

## Future advantages in energetics, activity time, and habitats predicted in a high-altitude pit viper with climate warming

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### Summary

1. A future warmer climate is generally predicted to threaten reptiles. But many high-altitude reptiles that rely on external heat to survive current cold climate may benefit from future warmth. This prediction can be tested by simulating activity time and energetics of reptiles with a biophysical model.

2. We modelled the potential response of a high-altitude snake, *Trimeresurus gracilis*, to a 3 °C increase in air temperature, using the biophysical/behavioural NicheMapper model. Using animal and environmental properties, we first analysed the effects of shade level (i.e. the reduction of solar radiation) on activity time and energetics of *T. gracilis*. We then computed activity time, energetics and potential habitats in its current range of Taroko National Park, Taiwan (> 1800 m in altitude), with a spatial climate, vegetation and topography data set.

3. In the current climate, increased shade levels were predicted to decrease activity time, maintenance energy requirements and discretionary energy (i.e. energy left after maintenance costs are met). In heavy shade (i.e. 81–100% reduction of solar radiation) at 3000 and 3500 m, *T. gracilis* was predicted to have impaired digestive capacity and hence to be unable to meet basic maintenance costs for survival. In a warmer climate, the predicted digestive capacity, energetics and activity time of *T. gracilis* increase. But in heavy shade at 3500 m, the digestive capacity was predicted to remain impaired for supporting basic energy requirements for survival.

4. In the current climate, the predicted suitable habitat area (i.e. where *T. gracilis* obtains positive discretionary energy) in coniferous and coniferous–broadleaf forests decreased with increasing elevation. At elevations higher than 3000 m, most suitable habitats were in open areas like grasslands where *T. gracilis* was also predicted to have more discretionary energy than in heavily forested habitats. Our field sightings agreed with model predictions. A warmer climate was generally predicted to increase the activity time, energetics and habitat area, given the current vegetation pattern.

5. Overall, we demonstrate that metabolism, digestive function and vegetative shade levels are critical elements affecting *T. gracilis*' energetics and habitats with climate change. *Trimeresurus gracilis* is likely to benefit energetically from future warmth.

**Key-words:** climate change, digestion, elevation, mechanistic model, metabolism, reptile, temperature, *Trimeresurus gracilis*

### Introduction

Recent climate change has had substantial consequences for mountain species, including population decline/

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extinction, range contractions and phenological changes (Pounds, Fogden & Campbell 1999; Inouye *et al.* 2000; Moritz *et al.* 2008). Globally, reptiles are also documented and predicted to be threatened by warming effects (Raxworthy *et al.* 2008; Tewksbury, Huey & Deutsch 2008; Huey *et al.* 2009; Sinervo *et al.* 2010). However, to survive cold mountain climates, many high-altitude reptiles require an external heat source (Hertz & Huey 1981; Marquet *et al.* 1989; Christian 1998) to elevate their body temperatures and physiological function. Therefore, a moderate increase in air temperature may benefit these thermoregulating reptiles by alleviating the negative impact of the current cold climate at high altitudes. The response of high-altitude reptiles to future warming within their particular landscape context has never been investigated based on a mechanistic understanding. This prediction requires an understanding of the interaction of the animal with its environment. Such a mechanistic prediction has implications for conservation and can aid in quantifying warming effects on mountain animals.

A practical approach to predicting warming effects on mountain reptiles is to estimate changes in their energetics and potential activity time in response to changing temperature. Whether reptiles can attain a positive energy balance and achieve enough activity time determines their survival and fitness (Sinervo *et al.* 2010). Due to long hibernating seasons, high-altitude reptiles greatly depend on the short active season to maximize growth, reproduction and energy storage. Reptiles' energetics and activity time are dependent on their body temperature. If the environment permits, reptiles can maintain their body temperature within a preferred range, maximizing physiological function. However, if the environment constrains reptiles' capacity to maintain this range, physiological and behavioural functions could be impeded (e.g. digestion, feeding, Stevenson, Peterson & Tsuji 1985; Hailey & Davies 1987; Tsai, Lee & Tu 2008), leading to a negative energy balance and/or very short activity time. For example, a shady, cold and windy place at high altitude could preclude reptiles' normal physiological function, causing them to hibernate longer and consume more energy than they have stored. Hence, the physical conditions in their living environment are also important in analysing the energetic responses of reptiles to temperature changes.

Predicting reptiles' energetics and activity time in response to climate change requires a model that can calculate the interaction between animal and environment. The biophysical/behavioural NicheMapper model (Porter & Mitchell 2006) calculates heat and mass transfer between an animal and its environment based on the principle of energy conservation. In particular, this model is able to estimate an animal's local microenvironment based on topographic and climate data (e.g. temperature, elevation, shade). The animal properties (morphology, physiology and behaviour) are also taken into account to compute the animal's body temperature, energetics and potential activity time in time and space (Porter & Gates 1969; Porter

*et al.* 1973). NicheMapper has also evaluated the warming effects on many species (amphibians: Kearney *et al.* 2008; lizards: Mitchell *et al.* 2008; Kearney, Shine & Porter 2009a; insects: Kearney *et al.* 2009b, 2010).

The potential activity time and energetics of high-altitude reptiles in response to vegetation variation and climate change have never been explored from an energetic point of view at a landscape scale. This study aimed at evaluating the warming effect on a high-altitude pit viper, *Trimeresurus gracilis* Oshima (Viperidae: Crotalinae; Fig. 1; altitudinal distribution >1800 m, Lue, Tu & Hsiang 1999), a protected and rare species endemic to Taiwan. Adult snakes frequently bask in the sun in open places such as rocky slopes, vegetable farms and grasslands during the active season, suggesting that thermoregulation is important in enhancing their physiological function in cold climates. Due to very rare occurrence data and secretive habits, estimating potential climate change impacts on *T. gracilis* with 'correlative' ecological modelling (review by Guisan & Zimmermann 2000; Stockwell & Peterson 2002) is challenging.

This study applied the NicheMapper model to predict physiological, behavioural and distributional responses to an increase of 3 °C air temperature on *T. gracilis*. The first goal was to enhance the NicheMapper model to estimate the digestive capacity of *T. gracilis* in the field, enabling further calculation of the discretionary energy, that is, the energy left after maintenance costs are met. We measured the following functional traits of *T. gracilis* for simulation: the preferred body temperatures and skin solar reflectivity. Standard metabolic rates (SMR; S.P. Huang & M.C. Tu, unpublished data) and digestive physiology data obtained from this species (Chu *et al.* 2009) and the closely related *T. stejnegeri stejnegeri* (Tsai, Lee & Tu 2008) were incorporated in simulating the energetics of this species.

The second goal was to predict the changes in the energetics and activity time of this species in response to a warming climate and to offer a plausible explanation for the changes. First, the impact of vegetative shade on



**Fig. 1.** A basking adult pit viper *Trimeresurus gracilis* Oshima. Photograph taken by Ming-Chung Tu.

*T. gracilis* was analysed by simulating the snake's activity time and energetics at five shade levels (i.e. the reduction of solar radiation: 0–20%, 21–40%, 41–60%, 61–80% and 81–100%) and three elevations (2000, 3000 and 3500 m) in both the current and future warming climates. Next, this study evaluated the effects of landscape characteristics on the activity time and energetics of this species, using a fine-scale spatial data set collected in its current range in Taroko National Park (longitude, latitude, topography, vegetation type and climate, 40 m × 40 m per grid cell). The warming effect on *T. gracilis* was evaluated based on the changes in activity time, energetics and thermally suitable habitats when the air temperature is 3 °C higher than the current temperature. The increase of 3 °C air temperature is based on the Intergovernmental Panel on Climate Change (IPCC) 4th Assessment Report (AR4) predicting that global air temperature will increase 2.0–5.4 °C by the year 2100 (A2 scenario; Meehl *et al.* 2007).

