



The importance of assessing parameter sensitivity when using biophysical models: a case study using plethodontid salamanders

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Abstract Landscapes are continually changing due to numerous assaults, including habitat alteration, anthropogenic disturbances, and climate change. Understanding how species will respond to these changes is of critical importance for conservation and management. Mechanistic models, such as biophysical models (BPMs), are an increasingly popular tool to predict how local population dynamics or species' distributions may be altered in response to environmental and climate changes. By mechanistically modeling relationships between environmental conditions, physiology and behavior, it is possible to make accurate predictions about how species may respond. However, BPMs are often difficult to implement due to lack of appropriate, species-specific data that is biologically realistic or relevant. In this study, we present a BPM for the salamander *Plethodon jordani* and assess how adding more biological realism has potential to alter model predictions about annual energy budgets. Additionally, we conducted local and global sensitivity analyses to evaluate the importance of accurately specifying model parameter values and functional relationships. We found that the addition of biological realism resulted in greater model complexity as well as substantially different estimates of energy balance. Correct parameterization of biophysical models is also critical, as small changes in parameter values can result in disproportionately large changes in downstream model estimates. Our model highlights the overall importance of using ecologically relevant and specific data for input parameters, as well as careful

assessment of parameter sensitivity. We encourage researchers to be aware of the data they are using to parameterize BPMs, and urge the collection of system-specific data that is relevant in spatial and temporal scale. We also recommend greater and more transparent use of sensitivity analyses to provide a better understanding of the model, as well as greater confidence in model predictions.

Keywords Biophysical model · Energy budget · Global sensitivity · Mechanistic model · *Plethodon* · Sensitivity analysis

Introduction

Understanding how abiotic and biotic factors affect the behavior and distribution of species across a landscape is critically important to inferring how species may persist in the future. Factors such as habitat loss and fragmentation, anthropogenic pressures, exotic invasions, emerging disease, among many others, are reshaping current geographic distributions of many species, both plant and animal (Wilcove et al. 1998; Parmesan and Yohe 2003). Global climate change has received a considerable amount of attention regarding its impacts on species distribution. In response to a warming climate, species have been found to shift across both latitude (Parmesan and Yohe 2003) and elevation (Moritz et al. 2008), thereby expanding and/or contracting historic species' ranges and distribution. The ability to predict how distribution and potential ranges may shift in the face of global climate change is critical to the conservation and management of at-risk species, and a number of tools have been developed to forecast future range shifts.

Environmental niche modelling has emerged as one of the primary methods for predicting both constraints and

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responses of a species to a changing environment, which depends on both abiotic and biotic factors (Elith and Leathwick 2009; Morin and Thuiller 2009). However, the usefulness of such models depends on the type and level of accuracy of the data used. Both correlative and mechanistic approaches have been used to effectively model variations and changes in contemporary species under predicted climate change scenarios (reviewed in Kearney and Porter 2009; Morin and Thuiller 2009). Correlative models relate occurrence data (presence only or presence/absence) to spatial and environmental data, and attempt to model and forecast possible range shifts. Correlative models have been widely used across taxa because they require little species-specific data and have therefore, relatively abundant and easily accessible data (Morin and Thuiller 2009). Yet, correlative models exclude potentially important processes and mechanistic effects that may dictate distribution and limit ranges of species (Kearney and Porter 2009). Mechanistic models, such as biophysical models (BPMs), link species-specific parameters, such as dispersal ability, demographic traits, physiological traits, species interactions, evolutionary history, and adaptation with relevant climatic data (Kearney and Porter 2009; Riddell and Sears 2015; Urban et al. 2016). Biophysical models explicitly seek to mathematically model biological processes through mechanistic relationships of physical processes and the environment using basic laws of physics, such as heat and mass transfer. Thus, BPMs explicitly relate processes that constrain species with the climate they specifically experience (Kearney and Porter 2009).

BPMs are increasing in popularity, especially with open-access data repositories that provide greater availability to data and previous models (Kearney et al. 2014). However, parameterization and implementation of these models is still difficult. By virtue of mechanistic models, obtaining greater amounts of detailed information per species is required to fully parameterize a species-specific model. Lack of such data, or uncertainty in parameters, can lead to inaccurate predictions (Buckley et al. 2010). Often, the data used for model parameterization is from either small-scale lab studies or small and limited data sets (e.g., Kearney et al. 2009; Gifford and Kozak 2012). For example, Buckley et al. (2010) used minimal activity time for population persistence in the lizard species *Sceloporus undulatus* as a parameter in their BPM, which has not been reliably measured in the field. Due to limited available data, Gifford and Kozak (2012) used the same surface active thermal ranges for salamander species that are currently found at different elevations to model energy budgets and population dynamics. Further, despite genetic variability and physiological and behavioral plasticity observed in species across their ranges (Sultan 2000; Angilletta 2001; Kolbe et al. 2014; Seebacher et al. 2015), few studies have incorporated such range-wide variation into BPMs (but see Buckley 2008). Parameterizing

BPMs with readily available existing data likely does not wholly or accurately reflect the biological constraints of a particular species (see Urban et al. 2016 for review), and there is an immediate need to collect data that accurately represents biological mechanisms of species' in relation to their environment.

An important factor in formulating accurate and descriptive models of any kind is assessment of the sensitivity of parameters used in a model. Local sensitivity analyses vary one input parameter while holding all others constant to understand downstream effects of the varying parameter on model predictions (Confalonieri et al. 2010), while global sensitivity analyses seek to assess the contribution of each parameter as they interact with all other parameters (Saltelli et al. 2008). Understanding the sensitivity of each parameter can provide greater insight into the influence of a particular parameter, and emphasizes the importance of accurately determining parameter values (Confalonieri et al. 2010). The value of sensitivity analyses has been previously demonstrated in the context of BPMs (Mathewson and Porter 2013; Fitzpatrick et al. 2015), but sensitivity analyses in BPM studies to date have generally been vague or lack quantitative details of how varying input parameters impacts model outputs (Jonsson et al. 2008; Buckley et al. 2010; Gifford and Kozak 2012; Sears et al. 2016). To better understand such effects, and to accurately parameterize models, a greater amount of specific empirical data on the species of interest, in the region of interest, must be obtained (Urban et al. 2016).

The need for including more biological realism in BPMs is of utmost importance for accurate predictions of species' responses to climate change. The present paper investigates a plethodontid salamander species and assesses parameterization and sensitivity of parameters influencing the frequency and duration of salamander surface activity and energy balance: factors that likely limit their elevational and geographic ranges. It is anticipated that plethodontid salamanders will be substantially impacted by climate change as a consequence of their unique physiology and specific habitat requirements (Wells 2007), and correlative models have predicted significant contraction of species' ranges or complete loss of species as a consequence of climate change (Milanovich et al. 2010). Plethodontid salamanders are lungless and respire cutaneously (Gatz et al. 1975). Due to their unique physiological requirements, plethodontid salamanders generally inhabit cool, moist habitats and can have limited or periodic surface activity. The duration or frequency of surface activity is likely to influence foraging, movement, and mating behaviors, which consequently can affect individual survival and population persistence (Feder 1983; Feder and Londos 1984). The behavior and physiology of plethodontids is strongly driven by environmental variables such as rainfall, temperature, elevation, slope, aspect,

and leaf litter cover; all of which vary across a species range. For example, different plethodontid species have variable aggressive interactions and responses given temperature and elevation (Nishikawa 1987; Anthony et al. 1997; Clay and Gifford 2016), and physiological resistance to water loss can also vary across elevation (Riddell and Sears 2015). Here, we modify and extend an existing BPM by including more relevant behavior, and demonstrate how varying critical parameters can influence model inferences for *Plethodon jordani* (Blatchley). We also stress the importance of collecting empirical, species-specific data for model parameterization, as well as incorporation of sensitivity analyses to better understand the influence and parameters on model outputs.

