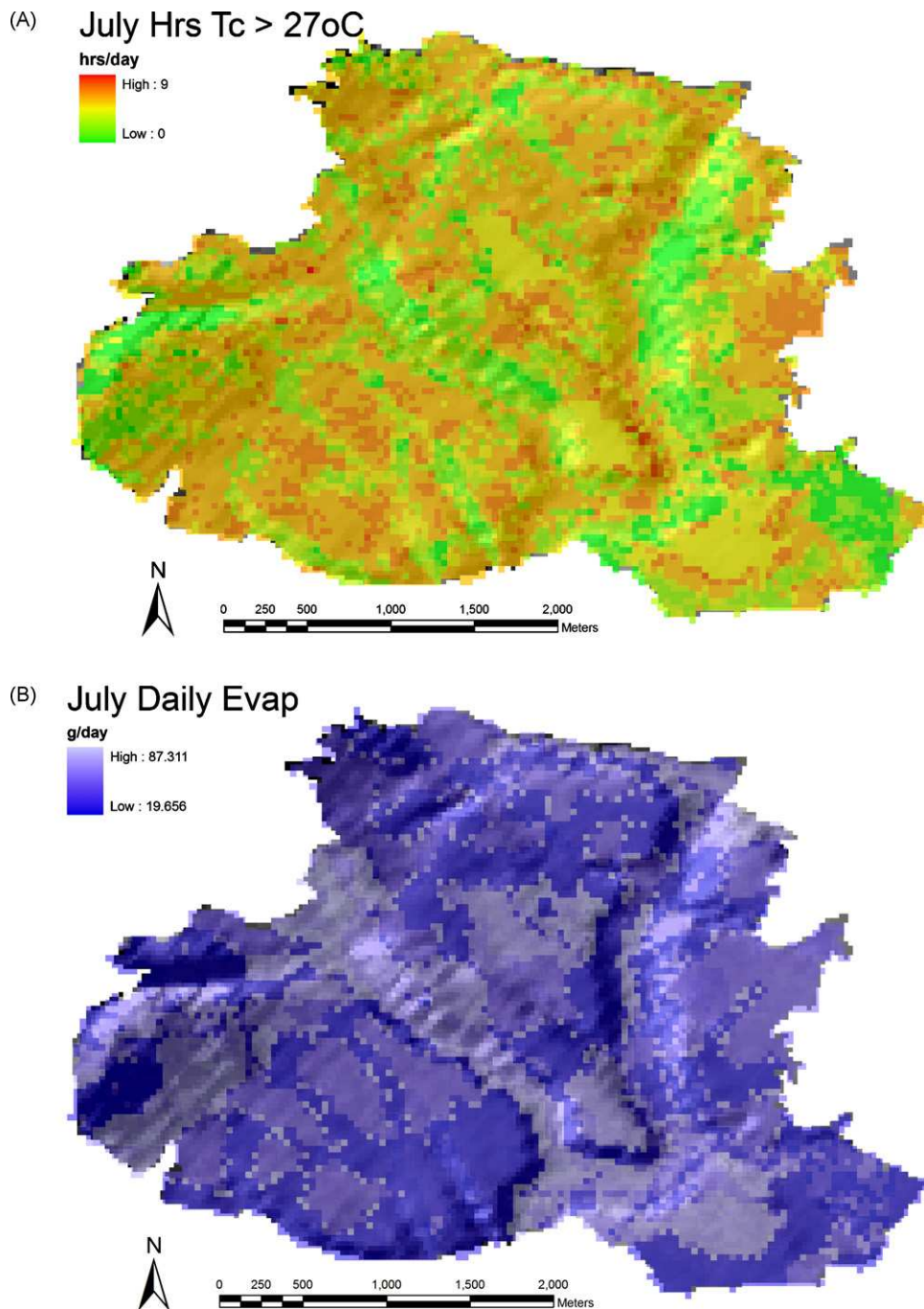


Fig. 6. (A) The Stamp Meadows area (southeastern Idaho) reclassified to map areas where a toad could maintain a warm body temperature ($T_c > 27^{\circ}\text{C}$) for different lengths of time. (B) The Stamp Meadows area (southeastern Idaho) reclassified to map rates of evaporative water loss (EWL), reflecting relative costs to a toad.