## Materials and methods

### MEASUREMENT OF PHYSIOLOGICAL TRAITS

#### Study animal, collection and maintenance

*Trimeresurus gracilis* is a small viviparous pit viper (body length <60 cm). It is active from April to October and hibernates from November to March. The diet of juvenile snakes is mainly lizards, and the diet of adult snakes is mainly mammals, including rodents and shrews (Lin & Tu 2008). Animals were collected from Yilan, Hualien, Miaoli, Kauhsiung, Taitung and Nantou counties during 1998, 1999 and 2001. They were maintained on a 12 : 12 h light/dark photoperiod at 20–25 °C in the laboratory. The snakes were kept individually in plastic cages (27 cm long × 18 cm wide × 16 cm high) containing a layer of wood shavings as substrate and a piece of tile as shelter. They were fed mice (10–20% snakes' body mass) once every 2 weeks and had unlimited access to water.

#### Measurement of skin solar reflectivity

A frozen intact male *T. gracilis* (43.7 g, SVL = 41.5 cm) was used for solar reflectivity measurement. The male snakes are brown-beige with dark brown blotchy patterns. The measured specimen had the most common skin colour pattern. The sample was thawed to room temperature (c. 25 °C) before measurement. The skin reflectivity of the dorsal mid-body was measured using an ASD portable spectroradiometer (Analytical Spectral Devices Field Spec Pro ASD, Boulder, CO, USA, spectral range = 350–2500 nm) with a circular quartz sensor window 1 cm in diameter.

#### Measurement of preferred body temperature

The preferred body temperatures ( $T_{\text{pref}}$ ) of the snakes were measured during 2000–2001 (body mass of males: median = 34.5 g, range = 11.9–60.0 g,  $n = 12$ ; body mass of females: median = 52.7 g, range = 12.7–80.6 g,  $n = 13$ ). Gravid females were excluded. The  $T_{\text{pref}}$  in the fasting state were measured in four seasons ( $n = 11$ –16 per season). Some individuals were measured in more than one season. Fasting  $T_{\text{pref}}$  were obtained after a 2-week fast at 20 °C. The  $T_{\text{pref}}$  in the postprandial state were measured using another set of snakes during May–July (body mass of

males: median = 37.3 g, range = 32.9–60.0 g,  $n = 5$ ; body mass of females: median = 63.7 g, range = 42.9–80.6 g,  $n = 5$ ).

The  $T_{\text{pref}}$  of the snakes were measured using a laboratory thermal gradient (150 cm long × 20 cm wide × 35 cm high; for details see Appendix S1, Supporting information). The thermal gradient, which generated temperatures ranging from 5 to 40 °C, was placed in a 5 °C walk-in chamber. The  $T_{\text{pref}}$  were obtained by measuring body temperature ( $T_b$ ) of snakes inside this gradient. Snakes'  $T_b$  was measured by the thermocouple and was recorded automatically with a data logger (Thermolog 306; Center Technology Corp., Taipei, Taiwan) every 10 min for 48 h. In the fasting state, the minimum and maximum  $T_b$  recorded during the 48 h measurement was defined as the voluntary thermal minimum ( $VT_{\text{min}}$ ) and voluntary thermal maximum ( $VT_{\text{max}}$ ), respectively. In the digestive state, the mean value of the  $T_{\text{pref}}$  recordings on the second day was defined as the postprandial  $T_{\text{pref}}$ .

### NICHEMAPPER MODEL

NicheMapper operates with a microclimate model and an ectotherm model. A detailed description of these two models has been reported elsewhere (Porter *et al.* 1973; Porter & Mitchell 2006) and at <http://www.zoology.wisc.edu/faculty/Porter/Port.html>.

#### Microclimate model

The microclimate model computes the hourly temperature profile, wind speed and clear-sky solar radiation of each location (pixel) for each month. The microclimate model has been tested in various environments (e.g. Porter *et al.* 1973; Kearney & Porter 2004; Kearney, Shine & Porter 2009a; Bartelt, Klaver & Porter 2010). The hourly outputs of the microclimate model were used as inputs for the ectotherm model (for details, see Porter *et al.* 1973, also Appendix S2, Supporting information) to calculate an animal's potential activity time, energetics and habitat suitability. The input variables are briefly described in Appendix S2 (Supporting information) and are listed in Table S1 (Supporting information). We validated soil temperature output from the microclimate model with corresponding recordings collected at two localities in the study area: Siaofenkou (altitude: 3005 m, data provided by Endemic Species Research Institute, Taiwan, 2006–2009) and Guanyuan (altitude: 2347 m, December 2004). Figure S1 (Supporting information) indicates that the simulated temperatures generally fell in the ranges of real temperature recordings.

#### Ectotherm model

As  $T_b$  is the critical factor affecting physiology and activity, the ectotherm model first estimated hourly core body temperatures ( $T_{b,t}$ ) in the middle Julian day of each month. Using climate outputs generated from the microclimate model, the ectotherm model computed the snakes'  $T_{b,t}$  by iteratively solving the steady-state heat balance equation:

$$Q_{\text{gen}} + Q_{\text{solar}} + Q_{\text{infra,in}} = Q_{\text{evap}} + Q_{\text{conv}} + Q_{\text{infra,out}} + Q_{\text{cond}} \quad \text{eqn1}$$

where  $Q_{\text{gen}}$  represents generated metabolic heat;  $Q_{\text{solar}}$  represents solar energy;  $Q_{\text{infra,in}}$  and  $Q_{\text{infra,out}}$  are incoming and outgoing thermal infrared radiation; and  $Q_{\text{evap}}$ ,  $Q_{\text{conv}}$  and  $Q_{\text{cond}}$  are evaporative heat, convective heat and conductive heat transfer, respectively. Basic elements for each term are described elsewhere (Porter *et al.* 1973; Porter & Mitchell 2006). As small animals may easily find sunny spots and vegetative shade in any location regardless of shade level, the ectotherm model allows snakes to adjust the amount of solar radiation they absorb from 0% to



100% of the amount of solar radiation equivalent to that in an open place. Shade levels thus only apply to the local microclimate conditions such as surface temperature.

The monthly activity time and metabolism requirement were obtained by multiplying the daily activity time and metabolism requirement estimated in the middle Julian day of each month by the number of days of that month. The activity time refers to the duration in which the environment is suitable for the snakes to be active above-ground. The maintenance energy requirement is the energy required for survival, including the cost of thermoregulation. The discretionary energy is the amount of energy that snakes can invest in other activities such as hunting, reproduction and accumulating fat.

**Estimation of active and hibernating months:** An active month is defined as a month in which snakes were able to complete digesting a meal, whereas a hibernating month is defined as a month in which snakes were not able to complete digesting a meal. We assumed a meal weighing 20% of the snake's body mass because (i) this is supported by the best available data (Tsai, Lee & Tu 2008) and (ii) this meal size is within the range of the body mass of its main mammalian prey (*Soriculus fumidus*, body mass *c.* 4–8 g, Lin & Tu 2008).