Methods

Model description

The mechanistic model used in this study was adapted from Gifford and Kozak (2012), hereafter referred to as the G-K model. The G-K model was developed as a spatial model to estimate annual energy budgets of two terrestrial plethodontid salamander species in the Great Smoky Mountains, USA to understand the biotic and abiotic factors constraining their distribution. Operative body temperature, food consumption, metabolic rate, and water loss were modeled as functions of environmental conditions (e.g., relative humidity, air temperature, wind speed). The spatial variation in the estimated annual budget of the G-K model for *Plethodon jordani* generally conformed to the known distribution of the species in the field (Dodd 2004; Gifford and Kozak 2012). However, the G-K model makes several simplifying assumptions about salamander behavior. A driving motivation for this study was to incorporate more relevant behavior into G-K biophysical model. First, the G-K model assumes that salamanders are surface active during all nighttime hours that conform to the temperature range that salamanders can be active (3–20 °C in the G-K model). This generally does not align with our field experiences in this system, or with the literature. Connette and Semlitsch (2015) found that the probability of surface activity declined with days since rainfall. Therefore, we propose modeling surface activity as a probabilistic function of days since rain. Additionally, the G-K model assumes a fixed and constant threshold of water loss (10%). Riddell et al. (2016) used a much more conservative value (3.8%), and results from Feder and Londos (1984) suggest that the maximum dehydration deficit a salamander will tolerate can vary as a function of the vapor pressure gradient. In short, the pattern observed by Feder and Londos (1984) suggests that if salamanders are losing water at a high rate (as a result of a large vapor pressure gradient), then they will forego surface activity at a lower dehydration threshold than when the rate of water loss is more

moderate. In this study, we assess both the sensitivity to varying the fixed dehydration threshold as well as incorporate a function to relate the maximum dehydration threshold with the vapor pressure gradient of the atmosphere. Finally, the original G-K model borrows foraging and digestive efficiency relationships from studies of a distantly related plethodontid salamander, *Plethodon cinereus*. A more relevant performance curve describing the amount of energy assimilated as a function of temperature is now available for *P. montanus* (Clay and Gifford 2017), a species more functionally and genetically similar to *P. jordani*, our focal species in this study (Kozak and Wiens 2010).

Our modified G-K model estimates annual foraging time (hours), energy consumption (kJ), energy expenditure (kJ), and energy balance (kJ). In this study, we focus primarily on energy balance as a response when conducting sensitivity analyses. These estimates are derived from three interacting submodels: (1) an environmental temperature submodel; (2) an operative body temperature submodel; (3) an activity submodel. Hourly air and soil temperatures were estimated from daily maximum and minimum temperatures (Campbell and Norman 1998). Because salamanders readily seek refuge underground during the day or when inactive at night (Petranka 1998), soil temperatures were calculated at the surface and at 30 and 100 cm below the surface (Campbell and Norman 1998). Salamanders were assumed to be at a depth of 30 cm below ground when ceasing activity during suitable nighttime conditions, and were otherwise assumed to be at a depth of 100 cm when not surface active. Salamander operative body temperature was calculated from these modeled temperatures using standard equations for absorbed and emitted radiation (Gates 1980; Campbell and Norman 1998), as detailed in equations in Table 1 as well as the Appendix of Gifford and Kozak (2012). We assume a constant wind speed of 0.1 m/s, measured at the height of a salamander (5 mm). We have made no further modifications to how operative body temperature is calculated by the G-K model, and therefore refer readers to the Appendix of Gifford and Kozak (2012) for the full description of all equations, parameters, and their modeled values. Potential activity time was then modeled as a function of days since rainfall, temperature, and dehydration state (Feder and Londos 1984; Connette and Semlitsch 2015). The probability that a salamander is surface active, p_a , was modeled as.

$$\text{logit}(p_a) = 0.75 - 0.34 \times \text{dry}, \quad (1)$$

where dry is the number of days since a rainfall of ≥ 5 mm (O'Connor et al. 2006). This relationship was adapted from Connette and Semlitsch (2015), who studied the closely related *P. shermani*. Surface activity, S_A , was then stochastically determined:

$$S_A \sim \text{Bernoulli}(p_a) \quad (2)$$

Table 1 Functions used to model mechanistic biophysical relationships. More detailed descriptions of functions can be found in the references provided

Parameter	Function	Equations	References
Operative environmental temperature	$T_e = T_a + \frac{R_{abs} - \epsilon \sigma (T_a + 273.15)^4}{c_p(g_r + g_{Ha})}$		Bakken 1992; Campbell and Norman 1998; Gifford and Kozak 2012
Radiation absorbed by animal	$R_{abs} = \alpha_L(F_a L_a + F_g L_g)$		Gates 1980; Campbell and Norman 1998; Gifford and Kozak 2012
Radiative conductance	$g_r = \frac{4\sigma(T_a + 273.15)^4}{c_p}$		Campbell and Norman 1998
Boundary layer heat conductance	$g_{Ha} = 1.4 \times 0.135 \sqrt{\frac{u}{d}}$		Campbell and Norman 1998 Mitchell 1976
Clear atmosphere emissivity	$\epsilon_{ac} = 9.2 \times 10^{-6} (T_a + 273.15)^2$		Gifford and Kozak 2012; Swinbank 1963
Probability of surface activity	$\text{logit}(p_a) = 0.75 - 0.34 \times dry$	(1)	Feder and Londos 1984 Connette and Semlitsch 2015
Surface activity	$S_A \sim \text{Bernoulli}(p_a)$	(2)	
Duration of activity	$\text{logit}(d) = -2.541 - 1.511 \times VPG$	(3)	Feder and Londos 1984
Vapor pressure gradient	$VPG = (vp_s - vp) \times 0.001$	(4)	
Saturation vapor pressure density	$vp_s = a \times \exp\left(\frac{bT_a}{T_a + c}\right)$	(5)	Campbell and Norman 1998
Vapor pressure as a function of the minimum daily temperature	$\exp(vp) = 6.457 + 0.0657 \times T_{mn}$	(6)	This study
Snout-vent length (SVL, mm)	55		Kozak et al. 2009
Salamander surface area (cm ²)			Whitford and Hutchinson 1967
Energy assimilation (E_a , kJ ^{-hr})	$E_a = a \times \left(\frac{b-T_b}{b-c} \times \frac{T_b}{c} \frac{c}{b-c}\right) \times \left(\frac{m}{24}\right)$	(7)	Clay and Gifford 2017
Mass (m , g)	$m = 4599.1 \times (SVL \times 0.001)^{2.5297}$	(8)	Gifford and Kozak 2012
Resting metabolic rate*	$\log_{10}MR = 0.036 \times T_b + (0.57 \times \log_{10}m) - 1.95$	(9)	Gifford and Kozak 2012
Energy expended	$E_{out} = MR \times 0.001 \times k \times J$	(10)	
Annual energy balance	$E_b = E_a - E_{out}$	(11)	
Activity temperature range (°C)	5–25		Feder et al. 1982

