

# Effect of species interactions on landscape abundance patterns

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## Summary

1. We develop a process-based bioenergetic model that incorporates population dynamics to predict the abundance trends for *Anolis* lizards along elevation gradients in the Lesser Antilles islands. Model outcomes are compared with empirical abundance trends on islands with and without species interactions and with differential topography.

2. The bioenergetic model incorporating body size, thermal physiology and prey abundance qualitatively predicts how lizard abundance declines with elevation for solitary anole species. Empirical elevation trends on northern and southern one-species islands have similar slopes but different intercepts at sea level. The greater anole abundance on the southern islands is predicted by the model when parameterized with the empirically observed higher insect abundance.

3. Anole abundance patterns on two-species islands diverge from the bioenergetic model predictions. One species is more abundant at sea level and the other more abundant at higher elevations compared with the trend for solitary anoles. Species interactions modify population responses to elevation gradients.

*Key-words:* bioenergetic model, competition, environmental gradient, habitat selection, lizard physiology.

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## Introduction

Environmental temperatures and topographic diversity are primary determinants of a solitary species' distribution. Interactions of two or more species along an environmental gradient modify responses to these factors (Heller & Gates 1971; Heller 1971; MacArthur 1972; Lawton 1993; Gaston 2003). Geographic range boundaries often coincide with identifiable climatic conditions (Muth 1980; Rogers & Randolph 1986; Caughley *et al.* 1987; Root 1988; Taulman & Robbins 1996). However, establishing whether climate causes observed correlations is difficult (Huntley 1994; Sykes, Prentice & Cramer 1996; Hill, Thomas & Huntley 1999; Gioia & Pigott 2000). Models that use environmental temperatures to predict species distributions of birds (Root 1988), butterflies (Kingsolver & Watt 1983; Bryant, Thomas & Bale 2002), mammals (Porter *et al.* 1994), and reptiles and amphibians (Tracy 1982; Porter & Tracy

1983; Porter 1989; Huey 1991; Grant & Porter 1992) are becoming increasingly mechanistic. However, this study is one of the first to couple energetic and population dynamic models to project species abundances on to a landscape.

Temperature-dependent metabolism has gained attention as a means to predict population growth rates (Savage *et al.* 2004) and species richness or distributions (Porter *et al.* 2000; Allen, Gillooly & Brown 2002). We use simple *Anolis* lizard communities on the Lesser Antilles islands to investigate how thermal energetics influence species distributions. Integrating individual energetic and population dynamic models is desirable but often prevented by community complexity and insufficient knowledge of life histories (Lawton 1991; Chown, Gaston & Robinson 2004).

How species interactions affect elevation trends in abundance has not been demonstrated (although the influence on distributions has been well demonstrated; Heyer 1967; Sullivan 1981; Conroy 1999). Environmental temperature interacts with species interactions and dispersal to determine species distributions, adding difficulty to isolating how each factor influences distributions in complex communities (Pearson & Dawson 2003). Our bioenergetic null-model provides a spatially explicit

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demonstration of how species interactions alter landscape-scale abundance patterns.

Our model of temperature-dependent foraging energetics predicts lizard abundance trends along an elevation gradient. We compare model outcomes with empirical abundance patterns on Lesser Antilles islands with and without species interactions and with differential topography. At the landscape scale, we hypothesize that abundance will decline with elevation due to thermal constraints on locomotion and metabolism. Further, we hypothesize that competing species partition the available energetic resources along the elevation gradient to enable coexistence.

#### LESSER ANTILLEAN ANOLIS MODEL SYSTEM

The simple anole communities on the Lesser Antilles islands enable understanding how competition and environmental temperatures interact to determine abundance distributions along elevation gradients. Each of the 27 Lesser Antilles islands contains either one anole species or a size-dimorphic pair of species (Creer *et al.* 2001; Schneider, Losos & deQueiroz 2001). Most species on the sympatric islands are separated in size by a factor consistent with Hutchinson's Rule, while most of those on one-species islands are of intermediate size (Schoener 1970). The degree to which sympatric anoles compete for resources is related to niche overlap in body size and perch position (Pacala & Roughgarden 1982) due to overlapping insectivorous diets (Schoener & Gorman 1968; Rummel & Roughgarden 1985).

Lizard survival varies inversely with island size and the number of bird species on small Bahamian islands (Schoener & Schoener 1978). As the species richness of birds, including predators, tends to increase with island size and with proximity to the equator (McLaughlin & Roughgarden 1989; Ricklefs & Lovette 1999), we would expect increasing predation with decreasing latitude. However, we observe a greater abundance of insects as well as lizards on the southern islands. This suggests that environmental temperature and prey abundance exert a greater influence on landscape-scale lizard abundance than predation on the study islands.

The northern and southern Lesser Antilles Islands are topographically distinct and their anole communities differ in phylogenetic origin. Northern anole species are related to anoles in Puerto Rico and western North America, whereas southern species have western South American affinities (Poe 2004). While the northern Lesser Antilles islands are predominately low elevation with steep mountains in the centre of the island, the southern islands tend to be more uniformly mountainous (Roughgarden 1995). By comparing altitudinal abundance patterns between the island groups, we can address whether the evenness of the distribution of area into elevation classes influences abundance patterns. The Lesser Antilles enable isolating the influence of species interactions and topography on habitat partitioning.

We examine these two factors – species interactions and topography – by comparing model outcomes to empirical abundance trends on four study islands. The northern one- and two-species study islands are Montserrat and St Kitts, respectively. The southern one- and two-species study islands are St Lucia and Grenada, respectively. On St Kitts, the smaller and larger species are *A. schwartzi* [mean snout vent length, SVL = 53.6 mm] and *A. bimaculatus* (78.5 mm), respectively. On Grenada, the smaller and larger species are *A. aeneus* (66 mm) and *A. richardi* (101 mm), respectively. On Montserrat and St Lucia, the solitary anole species are *A. lividus* (61 mm) and *A. luciae* (77 mm), respectively (Schoener 1970). Phylogenetic relatedness (Poe 2004; but see Losos *et al.* 2003) and similar habitat use (i.e. trunk-ground ecomorphs, Williams 1972) enable comparing habitat use by species on the one- and two-species islands. The island pairs have comparable topographic reliefs, vegetation types, and areas (with the two-species islands being somewhat larger than their one-species counterparts).

Anoles in the Lesser Antilles partition habitat at both local (within habitats) and landscape (between habitats along the elevation gradient) scales (Ricklefs & Schluter 1993). We focus here on landscape-scale habitat partitioning. A greater degree of broad scale habitat partitioning occurs in the southern islands (Roughgarden, Heckel & Fuentes 1983).

Among northern two-species islands, the smaller species numerically dominates everywhere on islands with size dimorphism and in higher-elevation forests on islands with little size dimorphism. A contrasting distribution pattern occurs on the southern islands, where the smaller lizard is restricted to open sites near sea level and the large anole is dominant in higher-elevation forests. Roughgarden *et al.* (1983) hypothesize that the more mountainous topography of the southern islands has resulted in a greater degree of landscape-scale habitat partitioning. We evaluate this hypothesis.

#### THE MODEL

Anole distributions are predicted using a behaviour-based model of anole population dynamics that predicts equilibrium abundance from foraging energetics. Foraging energetics provides a good basis for predicting lizard distributions as ectothermic lizards are strongly influenced by ambient temperatures (Spotila & Standora 1985) and foraging accounts for a large proportion of daily energy expenditures (Bennett & Gorman 1979). At the least, foraging energetics provides a sensible null model for addressing the influence of other factors such as species interactions and resource requirements (Muth 1980). The basic model, which we modify to incorporate thermal physiology by making the parameters temperature-dependent, is presented by Roughgarden (1997).

Briefly, the model assumes an individual anole is an energy maximizing sit-and-wait predator whose foraging

radius is limited by lizard density. The model is an animal counterpart for the neighbourhood model, where plants interact with their adjacent neighbours (Pacala & Silander 1985). The model assumes that the anoles forage on a linear interval ( $r$  to  $r + dr$ ). This simplifies spatial dynamics and produces model predictions that are comparable with empirical transect counts. This approach ignores the vertical distance an anole travels from its tree perch to its prey. The approximation is reasonable because anoles have similar intraspecific perch-height preferences (Schoener & Gorman 1968) and it is relatively seldom that multiple lizards are observed in the same tree at different heights.