We estimated digestive time ( $t_{\text{digest}}$ ) of snakes with fluctuating  $T_b$ s based on the degree–time concept. This concept was derived from empirical work indicating that the snakes'  $t_{\text{digest}}$  increased nonlinearly with decreasing  $T_b$ s and digestion ceased when  $T_b$ s are too low (e.g. regurgitation *c.* 10 °C for *Vipera aspis* and *Natrix maura*, Naulleau 1983; Hailey & Davies 1987). Here, a snake was postulated to require a minimum amount of accumulated thermal time (critical degree–time,  $C_{\text{crit}}$ ) to complete digestion of a meal, and the digestion would cease below a critical  $T_b$  ( $T_{b,\text{crit}}$ ). The  $C_{\text{crit}}$  and  $T_{b,\text{crit}}$  were calculated to be 127.29 °C-days (=3054.99 °C-hours) and 11.0 °C, respectively (detailed information in Appendix S3, Supporting information). The digestive time for each month ( $t_{\text{digest, moi}}$ ) was calculated using eqn 2:

$$t_{\text{digest, moi}} = \frac{C_{\text{crit}}}{\sum_{t=1}^{t=24} (T_{b,t} - 11.0^\circ\text{C})} \quad \text{eqn 2}$$

where  $T_{b,t}$  is the simulated core  $T_b$  at hour  $t$  (from  $t = 1$  for 1 am to  $t = 24$  for 12 am) in the middle Julian day of a month  $i$  ( $i = 1$  for January to  $i = 12$  for December). When  $T_{b,t} < 11.0$  °C, then  $T_{b,t} = 11.0$  °C.

**Estimation of annual maintenance energy requirements:** There are no quantitative data available to estimate the energetics of *T. gracilis* in the field. Many pit vipers are relatively sedentary, and many routine activities are perceived as slow and deliberate (Lillywhite 1987). The maintenance energy requirements were assumed to be 1.0 times standard metabolism (eqn in Table S1, Supporting information) in the hibernating season and 1.5 times standard metabolism in the active season when  $T_b$ s are above  $VT_{\text{min}}$ . A setting of 1.0 times standard metabolism was also used to test the sensitivity of the results to these two different settings. The annual maintenance energy ( $M_{\text{yr}}$ ) was the sum of the maintenance energy requirements for the active and hibernating seasons.

**Estimation of annual digestive capacity and annual discretionary energy:** The annual digestive capacity and annual discretionary energy were calculated assuming (i) food is always available and (ii) snakes do not consume a meal unless they have completed digesting a food item (Beaupre 2002). The annual digestive capacity is defined by the maximum number of mice a snake can digest ( $N_{\text{yr,max}}$ ). We solved  $N_{\text{yr,max}}$  by summing the maximum number of mice that a snake can digest in each month, which was calculated from dividing the number of days of each month ( $d_{\text{moi}}$ ) by  $t_{\text{digest, moi}}$ :

$$N_{\text{yr,max}} = \sum_{i=1}^{i=12} \frac{d_{\text{moi}}}{t_{\text{digest, moi}}} \quad \text{eqn 3}$$

The annual discretionary energy ( $E_{\text{dnrg}}$ ) was solved by subtracting the annual maintenance energy requirements ( $M_{\text{yr}}$ ) from the maximum energy obtained from ingested prey ( $E_{\text{abs}}$ ):

$$E_{\text{dnrg}} = E_{\text{abs}} - M_{\text{yr}} \quad \text{eqn 4}$$

The  $E_{\text{abs}}$  is the product of apparent assimilation efficiency, net assimilated energy from a mouse ( $E_{\text{net}}$ ), and  $N_{\text{yr,max}}$ . The apparent assimilation efficiency incorporates the loss of energy from digestion to faeces production and nitrogenous waste elimination; it is assumed to be 0.87 based on empirical data collected from *T. s. stejnegeri* (at 25 °C, Tsai, Lee & Tu 2008). The  $E_{\text{net}}$  is the difference between the total energy assimilated from a mouse and the specific dynamic action (i.e. SDA, the energy cost of digestion). The equations used in the above calculation are listed in Table S1 (Supporting information).

**Estimation of habitat suitability:** A suitable habitat is defined as a location where a snake can obtain annual positive discretionary energy, whereas an unsuitable habitat is defined as a location where a snake cannot obtain positive discretionary energy. This definition of habitat is based on an assumption that *T. gracilis* has a small home range size so that they stay in certain ranges. We often observed snakes on certain spots in sunny slopes and grasslands ( $n = 90$  sightings, 2002–2008), and some individuals implanted with an identification tag were recaptured within several miles across several years (M.C. Tu & C.F. Lin, unpublished data).

## SIMULATION OF POTENTIAL ACTIVITY TIME, ENERGETICS AND HABITAT

### Preparation of spatial data set

The data set of latitude, longitude, elevation, aspect, slope and vegetation/land types for the study area (>1800 m in Taroko National Park) was prepared using ESRI ARCMAP version 9.1 (40 m × 40 m per cell, 363 804 grid cells). The elevation and the major vegetation/land types in the study area are shown in Fig. 2. The aspect and slope data were calculated from a digital terrain map (40 m × 40 m grid, Aerial Survey office, Taiwan Forestry Bureau). The vegetation/land type data (Taiwan Forestry Bureau) and how their corresponding shade levels were assigned are described in Table S2 (Supporting information). We estimated the canopy covers of main type forests with fisheye lens photographs (Nikon Coolpix 4500 camera fitted with a Nikon FC-E8 fisheye converter lens (Nikon, Tokyo, Japan); for details see Table S2, Supporting information).

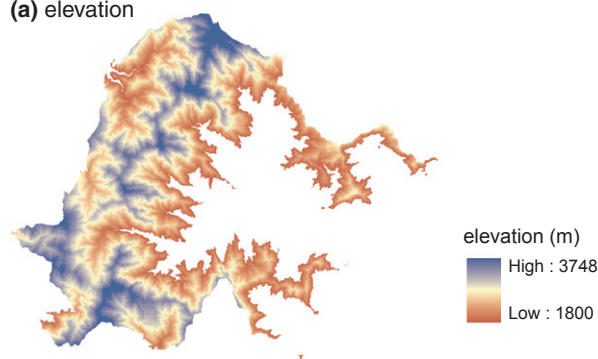
### Shade-level and landscape simulations

Shade-level simulation estimated the potential activity time and energetics of an adult male *T. gracilis* (32.0 g, total length = 42.9 cm) in five shade levels (0–20%, 21–40%, 41–60%, 61–80%, 81–100%) at three elevations (2000, 3000, 3500 m). The landscape simulation computed potential activity time, energetics and the potential habitats of two sizes of adult *T. gracilis* (small: 32.0 g, total length = 42.9 cm; large: 60.0 g, total length = 54.0 cm) in our study area.

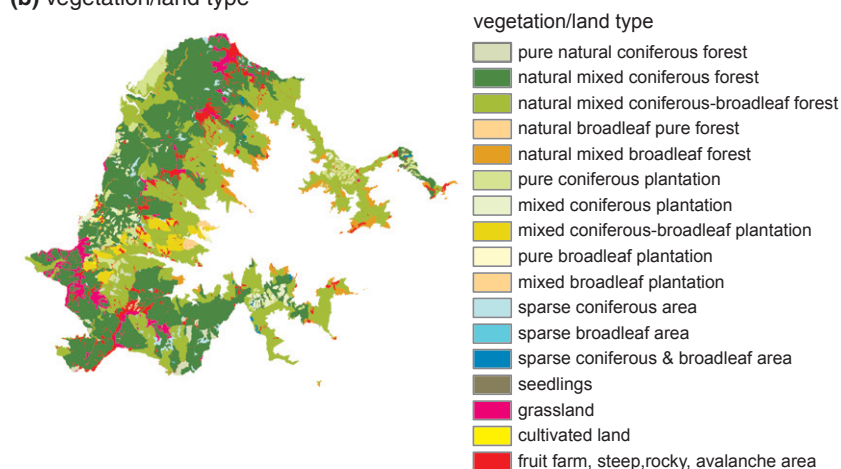
### Sensitivity tests

The sensitivity of the model to key parameters and settings used in the landscape simulations was tested in three vegetation/land types (open area, coniferous forest, coniferous–broadleaf forest) at three altitudes (2000, 3000 and 3500 m; see details in Appendix S4, Supporting information). The tested key parameters and

(a) elevation



(b) vegetation/land type



**Fig. 2.** The (a) elevation and (b) vegetation/land types of the study area in Taroko National Park.

settings are wind speed ( $0.1\text{--}1.0\text{ m s}^{-1}$ ,  $0.1\text{--}2.0\text{ m s}^{-1}$ ,  $0.1\text{--}4.0\text{ m s}^{-1}$ ), cloud cover (10% variance of mean) and the settings of multiplier (1.0, 1.5) of standard metabolism used in simulating energetics, skin solar reflectivity (6%, 10% and 14%) and oxygen extraction efficiency (5%, 10% and 15%).