average error rate of $\pm 1.6^{\circ}\text{C}$ would affect rates of CO_2 production by $\pm 8\%$ ($F_{1,85} = 1,027,616$, $p < 0.001$, $R^2 = 0.95$). This is within the range of temperature-induced changes in metabolic rates experimentally measured by Lillywhite et al. (1973) and Carey (1978) for *A. boreas*. Daily wet food requirements increased by 2.1% for 1°C error of T_c estimation ($F_{1,8189} = 23,859$, $p < 0.001$, $R^2 = 0.74$). In addition, physiological and ecological performance does not scale directly (Huey and Swenson, 1979). For example, improving physiological performance by 20% may not result in an equal improvement of ecological performance (e.g., activity time). Therefore, for the purposes and scale of this modeling, we consider the amount of error evident in T_c estimates by Niche Mapper to be inconsequential.

Our approach also places an emphasis on the cost of EWL among toad habitats (i.e., greater rates of EWL diminishes the ability of toads to maintain a warm T_c). The tendency of Niche Mapper to underestimate EWL (especially at higher rates of EWL) could be important in overestimating a toad's amount of activity time (Bartelt, 2000). Quantifying and correcting this EWL error greatly reduced the error produced in later landscape-scale tests.

4.2. Patterns of T_c and EWL

There were some distinct differences in the predictions of Niche Mapper compared to the actual field data. For example, maximum T_e predicted by Niche Mapper exceeded that of the field data and

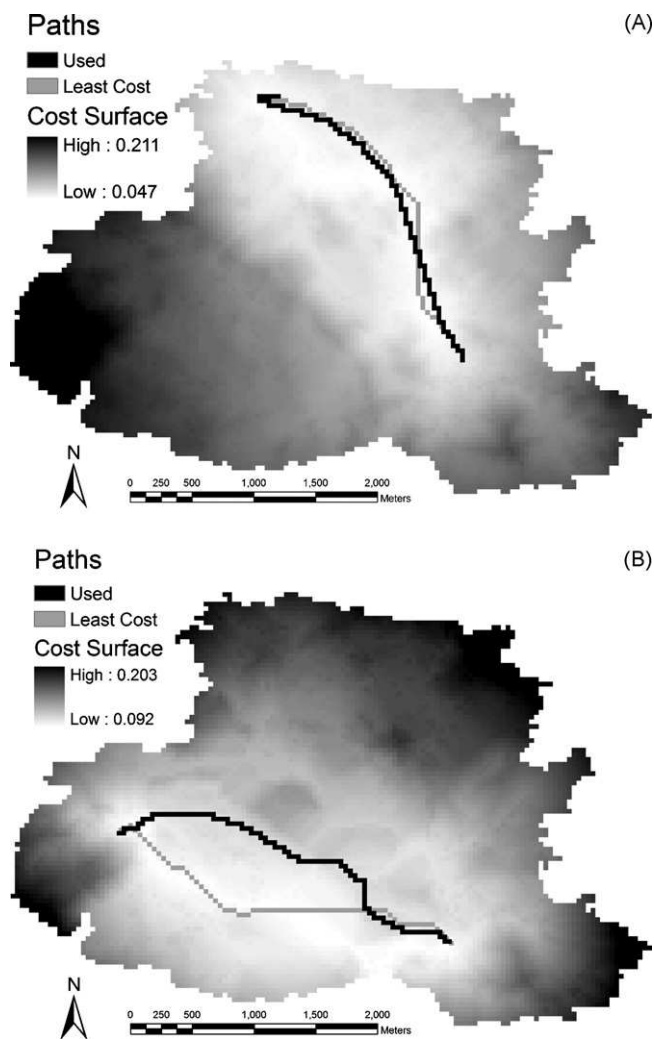


Fig. 7. (A) Using rates of EWL and cost-analysis to predict the movement of toad #31 across the Stamp Meadows landscape. (B) Using rates of EWL and cost-analysis to predict the movement path of toad #78 across the Stamp Meadows landscape.