The number of prey encountered in an interval is  $p(r)dr = adr$ , where  $a$  is prey density (insects per metre per second). If the cut-off distance, the maximum distance an anole is willing to run to obtain prey, is  $r_s$ , the average waiting time to encounter an insect is

$$t_w(r_s) = \frac{1}{\int_0^{r_s} p(r)dr} = \frac{1}{\int_0^{r_s} adr} = \frac{1}{ar_s} \tag{eqn 1}$$

and the average pursuit time, to the insect and return, is

$$t_p(r_s) = \frac{\int_0^{r_s} \left(\frac{2r}{v}\right)p(r)dr}{\int_0^{r_s} p(r)dr} = \frac{\int_0^{r_s} \left(\frac{2r}{v}\right)adr}{\int_0^{r_s} adr} = \frac{r_s}{v} \tag{eqn 2}$$

where  $v$  in the forager's sprint velocity. The foraging energetic yield per unit time,  $E(r)$ , of foraging within a radius,  $r$ , is derived as the energetic input less the energetic cost divided by the total foraging time:

$$E(r) = \frac{e_i - e_w t_w(r) - e_p t_p(r)}{t_w(r) + t_p(r)} \tag{eqn 3}$$

where  $e_i$  is the energy per insect;  $e_w$  and  $e_p$  is the energy per unit time expended waiting and pursuing, respectively, and  $t_w$  and  $t_p$  is time expended waiting and pursuing, respectively.

The handling time is assumed to be minimal and included in the pursuit time. The energetic cost of handling is included in the assimilation efficiency, as outlined below. At low lizard densities, the optimal cut-off distance for a solitary forager is the  $r_s$  that maximizes  $E(r_s)$ :

$$r_s = \frac{-(e_p - e_w) + \sqrt{(e_p - e_w)^2 + ave_i^2}}{ae_i} \tag{eqn 4}$$

Density dependence is introduced when crowding forces the territory size to be less than the  $r_s$  for solitary anoles. The model assumes that pairs of foragers are distributed facing each other along a circle of length  $L$  and that foragers equally partition foraging space (see Roughgarden 1997) for assumption rationale). The interindividual distance,  $d$ , for  $N$  foragers is then  $L/(N/2)$ , where  $L$  is the standard unit of length of a transect (1000 m).

To extend this model of individual foraging energetics to the scale of population dynamics, the change in population per unit time (production function) is calculated as the product of the population growth rate, based simply on birth minus death, and the population size,  $N$ , as follows:

$$\Delta N = (bE(r) - \mu)N \tag{eqn 5}$$

where  $\mu$  represents mortality and the reproductive cost of metabolism while not foraging and  $b$  is the reproductive rate per unit net energetic yield.  $\nu$  and  $b$  are lumped parameters,

$$\nu = \mu + m(\tau - \tau_f)e_r \tag{eqn 6}$$

$$b = m\tau_f \tag{eqn 7}$$

where  $\mu$  is the daily mortality,  $\tau$  is the day length ( $24 * 60 * 60$  s),  $\tau_f$  is the average daily foraging duration (seconds),  $e_r$  is the average metabolic rate while not foraging, and  $m$  is the quantity of eggs produced per joule of foraging yield times the probability of surviving to adulthood.

When the average distance between lizards on the transect is less than the energetically optimal foraging radius,  $r_s$ , each crowded lizard intakes less energy from foraging. This form of density dependence enables solving for the equilibrium population size. Explicit forms of the production function are used to solve for equilibrium population size (carrying capacity,  $K$ , where  $r = 0$ ) and the initial rate of population growth (the intrinsic rate of population increase,  $r_0$ ):

$$q_1 = be_p + \nu; q_2 = be_w + \nu; \tag{eqn 8}$$

$$q_3 = be_i a \nu + \sqrt{(be_i a \nu)^2 - 4a \nu q_1 q_2}$$

$$K = \frac{Lq_3}{2q_2 \nu} \tag{eqn 9}$$

$$r_0 = -\nu + b \frac{e_i - e_w / ar_s - e_p r_s / \nu}{1 / ar_s + r_s / \nu} \tag{eqn 10}$$

INCORPORATING TEMPERATURE DEPENDENCE

We make the model temperature-dependent by scaling running velocity and metabolic rates with temperature. Changes in lizard pursuit speed influence the energetically optimal foraging radius, the proportion of escaping insect prey, and the duration of foraging. Model predictions for population dynamics along the elevation gradient are contingent on whether the anoles are able to thermoregulate behaviourally along the elevation gradient.

Previous research on Caribbean anoles suggests that lizard habitat choice provides thermoregulation along elevation gradients (Huey & Webster 1976; Hertz 1979; Huey, Hertz & Sinervo 2003). While body temperature does drop somewhat with elevation, the drop is less

than the corresponding decline in environmental temperature (Hertz, Huey & Stevenson 1993; Huey *et al.* 2003). With increasing altitude, anoles perch in more open habitats (Rand 1964; Adolph 1990) and shift their activity times (Hertz 1981; Hertz & Huey 1981; Grant & Dunham 1990; Hertz 1992). Hertz & Huey (1981) show that, among anole populations along an altitudinal gradient, the degree of thermoregulation increases with increasing altitude. At the highest elevations, the slope of the regression of body temperature on ambient temperature is substantially less than 1 (Hertz & Huey 1981).

If we assume that active lizards are able to choose habitats to maintain their preferred body temperature, then metabolic rate and pursuit velocity are constant over the elevation gradient. In our model, a primary determinant of population dynamics is the time period during which a lizard is able to forage. When parameterizing the model with empirically observed environmental temperatures, the temperatures are never sufficiently warm to prevent midday foraging. Low temperatures at high elevation are the exclusive limitation to foraging duration in our model. Hence, populations of behaviourally thermoregulating lizards decline with elevation as their foraging duration declines. Conversely, metabolic rates and running speeds will vary along the elevation gradient and will influence abundance predictions if we do not assume that lizard habitat choice buffers changes in environmental temperature.

We examined the implications of behavioural thermoregulation along the altitudinal gradient by examining model outcomes under assumptions of both behavioural

thermoregulation and lack thereof. We only present predictions derived by assuming that lizards behaviourally thermoregulate to the temperature at which they reach maximum velocity, as empirical studies suggest that behavioural thermoregulation is quite effective and the model yields more realistic altitudinal patterns. The assumption may be approximate as lizards might thermoregulate to a temperature slightly below their optimal performance temperature (R. Huey, personal communication). We assume that the scale of dispersal relative to island size prevents intraspecific differences in thermal physiology along the elevation gradient (VanBerkum 1986; Sultan & Spencer 2002).

During periods of inactivity, we make the simplifying assumption that lizards are at their optimal body temperature. This assumption has a limited influence on energetics as the active metabolic rate is an order of magnitude greater than the inactive metabolic rate. We do not account for the thermal dependence of other metabolic parameters such as digestive rate (Vandamme, Bauwens & Verheyen 1991). Rates of digestion drop substantially as the body temperatures of inactive lizards declines with elevation (Angilletta 2001; McConnachie & Alexander 2004).

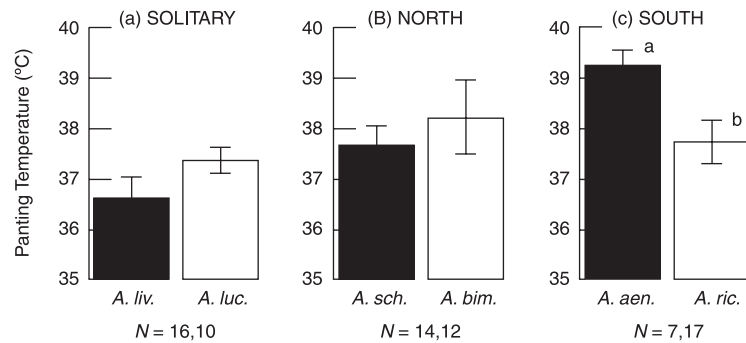
## MODEL PARAMETERIZATIONS

### Lizard parameters

Relations used to parameterize the bioenergetic model and their sources are presented in Table 1. Lizard mass is a power-law function of lizard SVL (Pough 1980;

**Table 1.** Relations for parameterizing the physiological model and their sources. Correlation coefficients are given when the relations were derived from data provided in the sources. Derivations of relations that are not directly reported in the source are provided in Appendix I