## Results

### MORPHOLOGY, BEHAVIOUR AND PHYSIOLOGY TRAITS

The dorsal skin solar reflectivity of the male *T. gracilis* specimen was 10%. The males and females did not differ significantly in both the  $VT_{\min}$  and  $VT_{\max}$  in four measured seasons and the postprandial  $T_{\text{pref}}$  (all  $P > 0.05$ , Kruskal–Wallis test); hence, the data collected from males and females were pooled together for further analysis. The range of mean  $VT_{\min}$  across four seasons was  $8.8\text{--}14.9\text{ }^{\circ}\text{C}$  (mean  $\pm 1$  SD. Spring:  $12.6 \pm 3.3\text{ }^{\circ}\text{C}$ , summer:  $14.9 \pm 3.2\text{ }^{\circ}\text{C}$ , autumn:  $10.1 \pm 6.8\text{ }^{\circ}\text{C}$ , winter:  $8.8 \pm 6.8\text{ }^{\circ}\text{C}$ ,  $n = 11\text{--}16$ ). The range of mean  $VT_{\max}$  was  $24.0\text{--}27.7\text{ }^{\circ}\text{C}$  (mean  $\pm 1$  SD. Spring:  $24.0 \pm 6.1\text{ }^{\circ}\text{C}$ , summer:  $27.7 \pm 4.0\text{ }^{\circ}\text{C}$ , autumn:  $26.1 \pm 7.4\text{ }^{\circ}\text{C}$ , winter:  $24.9 \pm 5.0\text{ }^{\circ}\text{C}$ ,  $n = 11\text{--}16$ ). The postprandial  $T_{\text{pref}}$  were  $23.8 \pm 9.3\text{ }^{\circ}\text{C}$  (mean  $\pm 1$  SD,  $n = 10$ ). Seasonal mean  $VT_{\min}$  and mean  $VT_{\max}$  of *T. gracilis* were used as the VT range for the ectotherm model. As large variance of VTs were found among individuals, a wide VT range (lower limit of 95%

CI for  $VT_{\min}$  and higher limit of 95% CI for  $VT_{\max}$ ) was used to test the sensitivity of the results to these two different settings. The other values of animal properties used in the ectotherm model are listed in Table S1 (Supporting information).

### RESULTS OF THE SENSITIVITY TEST

The results of the sensitivity test are shown in Appendix S4 (Supporting information). The model was very sensitive to wind speed. In general, an increasing wind speed (i) prolonged activity time in open areas but decreased activity time in the forest and (ii) decreased maintenance energy requirements and discretionary energy, with more profound effects in the forest than in open areas. In the coniferous forest at 3500 m, wind speed was not an influential factor because the snakes were predicted to hibernate underground all year. The model was also sensitive to the settings of the multiplier of standard metabolism used in simulating energetics. When using  $1.0 \times \text{SMR}$  for estimating energetics, the model predicted significantly less maintenance energy requirements and hence more discretionary energy than the reference values (set at  $1.5 \times \text{SMR}$ ) in all conditions tested, except in coniferous forest at 3500 m altitude where the snakes are predicted to hibernate all year. The model was not sensitive

to the cloud cover, skin solar reflectivity or oxygen extraction efficiency.

#### SHADE-LEVEL SIMULATION: EFFECTS OF SHADE LEVELS ON *T. GRACILIS* AT THREE ALTITUDES

Shade level was predicted to affect the digestive rate and  $T_b$  of *T. gracilis*. Using the digestive rate of *T. gracilis* in April as an example, Fig. 3 illustrates that increasing shade levels reduce  $T_b$  and consequently suppress digestive rates in general. In the current climate, the digestive rate was predicted to be severely suppressed in heavy shade levels (61–80%, 81–100%) at 3000 and 3500 m elevations due to very low  $T_b$ s. In the warmer climate, the predicted digestive rates increase in all simulated shade levels except heavy shade levels (61–80%, 81–100%) at 3500 m where the  $T_b$ s remain too low to support digestion (Fig. 3a).

The impact of the shade level on annual activity time, maintenance energy requirements and discretionary energy of *T. gracilis* in current and warmer climates is shown for snakes with mean VTs (Fig. 4) and snakes with a wide VT range (Fig. S2, Supporting information). In general, the impact of shade level on snakes predicted with these two sets of VT variables is similar. Therefore, only the results for a mean VTs snake are described below.

In the current climate, the predicted amount of annual activity hours was highest in the low and medium shade levels (Fig. 4a). The predicted active season was greatly reduced and even completely suppressed in the heavy shade level at 3000 and 3500 m. In the warmer climate, the predicted activity time is greater than that in the current climate for almost all shade levels at all three elevations.

The predicted annual maintenance energy requirements decrease with increasing shade levels at all three simulated elevations (Fig. 4b). Annual maintenance energy requirements in all shade levels increase in response to the warmer climate. In the current climate, the annual discretionary energy decreased with increasing shade levels at these three simulated elevations, and it was predicted to be very low or negative at heavy shade levels, that is, 61–80% and 81–100% (Fig. 4c). However, the discretionary energy is predicted to respond to the warmer climate differently across shade levels at these three elevations. At 2000 m, the predicted discretionary energy increases more in the heavy shade levels (61–80% and 81–100%) than in other shade levels because the digestive capacity is enhanced more in those heavy shade levels (Fig. 4c). But at 3000 and 3500 m, the predicted discretionary energy increases in all shade levels except in the heavy shade level (81–100%) at 3500 m. The impact of shade level on energetics of snakes in current and warmer climates estimated from a setting of 1.0 times standard metabolism for maintenance requirements is similar to the results reported above (Fig. S3, Supporting information).