Equation refers to the equation number in the main text

*Active metabolic rate modeled as $MR \times 1.375$ (Bennett and Houck 1983)

If $S_A = 1$, a salamander was considered active during nighttime hours if the air temperature was between 5 and 25 °C (Petranka 1998). The duration that a salamander remains active is a function of percent dehydration deficit (d), and the dehydration deficit that a salamander will endure before ceasing surface activity was modeled as a function of vapor pressure gradient (VPG), measured in kilopascals:

$$\text{logit}(d) = -2.541 - 1.511 \times VPG. \quad (3)$$

This relationship was derived from data presented in Feder and Londos (1984) in their study of *Desmognathus ochrophaeus*. VPG was calculated as:

$$VPG = (vp_s - vp) \times 0.001, \quad (4)$$

where vp_s is the saturation vapor pressure density of air measured in pascals, and vp is the vapor pressure of the air measured in pascals. Saturation vapor pressure density

was estimated using Teten's formula (Campbell and Norman 1998):

$$vp_s = a \times \exp\left(\frac{bT_a}{T_a + c}\right), \quad (5)$$

where $a = 610.78$ pascals, constant $b = 17.502$, constant $c = 240.97$ °C, and T_a is the air temperature in degrees Celsius. The vapor pressure density of air, vp , was estimated using a function derived from data downloaded from the Daymet climate database (Thornton et al. 2014). Daily climate data downloaded from the Daymet database has a daily average partial pressure of water vapor, measured in pascals. We used this estimate to derive a general equation ($R^2 = 0.998$) to estimate vapor pressure as a function of the minimum daily temperature in degrees Celsius (T_{mn}):

$$\exp(vp) = 6.457 + 0.0657 \times T_{mn}. \quad (6)$$

Spotila and Berman (1976) describe plethodontid salamander skin as a free water surface, and we modeled evaporative water loss in this manner, as detailed in Gifford and Kozak (2012). However, it should be noted that Riddell and Sears (2015) found that plethodontid salamander skin does exhibit a resistance, and that resistance to water loss appears to be a plastic trait. Further, Riddell et al. (2016) demonstrated that the boundary layer can significantly attenuate water loss. The total hours that a salamander was surface active (S_t) on a given night was determined as the total time until the dehydration deficit, d (Eq. 3), was reached, it was no longer nighttime, or temperatures were no longer suitable.

Our mechanistic model assumes that only surface active salamanders are foraging. As described by Clay and Gifford (2017) for the closely related *P. montanus*, energy assimilation (E_a , $\text{kJ}^{-\text{hr}}$) is a function of operative body temperature T_b , in degrees Celsius, using a beta performance curve:

$$E_a = a \times \left(\frac{b - T_b}{b - c} \times \frac{T_b^{\frac{c}{b-c}}}{c} \right) \times \left(\frac{m}{24} \right) \times S_t, \quad (7)$$

where a controls the maximum assimilation (0.107 kJ/g/day), b is the critical maximum temperature of the performance curve (33 °C), c is the optimal temperature for assimilation (22.7 °C), m is the mass of a salamander in grams, and S_t is the hours of surface active foraging time. Mass (m) was estimated using a function derived from empirical standard length (SVL , mm) and mass data collected on *P. jordani* (Gifford and Kozak 2012):

$$m = 4599.1 \times (SVL \times 0.001)^{2.5297}. \quad (8)$$

We set SVL equal to 55 mm, as used by Gifford and Kozak (2012). Metabolic rate, MR (oxygen consumption, $\text{ml}^{-\text{hr}}$), was calculated as

$$\log_{10} MR = 0.036 \times T_b + (0.57 \times \log_{10} m) - 1.95. \quad (9)$$

This relationship was derived for *P. jordani* by Gifford and Kozak (2012). We assume that the metabolic rate is 1.375 times greater when salamanders are active than when resting (Bennett and Houck 1983). The amount of energy expended by salamanders ($\text{kJ}^{-\text{hr}}$) was determined as

$$E_{out} = MR \times 0.001 \times k \times J, \quad (10)$$

where MR is converted to liters $^{-\text{hr}}$ and k is the number of kilocalories in 1 l of oxygen (5.0 kJ), and J is the amount of energy in 1 kcal (4.184 kJ). Annual energy balance (E_b , kJ) was then determined as:

$$E_b = E_{in} - E_{out}. \quad (11)$$

Equations and relevant references can be found in Table 1.

Data and modeling procedures

We obtained daily climate data for 1 January 2014–31 December 2014 from the Newfound Gap NOAA weather station (35°36'39"N, 83°25'44"W, elevation = 1536 m), located within Great Smoky Mountains National Park (Menne et al. 2012a, b). This weather station is located in the core of *P. jordani*'s elevational and geographic range (Dodd 2004), so the location is expected to be highly suitable for *P. jordani*. Temperature data from this weather station were collected at a height of 2 m above the ground, which may result in higher temperatures or greater daily fluctuation in temperature than near-ground temperatures typically encountered by salamanders. We therefore adjusted air temperatures to 5 mm above the ground following the correction used in NicheMapR (Kearney 2016), assuming 75% shade. This adjustment equation ($T_{ng} = 0.249 + 1.022T$; $R^2 > 0.999$) resulted in a nearly perfect relationship between weather station temperature (T) and near ground temperature (T_{ng}). For scenarios that modeled surface activity as a probabilistic function of time since rain (Eqs. 1, 2), we ran 1000 iterations of our model, calculating the mean and 95% confidence intervals of annual foraging time, energy consumption, energy expenditure, and energy balance. Prior to the sensitivity analysis, we ran four different permutations of our model to assess how the inclusion of context-dependent behavior affected output estimates: (1) salamanders are always surface active, maximum dehydration deficit fixed at 7.5% (average deficit in saturated air measured by Feder and Londos 1984); (2) salamanders are always surface active, maximum dehydration deficit variable and dependent on vapor pressure gradient; (3) surface activity dependent on time since rain, maximum dehydration deficit fixed at 7.5%; (4) surface activity dependent on time since rain, maximum dehydration deficit variable and dependent on vapor pressure gradient (Table 2). We also compared the energy balance of our model parameterizations with the energy balance estimate made by Gifford and Kozak (2012) at the location of the Newfound Gap weather station.