	Relation	Source
<i>Lizard parameters</i>		
Fresh mass, $M$ (g) from snout-vent length, SVL (mm)	$M = 3 \cdot 1 * 10^{-5} SVL^{2.98}$	Pough (1980)
Resting metabolic rate from mass, $M$ , and temperature, $T$ (°C) ( $O_2$ consumption, $mL O_2 h^{-1}$ )	$M R_{resting} = 0.28 M^{0.237-0.94}, r^2 = 0.57$	Bennett & Dawson (1976); Bennett (1982)
Maximum metabolic rate from mass, $M$ , and temperature, $T$ (°C) ( $O_2$ consumption, $mL O_2 h^{-1}$ )	$M R_{max} = 3.75 M^{0.0157-0.89}, r^2 = 0.72$	Bennett & Dawson (1976); Bennett (1982)
Metabolic rate conversion ( $mL O_2 h^{-1}$ to $J s^{-1}$ )	20.11	Bennett & Gorman (1979)
Maximal sprint speed ( $m s^{-1}$ ) from SVL (mm)	$v_{max} = 1.54 SVL^{0.30}, r^2 = 0.537$	Huey & Hertz (1982); Losos (1990)
Ratio of pursuit speed to maximum sprint speed	0.7	Irschick & Losos (1998)
Prey size (mm) from lizard SVL (mm)	$L_{insect} = 0.042 SVL + 0.15$	Schoener & Gorman (1968)
Proportion insect that can be assimilated	0.75 (approximate)	Kitchell & Windell (1972)
Assimilation efficiency (varied insectivorous diets)	0.75 (approximate)	Kitchell & Windell (1972)
<i>Foraging window parameters</i>		
Temperature, $T$ (°C), from elevation, $x$ (m), and hour, $h$	$T = 19.4 - 0.0065x + 1.58h - 0.06h^2$	Derived from NOAA NWS data
Temperature, $T_{maxv}$ (°C), of maximum velocity from panting temperature, $T_{pant}$ (°C)	$T_{maxv} = 0.8 T_{pant}$	Huey (1983); VanBerkum (1988)
Temperature, $T_{b80}$ (°C) of 80% of maximum sprint speed from $T_{maxv}$ (°C)	$T_{b80} = T_{maxv} - 4.6$	VanBerkum (1988)
Proportion of activity window that an individual lizard is active	0.75 (approximate)	Pacala (1982)
Proportion of activity time spent foraging	0.75 (approximate)	Bennett & Gorman (1979)
<i>Prey parameters</i>		
Insect abundance, $a$ (insects/(ms))	$0.016 \pm 0.003$	Unpublished data
Prey dry mass, $M$ (mg) from length, $L$ (mm)	$M_{insect} = 0.03 L^{2.5}$	Schoener (1977)
Prey energy content $J/mg_{drymass}$	23.85	Reichle (1971); Andrews & Asato (1977)



**Fig. 1.** The panting temperatures (°C) for (a) northern and southern solitary species; (b) northern sympatric species; and (c) southern sympatric species. The smaller and larger species of the species pairs are depicted with black and grey bars, respectively. Data are mean  $\pm$  SE. Bars with different letters are significantly different at  $P < 0.05$  ( $t$ -test). The smaller, southern sympatric species has a significantly higher panting temperature than the larger species.

Stamps, Losos & Andrews 1997). Lizard metabolic rate has been summarized at different body temperatures as a power-law function of mass, with the power-law exponent varying linearly with temperature (Bennett & Dawson 1976; Bennett 1982). Lizard maximum sprint speed is estimated as a power-law function of length (Huey & Hertz 1982; Losos 1990). We estimate lizard pursuit velocity as 70% of maximum sprint speed, corresponding to field observations by Irschick & Losos (1998).

#### Foraging window parameters

We calculate the foraging window using empirically derived diurnal trends for air temperature (NOAA NWS). The diurnal temperature trend was fit, using 2 years of hourly temperature data collected at sea level on St Lucia, with a parabola. Ocean buffering maintains fairly warm night-time temperatures, resulting in a parabola fitting the diurnal temperature trend better than a sine wave. The shape of the diurnal temperature trend at higher elevations is assumed to approximate that at sea level. Higher altitudes tend to experience larger diurnal temperature fluctuations (Rundel 1994). However, this trend is likely moderated by ocean buffering. Assuming that lizards maintain optimal body temperatures while inactive eliminates the need to account for the altitudinal trend in night-time temperature fluctuation. We use the wet adiabatic lapse rate (0.65°C per 100 m) to shift the diurnal temperature trend with elevation (Table 1). The environmental temperature (measured by a grey body or biophysical calculation; Roughgarden, Porter & Heckel 1981; Shine & Kearney 2001), is a better predictor of lizard body temperature than air temperature. However, we use air temperature data in this study as extensive time series data are available.

Once a site becomes sufficiently warm, lizard velocity increases linearly as a function of temperature to the lizard's maximum velocity. The velocity then remains near maximum before declining rapidly when approaching the upper critical temperature (VanBerkum 1986;

Hertz, Huey & Garland 1988; Bennett 1990; Irschick & Losos 1998). We assume that lizards thermoregulate to the temperature at which they reach maximum velocity, which consistently occurs at 80% of their critical upper temperature. The proportional temperature at which maximum velocity occurs is consistent for Costa Rican and Puerto Rican anoles (mean  $\pm$  SE = 0.80  $\pm$  0.010;  $n = 7$  species; Huey 1983; VanBerkum 1986, 1988).

We empirically estimated the upper critical temperature – the temperature at which lizards pant and are too warm for activity – by holding the lizards, caught at sea level, in the sun until they begin to pant (Hertz & Nevo 1981; Roughgarden 1995; Fig. 1). On the northern two-species island, the smaller species reaches its thermal maximum at a lower temperature, consistent with its lesser thermal inertia. In contrast, on the southern two-species island, the smaller species has a significantly greater panting temperature.

Foraging is restricted to periods of sunlight when the environmental temperature is sufficiently high for lizards to forage effectively. At what temperature can a lizard begin foraging? We conducted morning counts of active lizards. We confirmed that foraging begins at temperatures above the lowest temperature at which lizards are able to move (unpublished data). However, variability prevented our deriving a conclusive relation describing how temperature and time of day determine when lizards begin foraging. We assume that lizards forage when they can run at least 80% of their maximum sprint speed. The temperature breadth within which Costa Rican anoles can sprint at least 80% of capacity is consistent (mean  $\pm$  SE = 9.2  $\pm$  0.48;  $n = 7$ ; VanBerkum 1988). We thus assume that lizards initiate foraging at temperatures 4.6°C below the temperature of maximum velocity.

We assume that lizards are active for three-quarters of the activity window (Pacala 1982) and that three-quarters of the activity time is spent foraging (Bennett & Gorman 1979). We account for the metabolic cost (assuming the resting metabolic rate) for the portion of the activity window during which the lizard is not foraging.

*Prey parameters*

We account for decreasing proportional prey capture with decreasing lizard sprint speed by defining  $f$  as the probability per second that an insect moves from its initial location (Roughgarden 1995). We assume that the probability of the insect remaining stationary for  $t$  or more seconds is distributed exponentially with parameter  $f$ ,  $e^{-ft}$  (adapted from Roughgarden 1995). The successful fraction,  $F$  of all pursuits within the cut-off distance,  $r_s$ , where  $r$  is the distance from a given insect to the lizard and  $v$  is lizard velocity, is

$$F(r_s) = \int_0^{r_s} e^{-\frac{fr}{v}} = -v/f \left[ e^{-\frac{2fr_s}{v}} - 1 \right] \quad \text{eqn 11}$$

We reduce the energy input per insect by the proportion of pursued insect that are not caught.  $F$  is a free parameter as empirical data are unavailable. We estimate  $f$  to be 0.5 by solving for when the lizard foraging cut-off radius is 2 m, an empirically realistic value.

We estimate prey length as a function of lizard SVL using data from the intermediate sized anole, *A. roquet* on Martinique (Schoener & Gorman 1968). Although the data choice does not qualitatively change model outcomes, we chose their Martinique data over data for Grenada. The Grenada data predict that large lizards eat larger prey than characteristically available in some areas of the Lesser Antilles (Rummel & Roughgarden 1985). Conversions from insect head length to dry mass (Schoener 1977), energy content (Reichle 1971; Andrews & Asato 1977) and ultimately assimilated energy (Kitchell & Windell 1972) are provided in Table 1.

*Insect abundance*

We assume that insect abundance is log-normally distributed with mean 1.15 mm and variance 2 mm, corresponding to insect data for a tropical wet forest (Schoener & Gorman 1968). We determine the abundance of a specified prey size by multiplying the overall insect abundance by the probability density function for the specified prey size. As we lack data on the breadth of prey sizes consumed, we assume that the lizards are picky and calculate abundance based on a single prey size.