#### LANDSCAPE SIMULATION: POTENTIAL ACTIVITY TIME, ENERGETICS AND POTENTIAL HABITATS OF *T. GRACILIS*

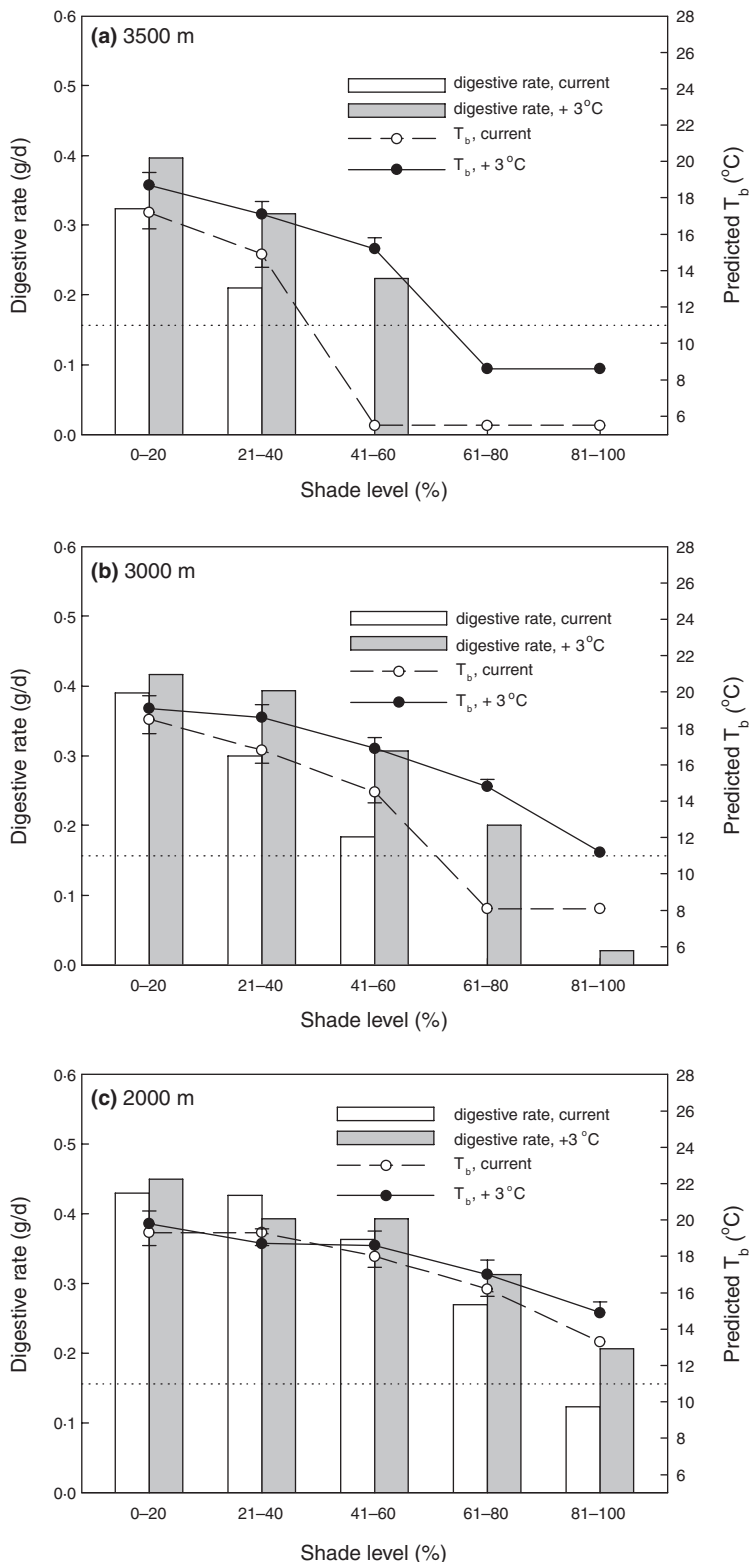
##### *In the current climate*

The estimated potential activity time, energetics and potential habitat sites of *T. gracilis* in the study area for a 32.0-g snake are shown in Fig. 5. The potential activity time (0–4078 h) was predicted to be highest along the eastern border and north-western margin and in many scattered sites within the study area (Fig. 5a). The annual maintenance energy ranged from 16.3 to 266.1 kJ (Fig. 5b), which required 3.3–53.9 g of food to support (Fig. 5c). The annual digestive capacity ranged from 0 to 140.9 g food (Fig. 5d). In a few places of the study area (11.8%), *T. gracilis* was predicted to be unable to complete the digestion of one mouse within a year. The discretionary energy was predicted to be zero or positive in about two-thirds of the study area (69.5%, c. 404.9 km<sup>2</sup>, Fig. 5e), indicated as thermally suitable habitats in Fig. 5f.

In general, the estimated suitable habitat area decreased with increasing elevation in two dominant forest categories (type A: natural coniferous forest/plantation, and type B: natural mixed coniferous-broadleaf forest/plantation; Fig. 6a, broken lines), but they did not significantly vary in other vegetation/land types among three elevation ranges (<2500 m, 2500–3000 m, >3000 m). The percentage habitable area (i.e. percentage area of a given vegetation/land category predicted to be habitable) in two dominant forest categories (type A and type B, Fig. 6b, broken lines) decreased markedly with increasing elevation, with a very minimal percentage of habitat at elevations higher than 3000 m (0.4% in type A, 7.4% in type B). Comparatively, the percentage habitable area in the other vegetation/land types did not vary significantly across the three elevation ranges (other types, 87.8–98.3%, Fig. 6b, broken lines). In general, the predicted discretionary energy of *T. gracilis* was lower in the types A and B forest habitats than that within other vegetation/land types (Fig. 6c, broken lines). At >3000 m elevation, the predicted discretionary energy in type A and type B habitats was extremely low (Fig. 6c). Our sightings were all located in suitable habitats ( $n = 90$ , in 27 grid cells, Fig. S4, Supporting information).

##### *In the future warmer climate*

In general, the activity time, maintenance energy requirements, food requirements and digestive capacity of a 32.0-g snake are all predicted to increase in the warmer climate in most of the study area (Fig. 7). Given the current pattern of vegetation/land types, suitable habitat (556.8 km<sup>2</sup>) increases mostly in the two dominant vegetation categories (type A and type B, Fig. 6a, solid lines). The percentage habitable area of these two categories significantly increases at elevations higher than 2500 m (type A and type B,