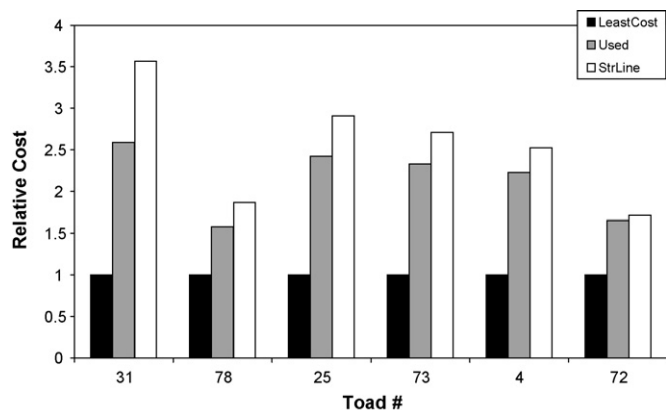


Fig. 8. Differences in relative costs of paths across the Stamp Meadows landscape. Because total distances traveled by toads were different, the costs of paths for each toad were standardized by the cost for its least-cost path to allow comparisons. Except for toad #78, as the total distance traveled by a toad decreased, so did the differences in cost between the three paths. From location to location, the care employed by toads to select lower cost travel paths may be small, but this difference becomes more important over longer distances.

briefly entered the range of the critical thermal maximum for *A. boreas* (Brattstrom, 1968). Why the mid-day T_e for the shrub habitat dipped briefly is unclear to us.

Computer models cannot capture the totality of natural variation. Comparing the T_e data recorded in the field among various habitats for a day to that calculated by Niche Mapper using weather data collected on the same day, Niche Mapper did not replicate the exact shading pattern of different habitats. For example, it did not replicate the periodic sun flecks as they moved across the physical models, briefly warming them. With the broader goal of modeling conditions across a landscape, however, capturing such minute details as periodic sun flecks may be less important than characterizing daily conditions available to amphibians in different habitats. Comparing the number of hours T_e was within different temperature ranges, Niche Mapper was within 1 h of the actual field data in 69% (11 out of 16) of the measurements. Because of our modification of correcting for shade change due to angle for this particular study site, the calculated estimates of EWL were very close to the measured field data.

4.3. Reclassifying the landscape

4.3.1. Habitat use

Comparing our results to those of Bartelt et al. (2004), we consider Niche Mapper to be a robust approach for modeling the distribution of suitable toad daily habitats across this landscape, because our modeling results closely reflect the actual patterns observed in these toads. For example, clear habitat selection patterns were discernable for female toads, but not male toads, because male toads remained within the vicinity of the breeding pond and this probably released them from the need to carefully conserve their body water. In Bartelt et al. (2004) and this study, the predictive models for females were stronger than those for males.

4.3.2. Movements

Using cost-analysis to predict the dispersal movements of these toads may have only limited value, because they moved primarily at night when temperatures were cooler and relative humidity was higher (Bartelt et al., 2004; Sullivan et al., 2008). Connecting sequential locations with straight lines very likely excludes much detail in their movement paths. In addition, the pattern evident in Fig. 8 (diminishing differences between used and straight-line paths as the total difference decreased) suggests that the cost of the path used by toads is more a function of distance traveled, rather than any discerning behavior of the toads. On the other hand, these differences also may suggest that while the toads did select sites with lesser costs, the differences, while real, were small and accumulated over longer distances. Regardless, given that a 60 g, free-ranging toad does not have the same total landscape perspective as does a computer, the spatial distribution of the idealized, least-cost paths compared to the paths used by toads suggests that this approach holds value. For example, although the path followed by toad #78 (Fig. 7B) did not closely follow the least-cost path, it does follow a least-cost corridor. Exceptions (i.e., near the west end of the path) occurred on rainy days when daytime activity costs were reduced.

4.3.3. Global climate change: an application

Like any other taxon, amphibians do not tolerate habitat modification/change well. Habitat loss and fragmentation is credited for being a principle (if not the most important) factor contributing to amphibian population declines (Green, 1997; Noss et al., 1997), and Gallant et al. (2007) suggests that continued trends of human population growth and resource use will continue the loss of habitat.