Sensitivity analysis

We assessed the sensitivity of model outputs to changes in the probability of surface activity (intercept of Eq. 1), fixed maximum percent water loss, the relationship of maximum water loss with vapor pressure gradient (hereafter VPG -dehydration; intercept of Eq. 3), and each of the three parameters of the beta performance curve for energy assimilation (Eq. 7). We conducted local sensitivity analyses for each of these model parameters using a one-factor-at-a-time (OFAT) approach to determine how changing values of each parameter affected the estimated annual energy balance. Parameters were varied as detailed in Table 3: surface

Table 2 Summary of BPM outputs for four different combinations of surface activity and maximum dehydration assumptions

Model settings	Foraging time (h)	Energy assimilated (kJ)	Energy expended (kJ)	Energy balance (kJ)
Surface activity: always active Percent dehydration: fixed (7.5%)	2954	22.62	11.57	11.05
Surface activity: always active Percent dehydration: variable ^a	1778	12.46	11.29	1.17
Surface activity: variable ^b Percent dehydration: Fixed (7.5%)	1178 (1018, 1346)	9.18 (7.72, 10.62)	10.94 (10.88, 11.01)	−1.76 (−3.16, −0.38)
Surface activity: variable ^b Percent dehydration: variable ^a	734 (622, 856)	5.19 (4.36, 6.07)	10.84 (10.79, 10.88)	−5.65 (−6.43, −4.81)

When surface activity was modeled as variable, the model was run for 1000 iterations, with mean and 95% confidence intervals of model outputs reported

^aMaximum percent dehydration deficit is a function of vapor pressure gradient (Eq. 3)

^bProbability of surface activity is a function of days since rainfall ≥ 5 mm (Eq. 1)

Table 3 Parameters assessed in one-factor-at-a-time sensitivity analyses

Parameter	Units	Equations	Modeled value	Sensitivity range	Energy balance range (kJ)
Surface activity probability	Probability (0–1)	(1)	0.750	0.50 to 0.98	−4.68 to 7.90
VPG-dehydration	Percent	(3)	0.073	0.015 to 0.150	−8.94 to 10.15
Maximum dehydration	Percent	NA	0.075	0.015 to 0.150	−6.28 to 11.28
<i>a</i> —Maximum assimilation	kJ/g/day	(7)	0.107	0.050 to 0.150	−0.96 to 20.04
<i>b</i> —Critical maximum temperature of beta performance curve	Degrees Celsius	(7)	33	25 to 36	−6.07 to 14.23
<i>c</i> —Optimal assimilation temperature	Degrees Celsius	(7)	22.7	15 to 25	3.48 to 24.28

Equation refers to the equation number in the main text. The modeled value is the value for each parameter used during BPM assessment and sensitivity range indicates the range of values assessed. Energy balance range demonstrates how annual energy budget, measured in kJ, was affected during the sensitivity analysis

activity probability from 0.50 to 0.98, percent VPG-dehydration from 0.03 to 0.15, maximum percent dehydration from 0.015–0.150, maximum energy assimilation from 0.05 to 0.15 kJ, critical maximum temperature from 25 to 36 °C, and optimal temperature for energy assimilation from 15 to 25 °C. All other parameters were held constant during sensitivity assessment. The ranges of values assessed for each parameter encompass plausible minima and maxima. The functional relationships of Eqs. 1 and 3 across the range of values assessed in the sensitivity analysis can be seen in Fig. 1.

In addition to OFAT, we also used global sensitivity analyses to assess how surface activity probability, VPG-dehydration, and the three beta performance curve parameters affected the annual energy balance (kJ). Specifically, we calculated Sobol' sensitivity indices using the R package 'sensitivity' (Baudin et al. 2016; Pujol et al. 2016). Sobol' sensitivity analyses are variance-based analyses that rely on Sobol' sequences to maximally cover parameter space (Saltelli et al. 2008). We used the Jansen method (Jansen 1999) to determine first and total order indices through Monte Carlo simulation estimation. First order indices report the variance explained by each parameter in isolation; total order

indices report the variance explained by each parameter plus its interaction with all other parameters.

Results

Annual foraging time and energy consumption were greatest when salamanders were active every night under suitable temperature conditions, and when they remain active until 7.5% of their body mass is lost through evaporative water loss (Table 2). This model estimates that salamanders will have a positive annual energy balance of 11.29 kJ. When the maximum dehydration deficit varies as a function of vapor pressure gradient, foraging time and energy consumption decline, and the annual energy balance is substantially reduced to 1.17 kJ. Modeling surface activity as a probabilistic function of time since rain with a fixed maximum dehydration deficit results in a further decline in foraging time and energy consumption (Table 2). As a consequence, there is a deficit of −1.76 kJ [95% CI (−3.16, −0.38) kJ] in the annual energy balance. The annual energy deficit increased to −5.65 kJ (−6.43, −4.81 kJ) when both surface activity and maximum dehydration deficit were modeled as functions

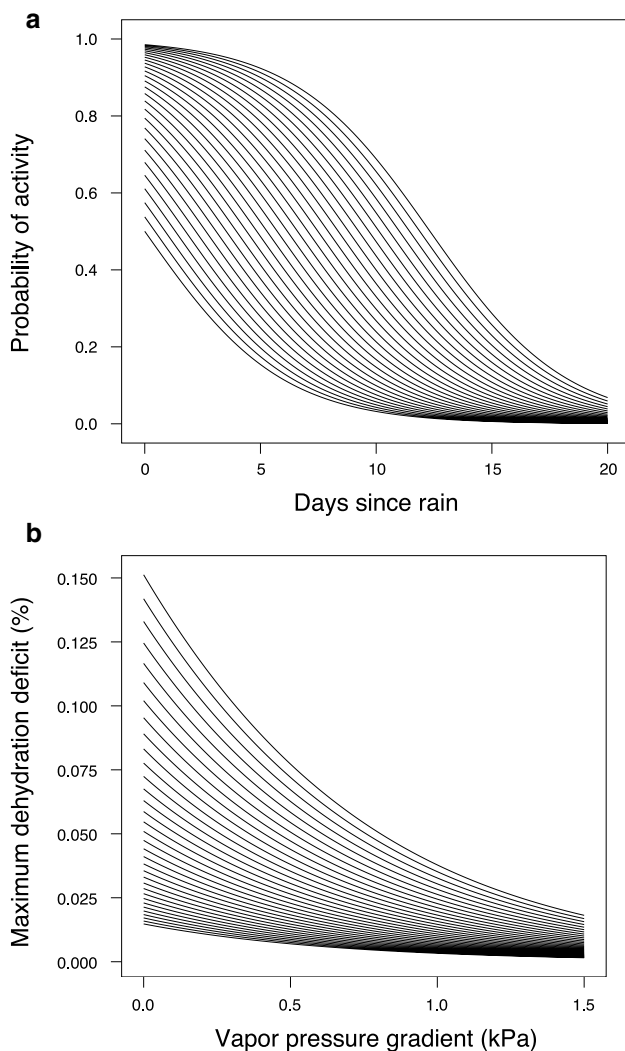


Fig. 1 Response plots demonstrating the range of values assessed during sensitivity analyses. The probability of surface activity, panel **a**, was modeled as a function of days since a rain event ≥ 5 mm (Eq. 1), with probability values ranging from 0.500 to 0.980 when time since rain is equal to zero. This relationship was adapted from Connette and Semlitsch (2015). **b** shows the relationship between vapor pressure gradient and the maximum dehydration deficit a salamander will undergo before abandoning surface activity. Maximum dehydration ranged from 0.015 to 0.150 when the vapor pressure gradient was equal to zero. This relationship was adapted from Feder and Londos (1984)

of climatological parameters (Table 2). As a comparison, the energy balance for this location in Great Smoky Mountains National Park was estimated to be 1.35 kJ by Gifford and Kozak (2012).

Our OFAT sensitivity analysis demonstrates that all six of the assessed parameters can substantially affect the calculation of annual energy balance (Fig. 2). Assuming the ranges of values assessed for each parameter are biologically relevant, annual energy balance can range from -7.5 kJ to nearly 25 kJ. Energy balance plateaued when assessing the

maximum percent water loss (Fig. 2a), and this is because salamanders could be surface active during all nighttime hours once the dehydration deficit threshold was $\geq 7.0\%$.