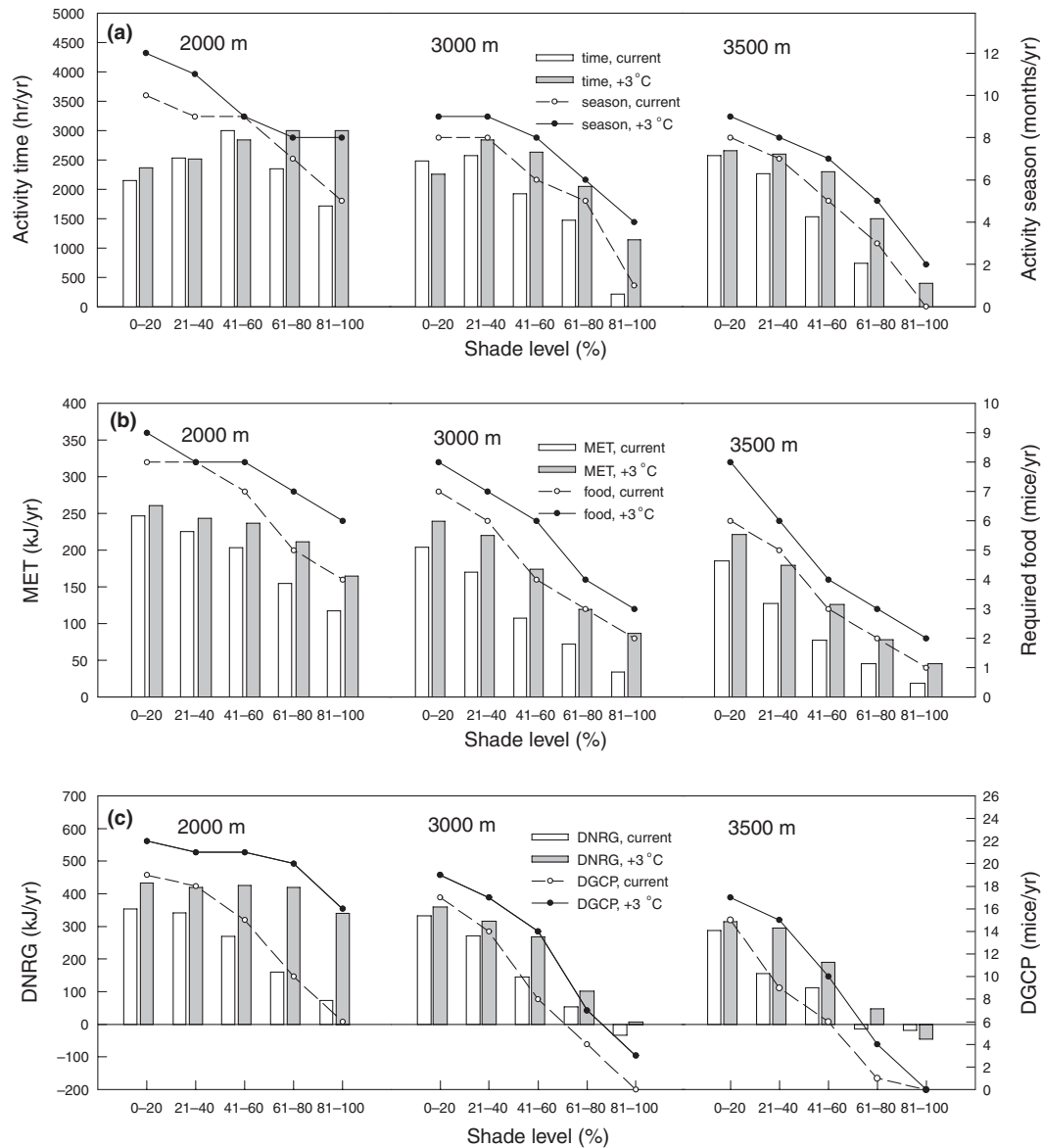
**Fig. 3.** The body temperature ( $T_b$ , mean  $\pm$  1 SE, shown in lines) and digestive rate (shown in bars) of a 32.0-g male *Triemesurus gracilis* in April in five shade levels at (a) 3500 m, (b) 3000 m and (c) 2000 m altitudes in current (hollow symbol/bar) and a 3 °C warmer climate (solid symbol/bar). The digestive rate (g per day) is converted from number of mice (6.4 g) digested in April. The means of  $T_b$  were calculated from 24-h body temperatures ( $T_{b,t}$ ) predicted for 15 April. The dashed line shows  $T_{b,crit}$ , the  $T_b$  at which digestion is assumed to cease.

Fig. 6b, solid lines). In general, the discretionary energy of *T. gracilis* in suitable habitat increases in the warmer climate (Fig. 6c, solid lines). Only in type A habitat higher than 3000 m does their discretionary energy remain low. The activity time, energetics and suitable habitat area of a 60.0-g snake in the current climate (Fig. S5, Supporting information) and the change of the above estimates in the

warmer climate are predicted to be similar to those of a 32.0-g snake (Figs S6 and S7, Supporting information).

## Discussion

The potential response of high-altitude reptiles to future warmer temperatures has never been explored from the



**Fig. 4.** Estimated annual (a) potential activity time, (b) maintenance energy requirements (MET) and (c) discretionary energy (DNRG) of a 32.0-g male *Trimeresurus gracilis* in five shade levels at three elevations (shown in bars). Estimated annual (a) number of active months, (b) required food for maintenance and (c) digestive capacity (DGCP; shown in lines).

energetic point of view in a landscape context. Here, NicheMapper incorporated the thermoregulation and characteristics of metabolism and digestion to estimate the energetics of *T. gracilis*, demonstrating that metabolism, digestive capacity and vegetative shade can be crucial elements affecting thermally suitable habitats in current and future climates. The shade level simulation provided an explanation of how shade levels at different elevations interact with climate to affect activity time and energetics. The landscape simulation showed that with climate change, the energetics and the assumed thermally suitable habitats of *T. gracilis* are dependent on vegetation/land types and elevation. These results have implications for future habitat management.

#### SHADE-LEVEL EFFECT ON ACTIVITY AND ENERGETICS OF *T. GRACILIS* AT HIGH ALTITUDES

Our results suggest that shade level is a crucial factor determining *T. gracilis*'  $T_{bs}$  and energetics. Higher shade levels reduce *T. gracilis*'  $T_{bs}$  and hence activity time, digestive capacity and energetics in general (Figs 3 and 4). The negative effect on activity time and maintenance energy requirements was particularly profound at heavy shade levels (e.g. 81–100% reduction of solar radiation) at 3000 and 3500 m. In these conditions, the digestive capacity of *T. gracilis* is predicted to be impaired, causing minimal or negative discretionary energy (Fig. 4). The ecological significance of such an impeded digestive capac-



ity is that heavily shaded places are energetically unsuitable for *T. gracilis*.

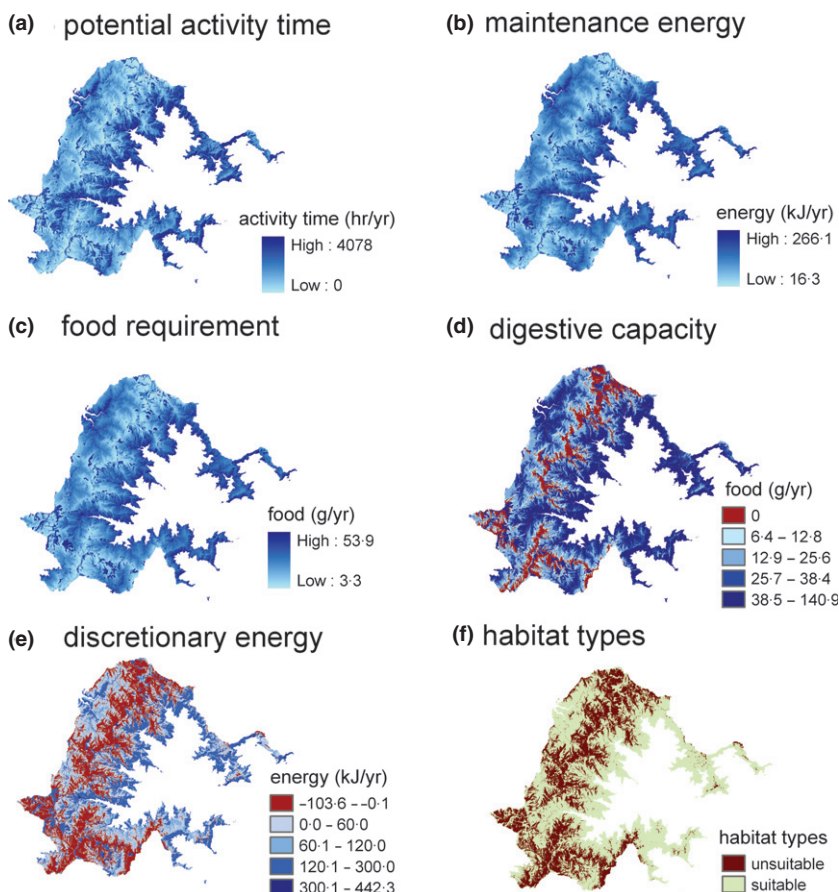
Our study addresses the temperature requirement of *T. gracilis*' digestion in high-altitude environments. Some evidence suggests *T. gracilis* prefers to utilize warm habitats in the active season despite good cold tolerance (e.g. low critical thermal minimum, Huang *et al.* 2007). This species exhibits obvious basking behaviour; they select for warm  $T_b$ s for digestion; and its feeding, defending and attacking behaviours showed optimal performance at  $T_b$ s higher than 20 °C and were severely reduced at low  $T_b$ s (below 10 °C; L. Chin & M.C. Tu, unpublished data). On the other hand, this study did not take into account the effect of mountain hypoxia on the energetics and activity time of *T. gracilis*. To the best of our knowledge, few studies report that reptiles are physiologically adapted to mountain hypoxia (e.g. Weathers & White 1972; Snyder & Weathers 1977; but Ruiz, Rosenmann & Nunez 1993). Hypoxia may have little impact on the energetics and activity time of *T. gracilis* due to their sedentary habits.