We empirically measured insect abundance along the elevation gradient on each island (methods in Appendix I). Elevation is not a significant determinant of insect abundance on any of the study islands (maximum likelihood mixed effect model with site as a random effect,  $F$ -test,  $P > 0.1$  for each island). Among the northern and southern two-species islands, the southern island has significantly more insects ( $F_{[8,231]} = 25.67$ ,  $P < 0.001$ , ANCOVA with elevation as the covariate). Although the difference is not significant, the southern one-species also tends to have more insects than the northern island ( $F_{[7,180]} = 0.67$ ,  $P < 0.5$ , ANCOVA with elevation as the covariate). The model was parameterized with island-specific insect abundances [St Kitts:

0.009 ± 0.0006,  $n = 96$ ; Grenada: 0.037 ± 0.006,  $n = 80$ ; Montserrat: 0.008 ± 0.0008,  $n = 80$ ; St Lucia: 0.011 ± 0.0007,  $n = 80$  insects/(m\*s) (mean ± SE)].

*Model sensitivity*

The most uncertain model parameter is insect abundance. Hence, we use the 95% confidence intervals of empirically measured insect abundance to depict the sensitivity of the model outcomes. This may underestimate the actual variance as insect measurements were conducted in a single day on each island. However, it does reveal how the relative abundance patterns of lizards respond to insect abundance. We also examine the model sensitivity to other less-certain parameters. Varying the proportion of maximum velocity at which a lizard begins foraging does not alter the predicted relative abundance patterns. Decreasing the proportion of maximum velocity at which foraging initiates primarily increases the maximum elevation at which the lizards are able to persist. Insect flightiness,  $f$ , is a free parameter. Varying  $f$  does not influence relative abundance patterns but does shift the absolute abundance trends. Increasing the insect flightiness decrements the energetic yield of foraging. Decreased energetic yield decreases both the predicted abundance and the maximum elevation at which lizards are able to persist. All other parameters are derived from empirically well established lizard morphology and physiology.

**Empirical methods**

## SITE SELECTION

We used topographic maps, digital elevation models and remotely sensed images (Landsat TM) to identify both windward and leeward elevation gradients on each island. Sites were distributed along the gradient and chosen to contain representative habitat types, a low abundance of cultivated species, relatively undisturbed habitat with a minimum of edge effects, and canopies less than approximately 10 m high to facilitate anole observations. Observations were conducted in June–August of 2002 and 2003, which is within the wet season. A total of 64 sites were distributed among the four islands. The two-species islands were visited both years and the one-species islands in the later year. We surveyed between the hours of 10:00 and 16:00 h to maintain temperatures and light intensities that are reasonably constant and adequate to enable microclimate partitioning. Day and time of observation were randomized with respect to site elevation.

Anole abundance was estimated by pacing an approximately 100-m linear transect for a constant search time (2 h). This method, analogous to bird point counts, allows greater geographical coverage than mark and recapture techniques with only a minor loss of accuracy for the present purposes (Diaz 1997). Repeat censuses of sites in the subsequent year confirms the robustness (both

relative and absolute abundance) of the censusing technique [mean abundance change:  $20\% \pm 0.08$ , mean species identity change:  $10\% \pm 0.09$  (data mean  $\pm$  SE,  $n = 9$ )]. The transect was chosen to be passable, representative and to have little or no elevation change. Vegetation was scanned for anoles from the forest floor to canopy within 2 m on each side of transect. If 100 m was travelled in less than 2 h, an additional transect was surveyed parallel to and approximately 5 m apart from the original transect. Upon observation of an anole, we recorded microclimate at the lizard perch and perch height measurements before resuming the survey. Estimates of abundance differences are conservative as more time was spent recording lizard data where lizards were more abundant. All surveys were conducted by the first author. We use the elevation mean of the two ends of the transect, measured using GPS and conformed using digital elevation models.

#### STATISTICAL ANALYSIS

All analyses were performed using R (R Foundation for Statistical Computing). Panting temperatures were compared using  $t$ -tests. Anole abundance trends as a function of elevation were fit using least squares algorithms. We report analysis of variance  $F$  statistics,  $P$ -values and coefficients of determination. For exponential fits, we note that the nonlinear analogue of  $r^2$  values is conservative, but violates the  $r^2$  identity as the residual sum of squares (SS) and regression SS do not sum to the total SS (Juliano & Williams 1987). We compare the slopes and intercepts among the one- and two-species islands using an analysis of covariance. Mean abundance is presented for resampled sites. Abundance data collected during the summer of 2002 for nine sites on St Kitts was adjusted, using time trials for collecting microclimate data, to account for instrument failure that prevented collecting microclimate data. A volcanic eruption on Montserrat in July 2003 influenced abundance estimates. Abundance outliers were identified by plotting Cook's distances and standardized residuals. Consequently, the Montserrat sites experiencing more than 2 cm of volcanic ash deposition were excluded from the plot and regression (Ash deposition map provided by the Montserrat Volcano Observatory).

## Results

#### VALIDATING THE MODEL FOR SOLITARY ANOLES

##### Model outcomes

We validate the model for northern and southern solitary anoles (Fig. 3). Once the model outcomes correspond to empirical abundance trends for solitary anoles, we can then transfer the model to two-species islands assuming noninteractive species and predict the sympatric species distributions in the absence of interactions. If we falsify these noninteractive predictions,

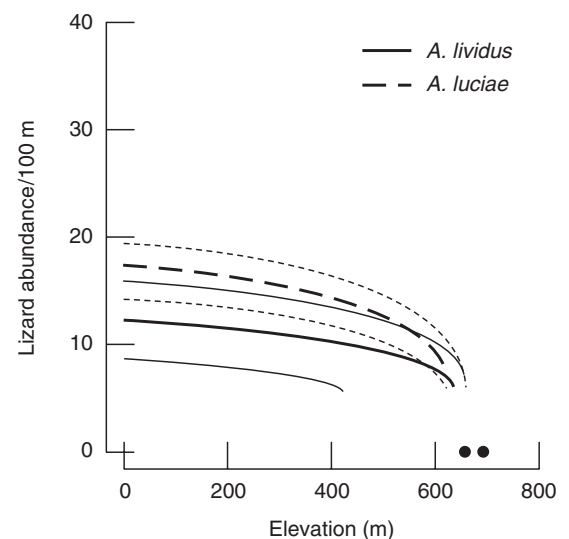
we can evaluate whether species interactions can account for the divergence from the bioenergetic null model.

The model yields undefined equilibrium anole abundance at high elevations where the predicted density of anoles drops below that required for density dependence. We use the density-independent cut-off radius,  $r_s$ , to solve for the elevation where the intrinsic rate of population increase declines to zero (i.e. where equilibrium abundance reaches zero). It is reasonable to extrapolate that abundance declines continuously to zero from the beginning of the density-independent zone to the elevation at which the intrinsic rate of increase is zero.

The model outcomes for solitary anoles show that abundance declines gradually at low elevation before rapidly decreasing at higher elevations. The model produces similar abundance trends for the northern and southern solitary anoles throughout the confidence interval for insect abundance. However, the southern species tends to be slightly more abundant and to persist at a slightly higher elevation along the elevation gradient, due to greater insect abundance (Fig. 2).

#### Empirical results

The empirical abundance of solitary anoles declines with elevation. The abundance pattern on the southern island, St Lucia, is well fit by a two-degree polynomial ( $r^2 = 0.81$ ,  $F_{[2,7]} = 14.93$ ,  $P < 0.01$ ). A linear trend fits as well ( $r^2 = 0.73$ ,  $F_{[1,8]} = 21.69$ ,  $P < 0.01$ ). On the northern island, Montserrat, the curvilinear fit ( $r^2 = 0.90$ ,  $F_{[2,5]} = 23.81$ ,  $P < 0.01$ ) is nearly linear and similar to



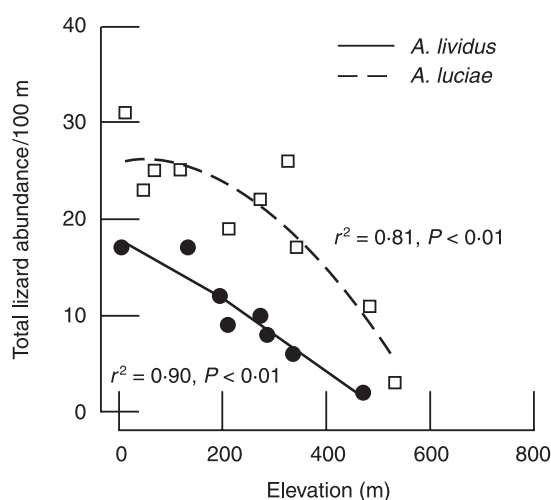
**Fig. 2.** Predicted lizard abundance per 100 m as a function of elevation on the single species islands. The model outcomes, produced by parameterizing the model with the mean and upper and lower 95% confidence intervals of island insect abundances, are presented to examine the model sensitivity. The predictions for the northern solitary species are depicted with a solid line, while those for the southern solitary species are depicted with a dashed line. The dots indicate the elevations where the intrinsic rates of increase reach zero. Lizard abundance is predicted to decrease with elevation. Higher insect abundance increases the predicted lizard abundance.

a linear fit ( $r^2 = 0.90$ ,  $F_{[1,6]} = 55.24$ ,  $P < 0.001$ ). The quadratic term does not significantly improve the fit on either Montserrat ( $F = 0.15$ ,  $P < 0.71$ , ANOVA) or St Lucia ( $F = 2.93$ ,  $P < 0.13$ , ANOVA). However, we depict the polynomial fits to correspond to the model outcomes and the trends on two-species islands. The linear abundance declines have nearly equivalent slopes on Montserrat and St Lucia (slopes  $\pm$  SE =  $0.035 \pm 0.0047$ ,  $n = 8$ , and  $0.0384 \pm 0.005$ ,  $n = 10$ , respectively). The difference in slopes is highly nonsignificant ( $F_{[1,14]} = 0.07$ ,  $P = 0.79$ , ANCOVA).