The global sensitivity analysis revealed that maximum percent water loss, as a function of vapor pressure gradient, was unequivocally the most influential parameter affecting annual energy balance, and this was evident when assessed in isolation and in combination with all other parameters (Table 4; Fig. 3). First order Sobol' indices indicate that 48% (42, 54% CI) of the variance in energy balance can be explained by the maximum percent water loss salamanders will endure, modeled as a function of vapor pressure gradient. This is ≥ 4.6 times more variation than any other parameter assessed (Table 4). Total order Sobol' indices indicate some support for the importance of interactions among the parameters assessed as the confidence intervals for most parameters exceeded the upper estimates for first order indices, and the sum of total order indices exceeded 1.0 (1.23).

Discussion

Biophysical models have tremendous potential to provide realistic predictions about biological responses to both fine-scale (e.g., habitat degradation) and large-scale (e.g., climate change) disturbances. However, accurate predictions from BPMs require detailed mechanistic understanding of behavior and physiology. The results of our study emphasize the potentially large effect of adding more ecological realism, but also the sensitivity of model outputs to parameter uncertainty. Simplifications of behavior and physiology can result in over- or underestimations of BPM model outputs. With the G-K model, using generalized salamander behavior and physiological parameters, such as all animals being surface active every night and animals remaining active up to a fixed dehydration threshold, resulted in energy estimates more than 10 times greater than if surface activity is variable and/or dependent upon time since rainfall (Table 2). Such findings underscore the need for studies designed to measure key model parameters, a sentiment echoed by Urban et al. (2016).

Intensive studies of plethodontid salamanders have convincingly demonstrated that salamanders are not surface active every night (Connette and Semlitsch 2015), and that nocturnal surface activity is affected by rainfall (Connette and Semlitsch 2013, 2015; Connette et al. 2015). Our inclusion of a function to relate surface activity with time since rain (Eq. 1) resulted in a negative energy balance (Table 2), which raises a number of questions. Is the 1 year of data modeled an aberrant year? Are salamanders expending more energy than they are consuming at this location? Is Eq. 1 appropriately parameterized? Is the functional relationship described in Eq. 1

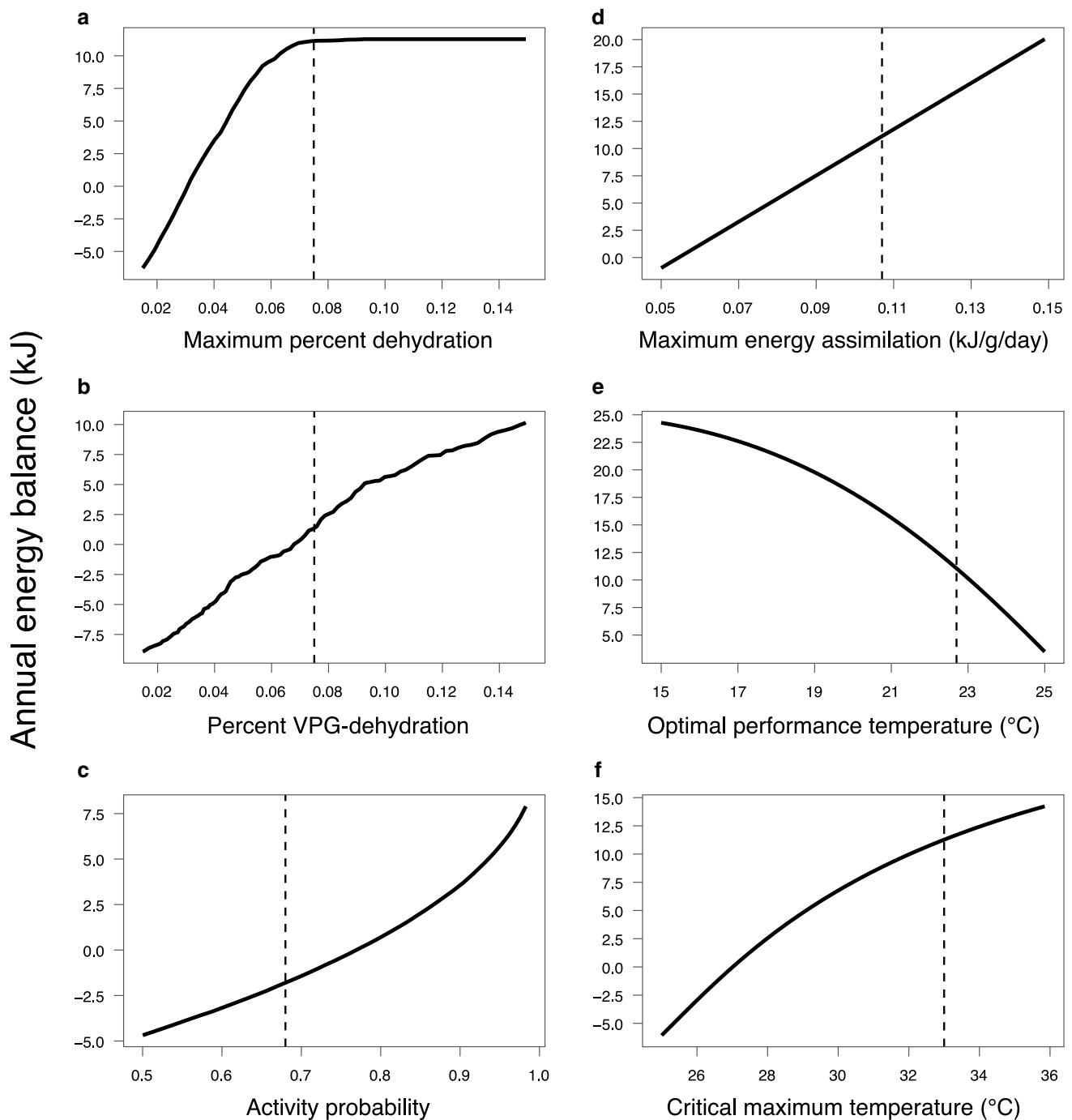


Fig. 2 Annual energy balance (kJ) estimated from sensitivity analyses of the biophysical model parameters maximum dehydration deficit, assuming salamanders are always active (**a**), maximum dehydration deficit as a function of vapor pressure gradient, assuming salamanders are always active (**b**), and probability of surface activity as a function of days since rain, assuming a fixed maximum dehydra-

tion deficit of 7.5% (**c**). The beta performance curve parameters of maximum energy assimilation (**d**), optimal performance temperature (**e**), and critical maximum temperature (**f**) were also assessed assuming salamander area always active with a fixed dehydration deficit of 7.5%. The *dashed vertical line in each plot* indicates the original modeled value of each parameter

correct? Are other functions in the BPM correct (e.g., energy assimilation, metabolic rate)? Answers to these questions are complex and difficult to answer, further

highlighting the challenges of using models that attempt to capture a greater range of, and more precise, biological realism.