#### INTERACTION OF WARMER CLIMATE AND SHADE-LEVEL EFFECT ON ACTIVITY TIME AND ENERGETICS OF *T. GRACILIS*

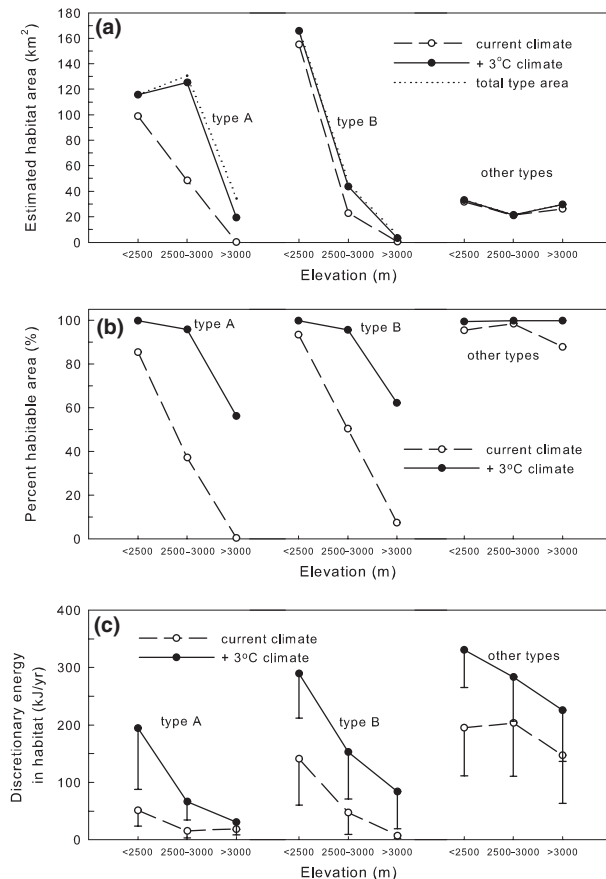
In a warmer climate, *T. gracilis* is predicted to increase activity time and maintenance energy in general (Fig. 4a, b). But the impact on discretionary energy and digestive

capacity among different shade levels varies among three elevations. At 2000 m, *T. gracilis* is predicted to have profoundly enhanced digestive capacity and hence more discretionary energy at heavy shade levels (e.g. 81–100%) than at other shade levels (Fig. 4c). In contrast, at 3000 and 3500 m in the heavy shade level (81–100%), the digestive function is predicted to rise very little or to remain impeded, barely covering the maintenance costs; in particular, at 3500 m, the discretionary energy is predicted to be more negative than it currently is.

These results contribute to a better understanding of the thermal ecology of high-altitude reptiles and their potential responses to climate change. First, our results offer a quantitative explanation of the importance of thermoregulation (e.g. Pearson & Bradford 1976; Christian 1998) to energetics and habitat utilization (Adolph 1990) in mountain reptiles. The effect of temperature on digestion has been widely studied in reptiles in the laboratory (Stevenson, Peterson & Tsuji 1985; Bedford & Christian 2000; Tsai, Lee & Tu 2008), but its influence on energetics in the field has never been analysed for high-altitude reptiles. Second, the vegetative shade can play an important but varying role in affecting reptiles' survival. It could be an environmental constraint to cold-climate heliotherms like *T. gracilis*, or it may be a vital cooling shelter for warm-climate heliotherms to avoid overheating (e.g. tropical species in Kearney, Shine & Porter 2009a). Third, our results suggest that shade level (vegetation) needs to be taken into



**Fig. 5.** Results of the simulations of (a) potential activity time, (b) maintenance energy requirements, (c) food requirements, (d) digestive capacity, (e) discretionary energy and (f) habitat type of a 32.0-g male *Trimeresurus gracilis*. Note the digestive capacity (g per year) is converted from number of 6.4 g mice. Maps (a–e) are annual simulations.



**Fig. 6.** The (a) estimated area of thermally suitable habitats, (b) percentage habitable area and (c) discretionary energy (mean  $\pm$  1SD) of a 32.0-g snake in three vegetation/land categories within three elevation ranges in the current climate and in an increase of 3 °C in air temperature. Percentage habitable area (%) =  $100\% \times (\text{predicted habitat area})/(\text{total area of the given vegetation type in the given altitude range})$ . Dotted lines in (a) show the total area of the vegetation/land types in each altitude range; these lines overlap the solid lines in some altitude ranges due to the scale of the figure. Vegetation/land types: type A: coniferous forest/plantation, type B: coniferous-broadleaf forest/plantation, other types: broadleaf forest/plantation, sparse coniferous/broadleaf/coniferous and broadleaf areas, grassland, seedlings, cultivated land, fruit farm, steep areas, rocky areas and avalanche areas.

account in future studies on the effect of climate change on heliothermic reptiles. A recent study (Sinervo *et al.* 2010) used a thermal model that employed only the mean  $T_b$  and the mean maximum air temperature to estimate the activity time of some reptiles. That approach may be reasonable for some thermoconforming reptiles, but it is not appropriate for heliothermic reptiles because the thermoregulation efficiency is shade dependent.

#### POTENTIAL ACTIVITY TIME, ENERGETICS AND HABITAT UTILIZATION OF *T. GRACILIS* IN THE STUDY AREA

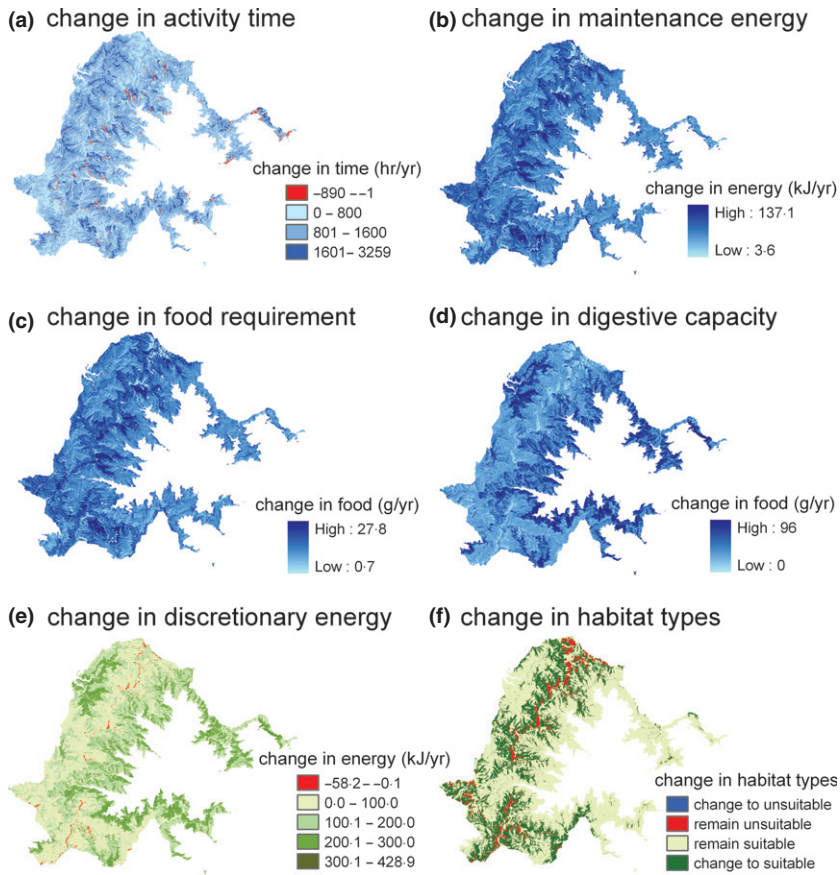
The majority (85.3%) of our study area is coniferous and coniferous-broadleaf forests/plantations (Fig. 2b). These

forests generate a cold microclimate for terrestrial animals by reducing solar radiation (up to 81.0%, T.H. Wey & P.H. Lin, pers. comm.). In the current climate, the habitable area predicted in the two dominant forest types decreases with elevation and becomes extremely small at >3000 m (Fig. 6a). At >3000 m, *T. gracilis* was predicted to have higher discretionary energy in habitats other than those in the two dominant forest types (Fig. 6c). This prediction agrees with our field observations, showing that *T. gracilis* is restricted to sunny places like rocky slopes and grasslands and is excluded from forest vegetation at altitudes >3000 m.