While the slopes of the abundance decline are indistinguishable between the islands, the estimated sea-level abundances (model intercepts) are significantly different. The estimated sea-level abundance on Montserrat (estimate  $\pm$  SE =  $18.6 \pm 1.30$ ) is approximately two-thirds that on St Lucia (estimate  $\pm$  SE =  $29.5 \pm 2.46$ ). The sea-level abundance difference between islands is highly significant ( $F_{[1,14]} = 35.77$ ,  $P < 0.0001$ , ANCOVA). We derive the same conclusion that the shapes of the abundance trend are indistinguishable ( $F_{[2,12]} = 0.59$ ,  $P = 0.57$ , ANCOVA) and that there is an island effect in abundance ( $F_{[1,12]} = 45.17$ ,  $P < 0.0001$ , ANCOVA) when considering polynomial regressions in the ANCOVA.

#### Comparing model outcomes to empirical patterns

The model succeeds in predicting the empirically observed decline in lizard abundance along the elevation gradient. However, abundance declines more rapidly with elevation than theoretically predicted on the one-species islands (Figs 2 and 3). The model correctly predicts that the southern solitary species will be more abundant everywhere (Fig. 2). Population abundance declines to zero at a lower elevation than predicted on both one-species islands.



**Fig. 3.** Anole abundance (along a 100-m transect) with respect to elevation on the two one-species islands. The southern solitary species is presented with open symbols and dashed regression lines. Abundance trends are fit with two-degree polynomials. Decreasing abundance with elevation is observed on all islands.

#### TESTING THE MODEL FOR SYMPATRIC ANOLES

##### Model predictions

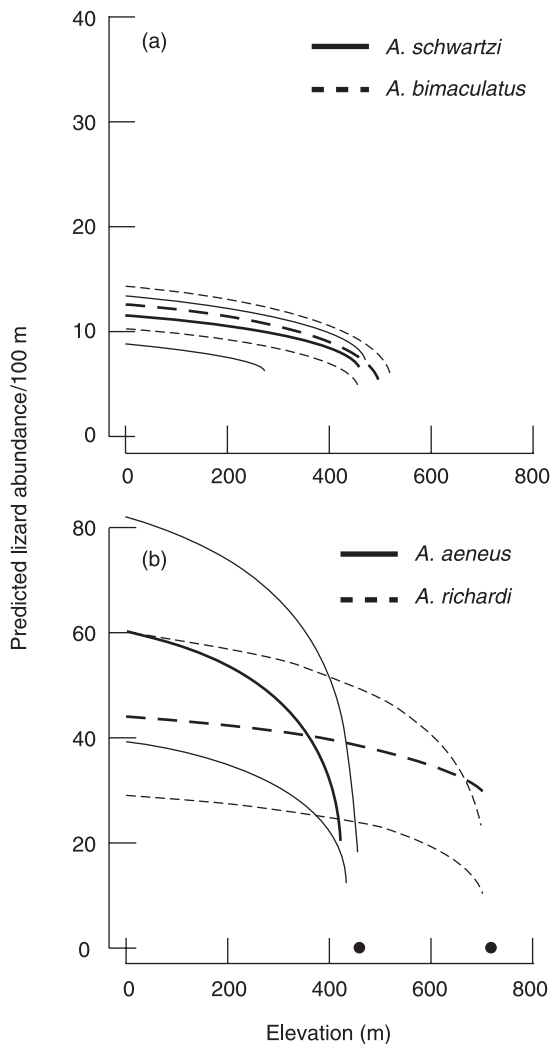
As the empirical data qualitatively matches the theoretical predictions for solitary anoles, we next compare the empirical data from two-species islands with the bioenergetic model outcomes. As the model is applied to each species independently, it serves as a null model to detect species interactions. Species-specific parameterizations enable addressing how morphology and physiology result in differential model outcomes for sympatric species. On the northern two-species island, the model cannot distinguish the abundance predictions for the smaller and larger species (Fig. 4a). On the southern two-species islands, we predict that the smaller, warm adapted lizard will be more abundant than the larger lizard at low elevation but will decline in abundance at a substantially lower elevation (Fig. 4b). The pattern holds throughout the confidence interval for insect abundance, as the insect abundance parameter will have the same value for both of the sympatric species on an island.

##### Empirical results

The trends for pooled species abundance on both the northern and southern two-species islands have a similar shape to the abundance trend on the one species islands, suggesting a systematic abundance response to elevation (St Kitts:  $r^2 = 0.60$ ,  $F_{[2,15]} = 11.06$ ,  $P < 0.001$ ; Grenada:  $r^2 = 0.54$ ,  $F_{[2,15]} = 8.93$ ,  $P < 0.01$ ; Fig. 5a,b). As with the one-species islands, pooled abundance is (nonsignificantly) higher on the southern two-species island compared with the northern two-species island ( $F_{[1,30]} = 2.59$ ,  $P < 0.12$ , ANCOVA). The shape of the abundance trend is indistinguishable between the northern and southern islands ( $F_{[2,30]} = 0.04$ ,  $P = 0.96$ , ANCOVA). Summed abundance declines to zero at a similar elevation on both two-species islands.

The empirical landscape-scale patterns of species abundance diverge from the trends for solitary anoles when an additional anole joins a community. The abundance trends are similar on both two-species islands with one species declining in elevation above sea level and the other species reaching peak abundance at mid elevation (Fig. 5c,d). We observe a reversal in the position of the larger species between the two islands. On the northern island, St Kitts, the larger species is most abundant as low elevation. On the southern island, Grenada, the larger species reaches peak abundance at mid elevation.

Both species are present at approximately equal abundance in the predominate low-elevation habitat on St Kitts (Fig. 5c). Above sea level, the smaller species, *A. schwartzi* increases in abundance to a maximum at mid-elevation, while *A. bimaculatus* abundance declines rapidly to zero. *A. schwartzi* abundance over the elevation



**Fig. 4.** Predicted lizard abundance per 100 m as a function of elevation for the (a) northern and (b) southern two-species islands. The model outcomes, produced by parameterizing the model with the mean and upper and lower 95% confidence intervals of island insect abundances, are presented to examine the model sensitivity. The predictions for the smaller sympatric species are depicted with a solid line, while those for the larger sympatric species are depicted with a dashed line. The dots indicate the elevations where the intrinsic rates of increase reach zero. Lizard abundance is predicted to decrease with increasing elevation. Higher insect abundance increases the predicted lizard abundance.

gradient fits a two-degree polynomial ( $r^2 = 0.59$ ,  $F_{[2,15]} = 10.66$ ,  $P < 0.001$ ). The abundance of *A. bimaculatus* declines exponentially with elevation ( $r^2 = 0.67$ ,  $F_{[2,16]} = 31.94$ ,  $P < 0.001$ ).

In contrast to the approximately equal species abundances at low elevation on St Kitts, the abundance of the smaller species on Grenada, *A. aeneus*, is spatially variable at low elevation (Fig. 5d). At every site below 50 m on Grenada, the density of one species is greater than or equal to the mean abundance, averaged across sites and species, while the abundance of the other species is less than the mean abundance. At higher elevations, *A. richardi* abundance gradually declines while *A. aeneus* remains present at low abundance.