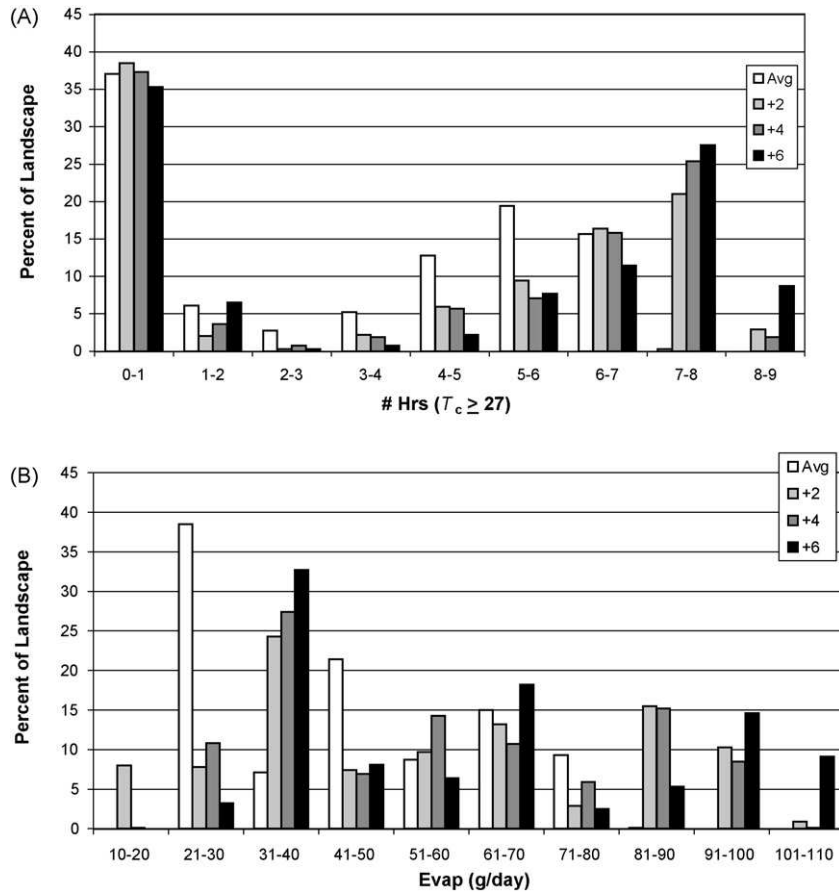


Fig. 9. The estimated effect of global warming on the Stamp Meadows landscape for toads, expressed as a percentage of the total landscape. (A) Niche Mapper predicts an increase in the percentage of the landscape where toads could achieve and maintain a warm body temperature ($T_c > 27$). (B) The rate of evaporation also will increase over a larger proportion of the landscape.

While the loss of habitat is an extreme change, what might be the effect of subtle changes (such as climate warming) in seemingly intact habitats on amphibians? The answer, of course, depends on the extent of change, but results from this study suggest that the Stamp Meadows landscape would become less friendly to toads by making it more difficult for them to balance their thermal and hydrological needs. Although a greater proportion of Stamp Meadows would support warmer body temperatures under climate warming (Fig. 9A), a greater proportion also would experience

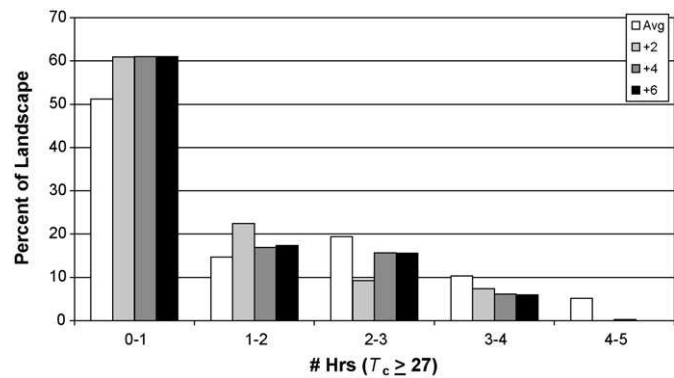


Fig. 10. The estimated effect of global warming on the Stamp Meadows landscape for toads. These results suggest that, because of increased rates of evaporation, less of the landscape would facilitate a toad's ability to maintain a warm body temperature ($T_c > 27$). Such an effect could reduce the connectivity of the landscape for toad movements, and/or reduce the amount of a toad's daytime activity (e.g., foraging and basking).