Table 4 Summary table of variance explained and 95% confidence intervals for Sobol’ sensitivity analysis; a global sensitivity analysis conducted to assess the effect and contribution of surface activity probability, maximum water loss as a function of vapor pressure gradient, maximum energy assimilation, critical maximum temperature of beta performance curve, and optimal temperature for energy assimilation on the annual energy balance (kJ)

Sobal’ index	Parameter	Variance explained	95% CI
First order			
	Surface activity probability	0.042	0.000, 0.101
	VPG-dehydration	0.481	0.422, 0.542
	<i>a</i> —Maximum assimilation	0.068	0.003, 0.128
	<i>b</i> —Critical maximum temperature of beta performance curve	0.013	0.000, 0.074
	<i>c</i> —Optimal assimilation temperature	0.104	0.040, 0.165
Total order			
	Surface activity probability	0.155	0.130, 0.182
	VPG-dehydration	0.634	0.576, 0.694
	<i>a</i> —Maximum assimilation	0.179	0.152, 0.206
	<i>b</i> —Critical maximum temperature of beta performance curve	0.059	0.044, 0.073
	<i>c</i> —Optimal assimilation temperature	0.199	0.157, 0.235

First order indices report the variance explained by each parameter in isolation, and total order indices report the variance explained by each parameter plus its interaction with all other parameters

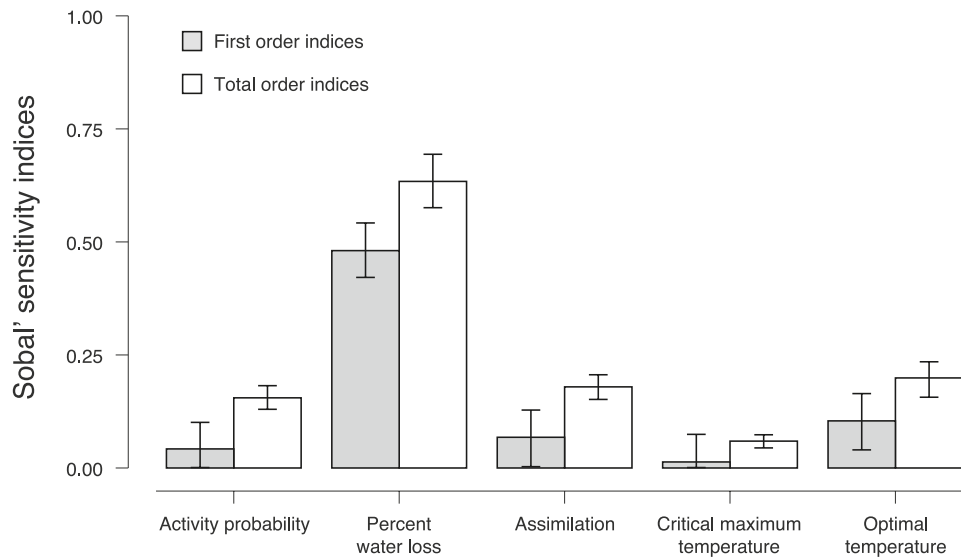


Fig. 3 Sobol’ sensitivity indices estimated from the global sensitivity analysis of five model parameters on the total annual energy balance (kJ): probability of surface activity (as a function of days since rain), maximum percent water loss (as a function of vapor pressure gradient), maximum energy assimilation of the beta performance curve, critical maximum temperature of the beta performance curve, and optimal temperature of the beta performance curve. First order indices

describe the variance in annual energy balance explained by each parameter in isolation, while total order indices describe the variance explained by each parameter plus its interaction with all other parameters. Global analyses were conducted with 2500 random combinations of these parameters. Mean index values are shown with error bars indicating the 95% confidence intervals determined from 1000 Monte Carlo iterations

Beyond our incorporation of more realistic behavior (i.e., variable surface activity and maximum dehydration deficit) and a more taxonomically relevant energy assimilation curve into the G-K BPM, other aspects should also be updated for future use. As demonstrated by (Riddell et al. 2016), accounting for boundary layer resistance to water loss may substantially increase activity time and energy balance estimates. Additionally, it is more biologically relevant to model humid operative temperatures for salamanders to account for the high rates of water loss, and consequent heat flux,

experienced by salamanders. It is possible that incorporation of these processes could result in a substantial increase in foraging time, and consequently, annual energy balance (Riddell et al. 2016). Future development of this model will seek to incorporate these features.

The sensitivity analyses used with our model showed that varying parameter inputs have the potential to change, sometimes drastically, model outputs. While changing the intercept of the functional relationship described in Eq. 3 resulted in moderate shifts in energy balance (Fig. 2b), Sobol’ indices

indicate that this parameter has >4 times an effect on energy balance than the other parameters when assessed in isolation, and >3 times the effect in combination with other parameters (Table 4; Fig. 3). Given that this relationship was originally described for a plethodontid salamander from another genus (*Desmognathus*) with a very different life history (i.e., biphasic life cycle), these findings should be interpreted with caution, but also highlight a deficit in our understanding of physiologically-mediated behavior in this system. Do terrestrial plethodontid salamanders from the genus *Plethodon* forego surface activity at a lower dehydration deficit when water is being lost at a rapid rate? Answering this question and understanding the relationship between maximum dehydration and vapor pressure gradients appears to be relevant and important to more accurately parameterizing BPMs for *Plethodon* spp. The apparent importance of water loss rate also reiterates the need for future models to accurately account for boundary layer effects (Riddell et al. 2016), as this can considerably attenuate water loss.

Including sensitivity analyses in BPMs is important for understanding how variation in inputs may impact downstream outputs, but they can also elucidate interesting interactions between parameters. Such analyses may also provide a method to decide the specific parameter inputs that will elucidate the clearest model results (Bonan 1991). For example, Bocci et al. (1997) used different model inputs when modelling sea grass in variable locations and environments due to the extreme sensitivity of respiration parameters. Using sensitivity analyses to determine the correct parameterization can critically contribute to more accurate and biologically relevant results. We therefore strongly encourage use of sensitivity analyses with BPMs, including presenting the analyses alongside the main model results. This can clearly and effectively be accomplished using tables similar to that of our Table 3 and Fig. 2 to explicitly show how changing a model parameter affects model outputs. Perhaps equally important are global sensitivity analyses, which can give insight into the partial and total contributions of model parameters. We found the variance-based Sobol' indices to be informative and to provide greater insight into our model than the OFAT sensitivity alone.

Absent from our model was any interaction with other sympatric salamanders. Gifford and Kozak (2012) did find that the inclusion of a competition coefficients in their model was necessary to accurately model the distribution of the low-elevation *P. tayahalee* living in association with *P. jordani*. However, at the elevation of the site assessed in our model, *P. jordani* is not directly in competition with another plethodontid salamander species (Dodd 2004). Nonetheless, species interactions are critical to understanding the effects of climate change on populations and should be included, when possible (Cahill et al. 2013). This also highlights another area of relevant research needed to

better parameterize models. Finally, critical model assessment requires empirical data to validate model outputs. For instance, Gifford and Kozak (2012) demonstrated that the number of surface active *P. jordani* increased with elevation, which also corresponded to increasing annual energy budgets. Such empirical data can be leveraged to determine the model parameter settings that best match observed patterns and behaviors.