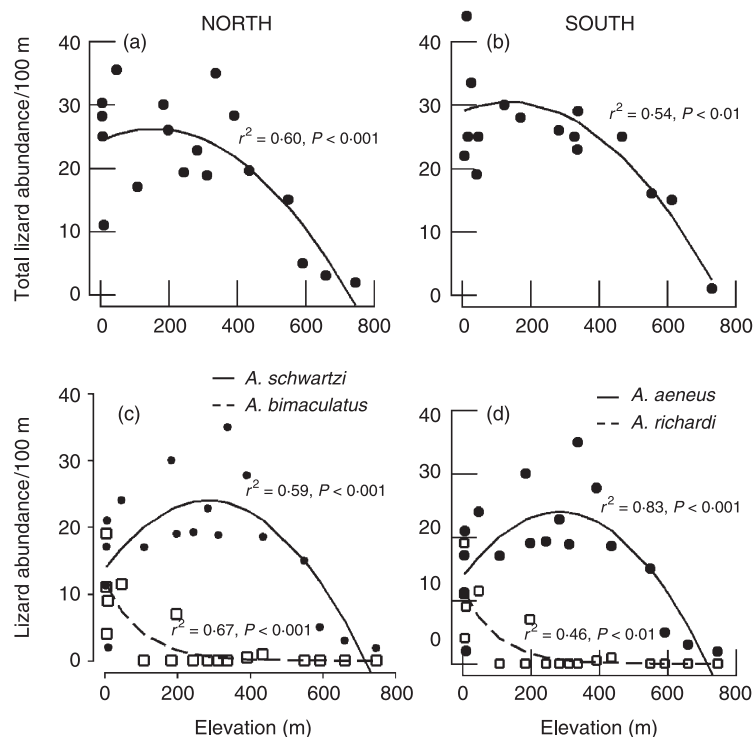
The site at an elevation of 125 m has exceptionally high *A. richardi* abundance. We excluded the site from the regression (by Cook's distances and standardized residual tests). *A. richardi* abundance along the elevation gradient at remaining sites with elevations greater than 50 m fits a two-degree polynomial ( $r^2 = 0.83$ ,  $F_{[2,8]} = 19.41$ ,  $P < 0.001$ ). The abundance of *A. aeneus* declines in a log-log-linear manner with elevation as it remains in the community at low abundance ( $r^2 = 0.46$ ,  $F_{[2,16]} = 13.67$ ,  $P < 0.01$ ).

#### Comparing model predictions to empirical patterns

The empirical abundance trends on the two-species islands falsify the outcomes of the bioenergetic null model. The model predicts humped-shaped abundance trends for all species (Fig. 4). In contrast, one species on each island has a convex declining abundance trend. The model predicts the observed mass reversal in the position of the species. In southern Grenada, the smaller species is warm adapted. Accordingly, the model successfully predicts that the larger species will persist in the community at substantially higher elevations than the smaller species (Fig. 5d). The model predicts that the smaller species will be more abundant at low to mid elevation than the larger species. Empirically, the smaller species exhibits a spatially patchy abundance pattern at low elevation before dropping to very low abundance not far above sea level. On the northern St Kitts, the sympatric species have indistinguishable thermal physiologies and are predicted to have similar abundance trends with elevation. Hence, the model fails to predict that the smaller lizard is more abundant everywhere and persists at higher elevations compared with the larger species (Fig. 5c).

#### Discussion

The landscape abundance patterns predicted by the bioenergetic model qualitatively correspond to empirical trends for both northern and southern solitary anoles. Quantitatively, the empirical abundance declines for solitary species are more continuous and steeper along the elevation gradient than the model outcomes. A declining ability to thermoregulate behaviourally to the optimal performance temperature at cooler, higher elevation sites would account for this quantitative divergence from the bioenergetic null model. Limited night-time digestion at high elevations may also contribute to the slope discrepancy (Angilletta 2001; McConnachie & Alexander 2004). The similar slopes of the abundance declines on the northern and southern one-species islands illustrate that environmental temperature influences population dynamics in a consistent manner (Hutchins 1947). Similarly shaped pooled abundance trends for the northern and southern sympatric anoles provide additional support for a systematic response to environmental temperature.



**Fig. 5** Anole abundance (along a 100-m transect) with respect to elevation on the two-species islands. The top row depicts abundance summed across the sympatric species. The bottom row depicts abundances individually for each sympatric species. The left and right columns present data for the northern and southern islands, respectively. The larger of the species pair is presented with open symbols and dashed regression lines. Abundance trends are fit with either a two-degree polynomial or exponential decline. The regression for *A. richardi* on Grenada is fit for sites above 50 m due to patchy abundances. Decreasing total abundance with elevation is observed on the two-species islands, but the trend diverges from hump-shaped trend for individual species.

The greater lizard abundance on both the southern one- and two-species islands, compared with the northern islands, corresponds to greater resource availability (i.e. insect abundance). The overall species richness of most animal groups is also greater in the southern islands. The two northern study islands each contain approximately 25 bird species, while the southern islands contain approximately 40 bird species (Ricklefs & Lovette 1999).

We falsify the bioenergetic model predictions for the abundance of each sympatric species. Among species pairs in both the predominately low elevation northern island and the more mountainous southern island, abundance trends for the sympatric anoles diverge from those for solitary anoles along the elevation gradient. One anole is more abundant at low elevation than predicted for a solitary anole; the other species is less abundant at low elevation and more abundant at mid elevation than predicted for a solitary anole. The greater spatial resolution of our study reveals more complex landscape abundance patterns than those observed in a preliminary study (Roughgarden *et al.* 1983).

Roughgarden *et al.* (1983) observed a greater degree of habitat specialization on islands with a more equitable distribution of area into elevation classes. High-forested and low-scrubby sites are more equitably distributed in the mountainous southern islands compared with

the predominantly low-scrubby northern islands. A theoretical model confirmed that species will specialize in habitats that are equally abundant, but coexistence is anticipated when a single habitat type dominates (Roughgarden *et al.* 1983). The initial observations found that the smaller species will be more abundant throughout the northern island (Roughgarden *et al.* 1983). We confirm this prediction and find that both species are present at approximately equal abundance at low-scrubby sites. At high-forested sites, the smaller *A. schwartzi* increases in abundance while the larger *A. bimaculatus* is entirely absent from the community. On the more mountainous southern island, Roughgarden *et al.* (1983) hypothesize that the larger anole specializes in high-forested sites, while the smaller anole specializes in low-scrubby sites. The larger *A. richardi* is indeed dominant in high-forested sites. However, the smaller *A. aeneus* is not dominant at all low elevation sites. Rather, it is patchily distributed, being numerically dominant at some sites and nearly absent from others.

The bioenergetic model examines how species specialize along altitudinal gradients, evaluating the height of 'mountain passes' in the tropics (Janzen 1967). Huey (1978) demonstrated that patterns of herpetile similarity are consistent with tropical species having narrower altitudinal ranges. The model is used to demonstrate that *A. aeneus*' higher panting threshold enables specialization to warmer, low-elevation sites. The model

parameterization assumes constant thermal constraints and morphological traits along the elevation gradient, due in part to dispersal between habitats (VanBerkum 1986; Sultan & Spencer 2002). This assumption is unlikely to influence elevation trends in abundance as the influences of morphological adaptations (e.g. colour and/or size) on population dynamics are overshadowed by behavioural differences (e.g. microhabitat choice) (Porter & Tracy 1983; Stevenson 1985; Huey *et al.* 2003).

Environmental temperatures govern anole distributions in the Lesser Antilles. Additional factors, such as water availability or the viability of eggs, may be the primary determinants of lizard distributions elsewhere (Muth 1980). In these cases, the bioenergetic model can be used as a null model to understand species distributions. Species interactions superimpose on the systematic, temperature-mediated responses to elevation gradients to produce novel spatial abundance patterns. A model has been developed that uses the energetic implications of environmental temperatures along the elevation gradient to successfully predict abundance declines for solitary anoles. The noninteractive model was falsified for two-species islands. Species interactions is the most tenable factor to account for the abundance trends on two-species islands.