greater amounts of EWL (Fig. 9B). When combined, a toad would be more constrained in maintaining warmer body temperatures and suitable hydration levels (Fig. 10); this would translate into reduced activity hours that could impact growth and reproductive potential for both individuals and populations. Constraining the amount of time that toads could maintain warm body temperatures would reduce their amounts of time for activities such as basking and foraging, which could also reduce physiological function including growth rates or the ability to produce eggs. For example, juvenile toads allowed access 5 h/d grew (snout-vent-length; SVL) four times faster over eight weeks than those allowed access to heat for only 1 h (Lillywhite et al., 1973). Similarly, P.S. Corn (pers. commun., 2007) measured growth (SVL) of brown morph leopard frog (*Rana pipiens*) metamorphs in Colorado as a function of degree-days. He estimated that a 20% change in degree-days would result in a 25% change in growth. Our study suggests a reduction by up to 40% for the amount of time that toads could effectively maintain a body temperature $\geq 27^\circ\text{C}$ (in effect, reducing its degree-days). Using the measurements of Lillywhite et al. (1973) and Corn, this could translate into a reduction in growth of up to 50%. While we don't know if adult toads would experience this much reduction, it seems clear their growth rates could be negatively affected under global warming.

The vulnerability of amphibians to certain diseases may also be exacerbated by climate change. A warming climate might affect the spread and incidence of *Batrachochytrium dendrobatidis*, a major and deadly pathogen of amphibians (Voyles et al., 2009). Our modeling approach may help address this relationship (e.g., Pilliod et al., 2010).

Increasing the physiological cost of a landscape could also affect amphibian populations by affecting dispersal patterns and metapopulation structure. Because frogs and toads may travel kilometers overland to reach other ponds, foraging areas, hibernacula, etc. (e.g., Pilliod et al., 2002; Muths, 2003), habitat fragmentation could be an important factor in amphibian population declines (Laan and Verboom, 1990; Funk et al., 2005). Before climate warming affects plants directly and alters the physical structure of habitats, results from this study suggest that microenvironmental conditions could be altered sufficiently to increase the cost of movements or diurnal activities such as foraging. Habitats may not be physically fragmented, but from an amphibian perspective, they could be “thermally fragmented.”

A different set of results could be produced under a different set of assumptions. Because the long-term Island Park data showed a very small difference in rainfall compared to, 1993 conditions, we assumed negligible differences in atmospheric moisture for the climate scenario tests. If rainfall increases proportionally to increases in temperature, then the resulting warming and more humid microenvironmental conditions of habitats might reduce the physiological cost of amphibian terrestrial habitats. On the other hand, in areas where rainfall and moisture is predicted to decrease (e.g., large portions of western and south-western U.S.), the physiological cost of landscapes could greatly increase.

5. Conclusions

A careful comparison of laboratory and field experimental data against Niche Mapper shows that robust estimates of body temperature, water loss rates, and likely movement and habitat use patterns of *A. boreas* on the landscape can be obtained knowing only measurable landscape and animal properties. We are working with other populations in other areas (central Idaho, Yellowstone National Park, northern Midwest) to begin assessing the applicability of these results to this and other species (*Rana luteiventris*, *R. pipiens*, *Anaxyrus americanus*).

The effect of a warming climate on these wet-skinned ectotherms depends also on changes in atmospheric moisture patterns. Under the assumptions of this study, relatively constant atmospheric moisture could accentuate drying conditions and further stress amphibians. A warmer climate with greater amounts of atmospheric moisture could benefit these wet-skinned ectotherms by reducing physiological costs. The resulting warmer T_c s might also reduce the incidence of chytridiomycosis (Woodhams et al., 2003; Rohr et al., 2008), although a connection between warmer T_c s and chytridiomycosis is uncertain (Pilliod et al., 2010). *A. boreas* can adapt to habitat change (e.g., fire; Hossack and Corn, 2007), provided water sources (Hossack and Corn, 2008) or adequate protective cover (Bartelt et al., 2004) are available. Our mechanistic modeling suggests that projections of consequences of climate change for toads and their climate constrained distribution limits in the future can be assessed reliably within the confidence limits of global climate simulations that drive these mechanistic models. Analogous calculations for Tuataras on coastal islands of New Zealand (Mitchell et al., 2008), Hawaiian honeycreepers on Maui (Porter et al., 2006), the endangered Japanese Serow deer on Honshu (Natori and Porter, 2007), cane toad and the mosquito, *Aedes aegypti* in Australia (Kearney et al., 2008, 2009) using the same software package suggest that this approach is robust for simulations of animals' energetics, behavior and distribution limits in the geological past, current climatic conditions and future climate events. As these calculations have also shown, different critical variables apply to different species depending on their properties, the properties of the landscapes that harbor them and the questions being asked.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2010.07.009.

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