There is tremendous power and potential for BPMs and other mechanistic models to provide realistic biological and ecological predictions (Buckley et al. 2010). However, the need for precise specification of model parameters poses considerable challenges to their practical application. In some instances, it may be possible to specify model parameters based on studies of closely related species. For example, Kearney et al. (2008) parameterized some aspects of their model for *Bufo marinus* based on parameters derived from the leopard frog, *Rana pipiens* (Kearney et al. 2008). Similarly, our BPM was built and used to make predictions for *P. jordani*, a large-bodied terrestrial plethodontid salamander. However, most of the functional relationships in our model rely on studies conducted with other species; energy assimilation from *P. montanus* (Clay and Gifford 2017); probability of surface activity from *P. shermani* (Connette and Semlitsch 2015); VPG-dehydration from *Desmognathus ochrophaeus* (Feder and Londos 1984). We have demonstrated that each of these relationships is sensitive to parameterization, further emphasizing the need to better understand these processes in salamanders generally, and in *P. jordani* specifically. While it may be necessary to use data from closely related species when specific data is lacking, researchers must be cautious in generalizing such results due to uncertainty, and make concerted efforts to collect organism-specific data.

The use of data that is collected over a short temporal scale and small spatial scale may result in further uncertainty in models. For example, Jonsson et al. (2008) modelled lichen hydration using parameter measures collected over 4 months, which is unlikely to encompass seasonal and annual environmental variation that may influence model outputs. Considering the scale of the data, both temporal and spatial, is of utmost importance to obtaining relevant and useful outputs (Wiens 1989). Our BPM used daily climatic data, whereas many other models have used monthly averages and/or ranges (Kearney et al. 2008; Gifford and Kozak 2012), seasonal averages (Bach 1993), or annual averages of environmental data (Pastres et al. 2004). Considerations of scale are invariably dependent on the model and study system. Plethodontid salamanders have unique activity patterns whereby emergence and surface activity typically only occur under specific climate conditions when temperature and moisture are optimal. Therefore, finer scale temporal data (daily climate data)

are necessary to model realistic behavior and elucidate relevant results. A clear understanding of the natural history of the species of interest, as well as surrogate species that may provide model parameter inputs, must be considered when constructing a BPM, and when interpreting their outputs.

Overall, data gaps exist across taxa (outlined by Urban et al. 2016), and it is critically important to collect long-term, robust, species-specific data wherever possible. In fact, Urban et al. (2016) have issued a call for global coordination and regional working groups to collect standardized data. We second such recommendations, and further urge the formation of local groups committed to collecting standardized and rigorous data on important demographic, behavioral, physiological, and environmental parameters on species of conservation and management interest. We also urge careful monitoring and assessment of the influence of input parameters by using sensitivity analyses, and explicitly presenting results of such analyses. BPMs are a potentially powerful tool that can be used to gain important insights into species' responses to climate change, but are only as powerful and relevant as the data used.

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References

- Angilletta MJ Jr (2001) Variation in metabolic rate between populations of a geographically widespread lizard. *Physiol Biochem Zool* 74:11–21
- Anthony CD, Wicknick JA, Jaeger RG (1997) Social interactions in two sympatric salamanders: Effectiveness of a highly aggressive strategy. *Behaviour* 134:71–88
- Bach HK (1993) A dynamic model describing the seasonal variations in growth and the distribution of eelgrass (*Zostera marina* L.) I. Model theory. *Ecol Model* 65:31–50
- Bakken GS (1992) Measurement and application of operative and standard operative temperatures in ecology. *Am Zool* 32:194–216
- Baudin M, Boumhaout K, Delage T, Iooss B, Martinez J-M (2016) Numerical stability of Sobol' indices estimation formula. In: Proceedings of the SAMO 2016 conference, reunion Island, France. pp 50–51
- Bennett AF, Houck LD (1983) The energetic cost of courtship and aggression in a plethodontid salamander. *Ecology* 64:979–983
- Bocci M, Coffaro G, Bendoricchio G (1997) Modelling biomass and nutrient dynamics in eelgrass (*Zostera marina* L.): applications to the Lagoon of Venice (Italy) and Oresund (Denmark). *Ecol Model* 102:67–80
- Bonan GB (1991) A biophysical surface energy budget analysis of soil temperature in the boreal forests of interior Alaska. *Water Resour Res* 27:767–781
- Buckley LB, Urban MC, Angilletta MJ, Crozier LG, Rissler LJ, Sears MW (2010) Can mechanism inform species' distribution models? *Ecol Lett* 13:1041–1054
- Buckley Lauren B (2008) Linking traits to energetics and population dynamics to predict lizard ranges in changing environments. *Am Nat* 171:E1–E19
- Cahill AE, Aiello-Lammens ME, Fisher-Reid MC, Hua X, Karanewsky CJ, Yeong Ryu H, Sbeglia GC, Spagnolo F, Waldron JB, Warsi O, Wiens JJ (2013) How does climate change cause extinction? *Proc R Soc Lond B* 280:20121890
- Campbell GS, Norman JM (1998) Introduction to environmental biophysics, 2nd edn. Springer, New York
- Clay TA, Gifford ME (2016) Thermal sensitivity of aggression in two terrestrial salamanders, *Plethodon cylindraceus* and *P. montanus*. *Ethology* 122:127–133
- Clay TA, Gifford ME (2017) Population level differences in thermal sensitivity of energy assimilation in terrestrial salamanders. *J Therm Biol* 64:1–6
- Confalonieri R, Bellocchi G, Bregaglio S, Donatelli M, Acutis M (2010) Comparison of sensitivity analysis techniques: a case study with the rice model WARM. *Ecol Model* 221:1897–1906
- Connette GM, Semlitsch RD (2013) Life history as a predictor of salamander recovery rate from timber harvest in southern Appalachian Forests, USA. *Conserv Biol* 27:1399–1409
- Connette GM, Semlitsch RD (2015) A multistate mark–recapture approach to estimating survival of PIT-tagged salamanders following timber harvest. *J Appl Ecol* 52:1316–1324
- Connette GM, Crawford JA, Peterman WE (2015) Climate change and shrinking salamanders: Alternative mechanisms for changes in plethodontid salamander body size. *Global Change Biol* 21:2834–2843
- Dodd CK (2004) The amphibians of the Great Smoky Mountains National Park. The University of Tennessee Press, Knoxville
- Elith J, Leathwick JR (2009) Species distribution models: ecological explanation and predictions across space and time. *Annu Rev Ecol Evol Syst* 40:677–697
- Feder ME (1983) Integrating the ecology and physiology of plethodontid salamanders. *Herpetologica* 39:291–310
- Feder ME, Londos PL (1984) Hydric constraints upon foraging in a terrestrial salamander, *Desmognathus ochrophaeus*. (Amphibia: Plethodontidae). *Oecologia* 64:413–418
- Feder ME, Papenfuss TJ, Wake DB (1982) Body size and elevation in neotropical salamanders. *Copeia* 1982:186–188
- Fitzpatrick MJ, Mathewson PD, Porter WP (2015) Validation of a mechanistic model for non-invasive study of ecological energetics in an endangered wading bird with counter-current heat exchange in its legs. *PLOS One* 10:e0136677
- Gates DG (1980) Biophysical ecology. Springer, New York
- Gatz RN, Crawford EC Jr, Piiper J (1975) Kinetics of inert gas equilibration in an exclusively skin-breathing salamander, *Desmognathus fuscus*. *Respir Physiol* 24:15–29
- Gifford ME, Kozak KH (2012) Islands in the sky or squeezed at the top? Ecological causes of elevational range limits in montane salamanders. *Ecography* 35:193–203
- Jansen MJW (1999) Analysis of variance designs for model output. *Comput Phys Commun* 117:35–43
- Jonsson AV, Moen J, Palmqvist K (2008) Predicting lichen hydration using biophysical models. *Oecologia* 156:259–273
- Kearney M (2016) NicheMapR: R implementation of Niche Mapper software for biophysical modelling. R package version 1.0.0
- Kearney M, Porter W (2009) Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecol Lett* 12:334–350
- Kearney M, Phillips BL, Tracy CR, Christian KA, Betts G, Porter WP (2008) Modelling species distributions without using species distributions: the cane toad in Australia under current and future climates. *Ecography* 31:423–434
- Kearney M, Porter WP, Williams C, Ritchie S, Hoffmann AA (2009) Integrating biophysical models and evolutionary theory to predict