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### References

- Adolph, S.C. (1990) Influence of behavioral thermoregulation on microhabitat use by two *Sceloporus* lizards. *Ecology*, **71**, 315–327.
- Allen, A., Gillooly, J. & Brown, J. (2002) Global biodiversity, biochemical kinetics, and the energetic equivalence rule. *Science*, **297**, 1545–1548.
- Andrews, R. & Asato, T. (1977) Energy utilization of a tropical lizard. *Comparative Biochemistry and Physiology*, **58A**, 57–62.
- Angilletta, M.J. (2001) Thermal and physiological constraints on energy assimilation in a widespread lizard (*Sceloporus undulatus*). *Ecology*, **82**, 3044–3056.
- Bennett, A.F. (1982) The energetics of reptilian activity. *Biology of the Reptilia* (eds C. Gans & F.H. Pough), Vol. 13, pp. 155–199. Academic Press, London.
- Bennett, A.F. (1990) Thermal-dependence of locomotor capacity. *American Journal of Physiology*, **259**, R253–R258.
- Bennett, A.F. & Dawson, W.R. (1976) Metabolism. *Biology of the Reptilia* (eds C. Gans & F.H. Pough), Vol. 13, pp. 127–223. Academic Press, London.
- Bennett, A.F. & Gorman, G.C. (1979) Population-density and energetics of lizards on a tropical island. *Oecologia*, **42**, 339–358.
- Bryant, S.R., Thomas, C.D. & Bale, J.S. (2002) The influence of thermal ecology on the distribution of three nymphalid butterflies. *Journal of Applied Ecology*, **39**, 43–55.
- Caughley, G., Short, J., Grigg, G.C. & Nix, H. (1987) Kangaroos and climate an analysis of distribution. *Journal of Animal Ecology*, **56**, 751–761.
- Chown, S.L., Gaston, K.J. & Robinson, D. (2004) Macro-physiology: large-scale patterns in physiological traits and their ecological implications. *Functional Ecology*, **18**, 159–167.
- Conroy, S. (1999) Lizard assemblage response to a forest ecotone in northeastern Australia: a synecological approach. *Journal of Herpetology*, **33**, 409–419.
- Creer, D., de Quiroz, K., Jackman, T.R., Losos, J. & Larson, A. (2001) Systematics of the *Anolis roquet* series of the southern Lesser Antilles. *Journal of Herpetology*, **35**, 428–441.
- Diaz, J.A. (1997) Ecological correlates of the thermal quality of an ectotherm's habitat: a comparison between two temperate lizard populations. *Functional Ecology*, **11**, 79–89.
- Gaston, K.J. (2003) *The Structure and Dynamics of Geographic Ranges*. Oxford University Press, Oxford.
- Gioia, P. & Pigott, J.P. (2000) Biodiversity assessment: a case study in predicting richness from the potential distributions of plant species in the forests of south-western Australia. *Journal of Biogeography*, **27**, 1065–1078.
- Grant, B.W. & Dunham, A.E. (1990) Elevation covariation in environmental constraints and life histories of the desert lizard *Sceloporus merriami*. *Ecology*, **71**, 1765–1776.
- Grant, B.W. & Porter, W.P. (1992) Modeling global macroclimatic constraints on ectotherm energy budgets. *American Zoologist*, **32**, 154–178.
- Heller, H.C. (1971) Altitudinal zonation of chipmunks (*Eutamias*): interspecific aggression. *Ecology*, **52**, 312–319.
- Heller, H.C. & Gates, D.M. (1971) Altitudinal zonation of chipmunks (*Eutamias*): energy budgets. *Ecology*, **52**, 424–433.
- Hertz, P. (1979) Sensitivity to high temperatures in three West Indian grass anoles, with a review of heat sensitivity in the genus *Anolis*. *Comparative Biochemistry and Physiology*, **63A**, 217–222.
- Hertz, P.E. (1981) Adaptation to altitude in two West Indian anoles (*Reptilia: Iguanidae*): field thermal biology and physiological ecology. *Journal of Zoology*, **195**, 25–37.
- Hertz, P.E. & Huey, R.B. (1981) Compensation for altitudinal changes in the thermal environment by some *Anolis* lizards on Hispaniola. *Ecology*, **62**, 515–521.
- Hertz, P.E. (1992) Temperature regulation in Puerto-Rican *Anolis* lizards – a field test using null hypotheses. *Ecology*, **73**, 1405–1417.
- Hertz, P. & Nevo, E. (1981) Thermal biology of four Israeli agamid lizards in early summer. *Israel Journal of Zoology*, **30**, 190–220.
- Hertz, P.E., Huey, R.B. & Garland, T. (1988) Time budgets, thermoregulation, and maximal locomotor performance are reptiles olympians or boy scouts? *American Zoologist*, **28**, 927–938.
- Hertz, P.E., Huey, R.B. & Stevenson, R.D. (1993) Evaluating temperature regulation by field-active ectotherms: The fallacy of the inappropriate question. *American Naturalist*, **142**, 796–818.
- Heyer, W. (1967) A herpetofaunal study of an ecological transect through Cordillera de Tilaran, Costa Rica. *Copeia*, **196**, 259–271.
- Hill, J.K., Thomas, C.D. & Huntley, B. (1999) Climate and habitat availability determine 20th century changes in a butterfly's range margin. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **266**, 1197–1206.
- Huey, R.B. (1978) Latitudinal pattern of between altitude faunal similarity: mountains might be higher in the tropics. *American Naturalist*, **112**, 225–229.

- Huey, R.B. (1983) Natural variation in body temperature and physiological performance in a lizard (*Anolis cristatellus*). *Advances in Herpetology and Evolutionary Biology: Essays in Honor of Ernest E. Williams* (eds A.G.J. Rhodin & K. Miyata), pp. 484–490. Museum of Comparative Zoology, Cambridge, MA.
- Huey, R.B. (1991) Physiological consequences of habitat selection. *American Naturalist*, **137**, S91–S115.
- Huey, R.B. & Hertz, P.E. (1982) Effect of body size and slope on sprint speed of a lizard *Stellio (Agama) stellio*. *Journal of Experimental Biology*, **97**, 401–409.
- Huey, R.B. & Webster, T.P. (1976) Thermal biology of *Anolis* lizards in a complex fauna *Cristatellus* group on Puerto Rico. *Ecology*, **57**, 985–994.
- Huey, R.B., Hertz, P.E. & Sinervo, B. (2003) Behavioral drive versus behavioral inertia in evolution: a null model approach. *American Naturalist*, **161**, 357–366.
- Huntley, B. (1994) Plant species' response to climate change: implications for conservation of European birds. *Ibis*, **8**, S127–S138.
- Hutchins, L.W. (1947) The bases for temperate zonation in geographical distributions. *Ecological Monographs*, **17**, 325–335.
- Irschick, D. & Losos, J. (1998) A comparative analysis of the ecological significance of maximal locomotor performance in Caribbean *Anolis* lizards. *Evolution*, **52**, 219–226.
- Janzen, D.H. (1967) Why mountain passes are higher in tropics. *American Naturalist*, **101**, 233–249.
- Juliano, S.A. & Williams, F.M. (1987) A comparison of methods for estimating the functional response parameters of the random predator equation. *Journal of Animal Ecology*, **56**, 641–653.
- Kingsolver, J.G. & Watt, W.B. (1983) Thermoregulatory strategies in *Colias* butterflies thermal-stress and the limits to adaptation in temporally varying environments. *American Naturalist*, **121**, 32–55.
- Kitchell, J. & Windell, J. (1972) Energy budget for the lizard, *Anolis carolinensis*. *Physiological Zoology*, **45**, 178–188.
- Lawton, J.H. (1991) From physiology to population dynamics and communities. *Functional Ecology*, **5**, 155–161.
- Lawton, J.H. (1993) Range, population abundance and conservation. *Evolution*, **8**, 409–413.
- Losos, J.B. (1990) A phylogenetic analysis of character displacement in Caribbean *Anolis* lizards. *Evolution*, **44**, 558–569.
- Losos, J.B., Leal, M., Glor, R.E., de Queiroz, K., Hertz, P.E., Schettino, L.R., Lara, A.C., Jackman, T.R. & Larson, A. (2003) Niche lability in the evolution of a Caribbean lizard community. *Nature*, **424**, 542–545.
- MacArthur, R.H. (1972) *Geographical Ecology: Patterns in the Distribution of Species*. Princeton University Press, Princeton.
- McConnachie, S. & Alexander, G.J. (2004) The effect of temperature on digestive and assimilation efficiency, gut passage time and appetite in an ambush foraging lizard, *Cordylus melanotus melanotus*. *Journal of Comparative Physiology-B Biochemical Systemic and Environmental Physiology*, **174**, 99–105.
- Mclaughlin, J. & Roughgarden, J. (1989) Avian predation on *Anolis* lizards in the northeastern Caribbean: an inter-island contrast. *Ecology*, **70**, 617–628.
- Muth, A. (1980) Physiological ecology of desert iguana *Dipsosaurus dorsalis* eggs: temperature and water relations. *Ecology*, **61**, 1335–1343.
- Pacala, S. (1982) *Population Experiments with the Anolis Lizards*. Dissertation, Stanford University.
- Pacala, S. & Roughgarden, J. (1982) Resource partitioning and interspecific competition in 2 2-species insular *Anolis* lizard communities. *Science*, **217**, 444–446.
- Pacala, S.W. & Silander, J.A. (1985) Neighborhood models of plant population dynamics 1. Single-species models of annuals. *American Naturalist*, **125**, 385–411.
- Pearson, R.G. & Dawson, T.P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, **12**, 361–371.
- Poe, S. (2004) Phylogeny of anoles. *Herpetological Monographs*, **18**, 37–89.
- Porter, W.P. (1989) New animal models and experiments for calculating growth-potential at different elevations. *Physiological Zoology*, **62**, 286–313.
- Porter, W. & Tracy, C. (1983) Biophysical analyses of energetics, time-space utilization, and distributional limits. *Lizard Ecology: Studies of a Model Organism* (eds R. Huey, E. Pianka & T. Schoener), pp. 55–83. Harvard University Press, Cambridge, MA.
- Porter, W.P., Munger, J.C., Stewart, W.E., Budaraju, S. & Jaeger, J. (1994) Endotherm energetics from a scalable individual based model to ecological applications. *Australian Journal of Zoology*, **42**, 125–162.
- Porter, W., Budaraju, S., Stewart, W. & Ramankutty, N. (2000) Calculating climate effects on birds and mammals: impacts on biodiversity, conservation, population parameters, and global community structure. *American Zoologist*, **40**, 597–630.
- Pough, F. (1980) The advantages of ectothermy for tetrapods. *American Naturalist*, **115**, 92–112.
- Rand, A.S. (1964) Ecological distribution in anoline lizards of Puerto Rico. *Ecology*, **45**, 745–752.
- Reichle, D. (1971) Energy and nutrient metabolism of soil and litter invertebrates. *Productivity of Forest Ecosystems* (ed. P. Devigneaud), pp. 465–475. UNESCO, Paris.
- Ricklefs, R.E. & Lovette, I.J. (1999) The roles of island area *per se* and habitat diversity in the species-area relationships of four Lesser Antillean faunal groups. *Journal of Animal Ecology*, **68**, 1142–1160.
- Ricklefs, R.E. & Schluter, D. (1993) Species diversity: regional and historical influences. *Species Diversity in Ecological Communities* (eds R.E. Ricklefs & D. Schluter), pp. 350–364. University of Chicago Press, Chicago, IL.
- Rogers, D.J. & Randolph, S.E. (1986) Distribution and abundance of tsetse-flies (*Glossina* spp). *Journal of Animal Ecology*, **55**, 1007–1025.
- Root, T. (1988) Energy constraints on avian distributions and abundances. *Ecology*, **69**, 330–339.
- Roughgarden, J. (1995) *Anolis Lizards of the Caribbean*. Oxford University Press, Oxford.
- Roughgarden, J. (1997) Production functions from ecological populations. *Spatial Ecology: the Role of Space in Population Dynamics and Interspecific Interactions* (eds D. Tilman & P. Kareiva). Princeton University press, Princeton, NJ.
- Roughgarden, J., Porter, W. & Heckel, D. (1981) Resource partitioning of space and its relationship to body temperature in *Anolis* lizard populations. *Oecologia (Berlin)*, **50**, 256–264.
- Roughgarden, J., Heckel, D. & Fuentes, E.R. (1983) Coevolutionary theory and the biogeography and community structure of *Anolis*. *Lizard Ecology: Studies of a Model Organism* (eds R.B. Huey, E.R. Pianka & T.W. Schoener), pp. 371–410. Harvard University Press, Cambridge, MA.
- Rummel, J.D. & Roughgarden, J. (1985) Effects of reduced perch-height separation on competition between two *Anolis* lizards. *Ecology*, **66**, 430–444.
- Rundel, P.W. (1994) Tropical alpine climates. *Tropical Alpine Environments: Plant Form and Function* (eds P.W. Rundel, A.P. Smith & F.C. Meinzer), pp. 21–44. Cambridge University Press, Cambridge.
- Savage, V., Gillooly, J., Brown, J., West, G. & Charnov, E. (2004) Effects of body size and temperature on population growth. *American Naturalist*, **163**, 429–441.
- Schneider, C.J., Losos, J.B. & deQueiroz, K. (2001) Evolutionary relationship of the *Anolis bimaculatus* group from the northern Lesser Antilles. *Journal of Herpetology*, **35**, 1–12.