#### POTENTIAL WARMING EFFECT ON ACTIVITY TIME, ENERGETICS AND HABITAT OF *T. GRACILIS* IN STUDY AREA

Our results predict that *T. gracilis* can benefit from increasing air temperatures by having more potential activity time, discretionary energy and thermally suitable habitat in general (Fig. 7). Understanding whether *T. gracilis* truly gains an energy advantage, and hence more habitat, from increasing temperatures requires more information on prey abundance and vegetative structures. Some empirical work also reports that cool-climate ectotherms have benefited from increasing warmth in the past decade(s) (e.g. lizard: increased survival rates, body size, female fecundity, Chamaillé-Jammes *et al.* 2006; frog: increased winter viability, McCaffery & Maxell 2010; insect: increased thermally suitable habitats Thomas *et al.* 2001; Davies *et al.* 2006). However, an elevation shift in montane herpetological assemblages due to upslope displacement was documented in the tropics (Raxworthy *et al.* 2008). That study draws attention to the diversity and conservation of reptiles that have been threatened by biological impacts (e.g. vegetation alteration, novel species interaction) and human destruction of habitats.

This study highlights the idea that animal-vegetation interactions can vary among elevations and could change in future warmer temperatures (Fig. 6). In general, in the current climate, the suitable habitats of *T. gracilis* decrease with increasing elevation in the two dominant forest types but not in open places (Fig. 6a). In addition, the increase in percentage habitable area due to a warmer climate varies with elevation and different vegetation/land types (Fig. 6b). Therefore, if the vegetation/land pattern changes in the future, the habitat areas predicted in this study could also change accordingly. For example, it has been documented during past decades that the coniferous forest has expanded into grasslands and moves upslope in our study area (C.T. Chen, unpublished data), like other mountain vegetation around the world (Walther 2003; Rull & Vegas-Vilarrúbia 2006). These dominant forests provide less percentage habitable area than do other land types like grasslands (Fig. 6b). Therefore, this upslope forest expansion could lead to less suitable habitat above 3000 m than that predicted by this study that used current vegetation



**Fig. 7.** Results of the simulations of a 3 °C increase in air temperature as it changes (a) activity time, (b) maintenance energy requirements, (c) food requirements, (d) digestive capacity, (e) discretionary energy and (f) habitat types of a 32.0-g male *Trimeresurus gracilis*. The digestive capacity (g per year) is converted from number of 6.4 g mice. Maps (a–e) are of annual summations.

patterns. In that case, *T. gracilis* would be likely to congregate more in open grassland places at this higher elevation or to move downslope, as forest may be an energetically suitable habitat at a lower elevation (e.g. <3000 m, solid line in Fig. 6c) in the warmer climate. If *T. gracilis* expands its habitat into forest areas, it may change biological interactions within the forest.

To the best of our knowledge, the crucial factor limiting the altitudinal distribution of *T. gracilis* likely involves prey abundance. The diet of juvenile snakes is mainly lizards (Lin & Tu 2008). We found that in an altitude range below the current altitudinal ranges of *T. gracilis* (e.g. 1500–2000 m), the lizard species are either very rare species (three *Ophisaurus* spp.) or species whose habits or habitats (i.e. four arboreal *Japalura* spp. and humid forested dweller *Plestiodon elegans*) are distinct from those of *T. gracilis* (terrestrial habit and sunny habitats; Lue, Tu & Hsiang 1999). This could cause juvenile *T. gracilis* to suffer from a food shortage and affect the altitudinal distribution of this species. It remains unknown whether the current altitudinal distribution of *T. gracilis* is caused by its inferior ability to compete with lowland species. If lowland species move upwards in the future, they could increase competition in the habitats of *T. gracilis*.

As the wind speed setting has strong effects on our simulation results, the potential influence of wind speed on our findings merits discussion. First, the prediction of a negative effect on this species from dense vegetation remains robust.

Although we set a low wind speed (i.e. 0.1–1.0 m s<sup>-1</sup> at 2 m high) within most forest vegetation, we found that higher wind speeds intensify the negative effect of vegetative shade on the snakes' estimated energetics and digestive capacity (Appendix S4, Supporting information). Second, the predicted advantage of this species in sparse areas and open places should generally be greater in calmer sites and lesser in windier sites relative to that predicted with the default wind speed setting (0.1–4.0 m s<sup>-1</sup>). Similarly, if future global warming causes significantly stronger wind speeds (comparative to the default setting), the predicted energetic advantage for this species may also be reduced.

#### LIMITATION, FUTURE EXTENSION AND APPLICATION OF NICHEMAPPER

This research remains preliminary in investigating the impact of a future increase of 3 °C air temperature on *T. gracilis*. First, cloud levels, fog and seasonal changes in precipitation may all modify local microclimates, typically cooling them as they increase. If the warmer habitats become drier, snakes might not be as active as we suggest due to behavioural changes related to dehydration, impacts on prey populations, etc. The changes in these climate factors were also predicted to threaten Andean communities (Bush 2002). Second, the prey and predator interaction and lowland species' upslope movement could affect species' response to climate change



(e.g. Raxworthy *et al.* 2008). In the future, NicheMapper can be extended to evaluate species interactions by calculating the overlap of energetic demand and activity time of different species (Porter *et al.* 1973, 2002; Porter & James 1979). Also, data on prey distribution could be projected onto the thermally suitable habitats for more comprehensive understanding about potential habitats. Our approach can be used to predict environmental impacts on rare species that requires significant efforts to collect occurrence data, provided that the animal and environmental properties are available.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Description of thermal gradient apparatus.

**Appendix S2.** Description of major variables used in microclimate model.

**Appendix S3.** Development of equations to estimate digestive time.

**Appendix S4.** Sensitivity analyses.

**Fig. S1.** Validation of the simulated temperatures with temperature recordings in two field sites.

**Fig. S2.** Simulation results for a 32.0 g *T. gracilis* with a wide VT range.

**Fig. S3.** Simulation results for a 32.0 g *T. gracilis* with 1.0 times standard metabolism set for maintenance requirements.

**Fig. S4.** The sightings and the predicted suitable habitats in Taroko National Park.

**Fig. S5.** Simulation results of a 60.0 g snake in Taroko National Park in current climate.

**Fig. S6.** Simulation results of a 60.0 g snake in Taroko National Park in warmer climate.

**Fig. S7.** Simulated changes in habitat and discretionary energy of a 60.0 g *T. gracilis* in Taroko National Park in warmer climate.

**Table S1.** The parameters and equations used in this study.

**Table S2.** The vegetation/land types and assigned monthly shade levels in the study area.