- climatic impacts on species' ranges: the dengue mosquito *Aedes aegypti* in Australia. *Funct Ecol* 23:528–538
- Kearney MR, Isaac AP, Porter WP (2014) microclim: Global estimates of hourly microclimate based on long-term monthly climate averages. *Sci Data* 1:140006
- Kolbe JJ, Ehrenberger JC, Moniz HA, Angilletta MJ Jr (2014) Physiological variation among invasive populations of the brown anole (*Anolis sagrei*). *Physiol Biochem Zool* 87:92–104
- Kozak KH, Wiens JJ (2010) Niche conservatism drives elevational diversity patterns in Appalachian salamanders. *Am Nat* 176:40–54
- Kozak KH, Mendyk RW, Wiens JJ (2009) Can parallel diversification occur in sympatry? Repeated patterns of body-size evolution in coexisting clades of North American salamanders. *Evol Int J org Evol* 63:1769–1784
- Mathewson PD, Porter WP (2013) Simulating polar bear energetics during a seasonal fast using a mechanistic model. *PLoS One* 8:e72863
- Menne MJ, Durre I, Korzeniewski B, McNeal S, Thomas K, Yin X, Anthony S, Ray R, Vose RS, E. Gleason B, Houston TG (2012a) Global Historical Climatology Network—Daily (GHCN-Daily), Version 3, Subset: USC00406500. NOAA Natl Clim Data Center. doi:10.7289/V5D21VHZ (Accessed 27 September 2016)
- Menne MJ, Durre I, Vose RS, Gleason BE, Houston TG (2012b) An overview of the global historical climatology network-daily database. *J Atmos Oceanic Technol* 29:897–910
- Milanovich JR, Peterman WE, Nibbelink NP, Maerz JC (2010) Projected loss of a salamander diversity hotspot as a consequence of projected global climate change. *PLoS One* 5:e12189
- Mitchell JW (1976) Heat transfer from spheres and other animal forms. *Biophys J* 16:561–569
- Morin X, Thuiller W (2009) Comparing niche- and process-based models to reduce prediction uncertainty in species range shifts under climate change. *Ecology* 90:1301–1313
- Moritz C, Patton JL, Conroy CJ, Parra JL, White GC, Beissinger SR (2008) Impact of a climate change on small-mammal communities in Yosemite National Park, USA. *Science* 322:261–264
- Nishikawa KC (1987) Interspecific aggressive behaviour in salamanders: species-specific interference or misidentification? *Anim Behav* 35:263–270
- O'Connor MP, Sieg AE, Dunham AE (2006) Linking physiological effects on activity and resource use to population level phenomena. *Integr Comp Biol* 46:1093–1109
- Parnesan C, Yohe G (2003) A globally coherent fingerprint of climate change. *Nature* 421:37–42
- Pastres R, Brigolin D, Petruzzo A, Zucchetto M (2004) Testing the robustness of primary production models in shallow coastal areas: A case study. *Ecol Model* 179:221–233
- Petranka JW (1998) Salamanders of the United States and Canada. Smithsonian Institution Press, Washington DC
- Pujol G, Iooss B, Janon A, with contributions from, Boumhaout, Veiga K, Fruth SD, Gilquin J, Guillaume L, Gratiot J, Lemaitre LL, Ramos P, Roustant B, Touati O, Weber T, Oomen F, Delage R T (2016) sensitivity: Global Sensitivity Analysis of Model Outputs. R package version 1.13.0
- Riddell EA, Sears MW (2015) Geographic variation of resistance to water loss within two species of lungless salamanders: implications for activity. *Ecosphere* 6:art86
- Riddell EA, Apanovitch EK, Odom JP, Sears MW (2016) Physical calculations of resistance to water loss improve predictions of species range models. *Ecol Monogr* 87:21–33
- Saltelli A, Ratto M, Andres T, Campolongo F, Cariboni J, Gatelli D, Saisana M, Tarantola S (2008) Introduction to sensitivity analysis. In: Saltelli A, Ratto M, Andres T, Campolongo F, Cariboni J, Gatelli D, Saisana M, Tarantola S (eds) Global sensitivity analysis. The primer. Wiley, Chichester, pp 1–51
- Sears MW, Angilletta MJ, Schuler MS, Borchert J, Dilliplane KF, Stegman M, Rusch TW, Mitchell WA (2016) Configuration of the thermal landscape determines thermoregulatory performance of ectotherms. *Proc Natl Acad Sci USA* 113:10595–10600
- Seebacher F, White CR, Franklin CE (2015) Physiological plasticity increases resilience of ectothermic animals to climate change. *Nat Clim Change* 5:61–66
- Spotila JR, Berman EN (1976) Determination of skin resistance and the role of the skin in controlling water loss in amphibians and reptiles. *Comp Biochem Phys A* 55:407–411
- Sultan SE (2000) Phenotypic plasticity for plant development, function and life history. *Trends Plant Sci* 5:537–542
- Swinbank WC (1963) Long-wave radiation from clear skies. *Q J R Meteorol Soc* 89:339–348
- Thornton PE, Thornton MM, Mayer BW, Wilhelm N, Wei Y, Devarakonda R, Cook RB (2014) Daymet: Daily surface weather data on a 1-km grid for North America; Version 2. Data set. Available on-line [<http://daac.ornl.gov>] from Oak Ridge National Laboratory Distributed Active Archive Center; Oak Ridge; Tennessee; USA. Accessed 15 Jan 2016
- Urban MC, Bocedi G, Hendry AP, Mihoub J-B, Pe'er G, Singer A, Bridle JR, Crozier LG, De Meester L, Godsoe W, Gonzalez A, Hellmann JJ, Holt RD, Huth A, Johst K, Krug CB, Leadley PW, Palmer SCF, Pantel JH, Schmitz A, Zollner PA, Travis JMJ (2016) Improving the forecast for biodiversity under climate change. *Science* 353:aad8466
- Wells KD (2007) The ecology and behavior of amphibians. University of Chicago Press, Chicago
- Whitford WG, Hutchison VH (1967) Body size and metabolic rate in salamanders. *Physiol Zool* 40:127–133
- Wiens JA (1989) Spatial scaling in ecology. *Funct Ecol* 3:385–397
- Wilcove DS, Rothstein D, Dubow J, Phillips A, Losos E (1998) Quantifying threats to imperiled species in the united states. *Bioscience* 48:607–615