- Schoener, T.W. (1970) Size patterns in West Indian *Anolis* lizards. II. correlations with sizes of particular sympatric species displacement and convergence. *American Naturalist*, **104**, 155–174.
- Schoener, T. (1977) Length-weight regression in tropical and temperate forest understory insects. *Annals of the Entomological Society of America*, **73**, 106–109.
- Schoener, T.W. & Gorman, G.C. (1968) Some niche differences in 3 Lesser Antillean lizards of genus *Anolis*. *Ecology*, **49**, 819–830.
- Schoener, T.W. & Schoener, A. (1978) Inverse relation of survival of lizards with island size and avifaunal richness. *Nature*, **274**, 685–687.
- Shine, R. & Kearney, M. (2001) Field studies of reptile thermoregulation: How well do physical models predict operative temperatures? *Functional Ecology*, **15**, 282–288.
- Spotila, J.R. & Standora, E.A. (1985) Energy budgets of ectothermic vertebrates. *American Zoologist*, **25**, 973–986.
- Stamps, J., Losos, J. & Andrews, R. (1997) A comparative study of population density and sexual size dimorphism in lizards. *American Naturalist*, **149**, 64–90.
- Stevenson, R.D. (1985) The relative importance of behavioral and physiological adjustments controlling body temperature in terrestrial ectotherms. *American Naturalist*, **126**, 362–386.
- Sullivan, B. (1981) Distribution and relative abundance of snakes along a transect in California. *Journal of Herpetology*, **15**, 247–248.
- Sultan, S.E. & Spencer, H.G. (2002) Metapopulation structure favors plasticity over local adaptation. *American Naturalist*, **160**, 271–283.
- Sykes, M.T., Prentice, I.C. & Cramer, W. (1996) A bioclimatic model for the potential distributions of north European tree species under present and future climates. *Journal of Biogeography*, **23**, 203–233.
- Taulman, J.F. & Robbins, L.W. (1996) Recent range expansion and distributional limits of the ninebanded armadillo (*Dasyurus novemcinctus*) in the United States. *Journal of Biogeography*, **23**, 635–648.
- Tracy, C. (1982) Biophysical modelling in reptilian physiology and ecology. *Biology of the Reptilia* (eds C. Gans & F. Pough), pp. 275–321. Academic Press, London.
- VanBerkum, F.H. (1986) Evolutionary patterns of the thermal sensitivity of sprint speed in *Anolis* lizards. *Evolution*, **40**, 594–604.
- VanBerkum, F.H. (1988) Latitudinal patterns of the thermal sensitivity of sprint speed in lizards. *American Naturalist*, **132**, 327–343.
- Vandamme, R., Bauwens, D. & Verheyen, R.F. (1991) The thermal dependence of feeding behavior food consumption and gut-passage time in the lizard *Lacertavivipara jacquin*. *Functional Ecology*, **5**, 507–517.
- Williams, E. (1972) The origin of faunas. Evolution of lizard congeners in a complex fauna: a trial analysis. *Evolutionary Biology*, **6**, 47–88.

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### Appendix I: notes on Table 1 parameterizations

**1 Fresh mass.** Data from 636 measurements of 47 species of lizards were used to estimate lizard mass as a function of SVL (mm) (Pough 1980). The regression corresponds closely to that derived for *Anolis* species (Stamps *et al.* 1997).

**2 Resting and maximum metabolic rate.** The 69 observations for resting metabolic rate were collected from 22 lizard genera. The 54 observations for maximum metabolic rate were collected from 14 lizard genera (Bennett & Dawson 1976; Bennett 1982). We use a non-linear least squares bivariate fitting function to predict metabolic rates as a function of mass and temperature.

**3 Maximal sprint speed from SVL.** Lizards sprint speed as a power-law of SVL was fit using data from 14 *Anolis* species on Puerto Rico and Jamaica (Huey & Hertz 1982; Losos 1990).

**4 Prey size.** Schoener & Gorman (1968) provide data from which we derive a relation between insect prey size (mm) and lizard head length, HL (mm):  $L_{\text{insect}} = 0.18\text{HL} - 0.11$ ,  $r^2 = 0.75$ ,  $n = 8$  means. Schoener & Gorman (1968) also provide data to convert from lizard head length (mm) to lizard SVL (mm):  $\text{SVL} = 4.16\text{HL} + 6.04$ ,  $r^2 = 0.96$ ,  $n = 219$ .

**5 Insect abundance.** Insect abundance was estimated by placing paper plates, each coated in the centre with a sticky substance (Tree tanglefoot, Tanglefoot Company, Grand Rapids, Michigan), in a habitat for 24 h. Sixteen plates were placed in a grid at four to five sites dispersed along the elevation gradient on each island. We convert the insect catch ( $\text{m}^{-2} \text{s}^{-1}$ ) to number of insects ( $\text{m}^{-1} \text{s}^{-1}$ ) by assuming that each lizard forages within 0.5 m to each side of the linear transect. We tested trends in lizard abundance using maximum likelihood mixed effects models, with the site as the random variable.