

# Climate, competition, and the coexistence of island lizards

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## Summary

1. The influence of environmental temperatures and competition combine to determine the distributions of island lizards. Neither a bioenergetic model nor simple models of competition alone can account for the distributions. A mechanistic, bioenergetic model successfully predicts how the abundance of a solitary *Anolis* lizard species will decline along an island's elevation gradient. However, the abundance trends for sympatric lizards diverge from the predictions of the non-interactive model.

2. Here we incorporate competition in the bioenergetic model and examine how different forms of competition modify the temperature-based abundance predictions.

3. Applying the bioenergetic model with competition to an island chain tests whether the model can successfully predict on which islands two lizards species will coexist.

4. Coexistence is restricted to the two largest islands, which the model predicts have substantially greater carrying capacities than the smaller islands. The model successfully predicts that competition prevents species coexistence on the smallest islands. However, the model predicts that the mid-sized islands are capable of supporting substantial populations of both species. Additional island characteristics, such as habitat diversity, resource availability and temporal disturbance patterns, may prevent coexistence.

*Key-words:* bioenergetic model, environmental gradient, habitat selection, species distributions, thermal physiology

*Functional Ecology* (2006) **20**, 315–322  
doi: 10.1111/j.1365-2435.2006.01095.x

## Introduction

Environmental temperatures and competition interact in a complex manner to determine species ranges (Maurer & Taper 2002; Gaston 2003; Case *et al.* 2005). The majority of attempts to understand species distributions regress observed distributions against environmental variables (Peterson & Vieglais 2001; Gaston 2003; Huntley *et al.* 2004; Parmesan *et al.* 2005). Geographical range boundaries often coincide with identifiable climatic conditions (Root 1988; Peterson *et al.* 2002), but establishing whether the relationship is causal is difficult. Attempts to predict species' responses to changing climates highlight the need for a more process-based understanding of how species distributions form. Most attempts at prediction assume that the species will follow shifting temperatures and precipitation to remain in a constant climate, a 'bioclimatic envelope' (Sykes, Prentice & Cramer 1996; Hill, Thomas & Huntley 1999; Gioia & Pigott 2000; Peterson *et al.* 2002; Oberhauser & Peterson 2003). Yet this approach fails to account for other factors that

may govern observed ranges, including dispersal limitations and species interactions (Pearson & Dawson 2003; Case *et al.* 2005).

Detailed, biophysical models have been developed to map the discretionary energy budgets of organisms and to examine spatially explicitly how factors such as topography and temperature influence these maps (Porter *et al.* 2000, 2002; Kearney & Porter 2004). We have developed one of the first bioenergetic models to couple energetic and population dynamic models to produce spatially explicit predictions of species abundances (Lawton 1991; Chown, Gaston & Robinson 2004). The mechanistic, bioenergetic model uses the temperature dependence of ectotherm energetics to predict spatial abundance distributions. The spatially explicit abundance predictions are derived by projecting the model outcomes in a geographic information system (GIS). The model was validated for solitary *Anolis* (Daudin 1802) lizards in both the northern and southern Lesser Antilles islands (Buckley & Roughgarden 2005).

Here we simulate competition in the population-dynamic, bioenergetic model. This allows evaluating how suites of species, rather than single species in isolation, respond to environmental temperatures. We parameterize the bioenergetic model with empirically measured morphological and environmental variables for the island of Grenada in the Southern Lesser Antilles,

which hosts two species of *Anolis* lizard. The bioenergetic model yields equilibrium abundances in the absence of competition (carrying capacities,  $K$ ). We then use Lotka–Volterra equations to approximate competition and fit the bioenergetic model with competition for Grenada. This yields equilibrium abundance in the presence of competition. We incorporate the form of competition observed on Grenada in the bioenergetic model. We then test the model on the Grenadines, an adjacent series of islands of variable size that host either the smaller or both of the species present on Grenada.

Approximating competition using a statistical model departs from the spirit of the mechanistic, bioenergetic model. Lotka–Volterra approximations are used, rather than developing an individual-based model of species interactions due to their well understood dynamics (May 1974; Roughgarden 1979; Case *et al.* 2005). This allows investigating how well understood forms of competition interact with the influence of temperature along the elevation gradient. The simulated competition attempts to account for all residual variation in the empirical abundance trends on Grenada. This approach will inform future mechanistic models addressing how temperature and competition interact to determine species distributions. The approach ignores deviations from model predictions resulting from simplifying thermal physiology and other ecological noise. Avian predation can be discounted as a primary determinant of lizard abundance patterns, as the biogeographical pattern of lizard abundance contrasts with the pattern of avian predator richness, and many mainland avian predators are absent from the islands (Andrews 1979).

The simple communities of *Anolis* lizards on the Grenadines islands are well suited for applying the bioenergetic model as a null model to understand species distributions and coexistence. The Grenadines vary from small, low-elevation, scrubby islands to larger, mountainous islands with complex forests and a variety of other habitats. They were a single land mass during periods of lower sea level (Heatwole & Mackenzie 1967). Hence extinction, rather than differential colonization, is the primary determinant of species occurrence on the study islands (Rand 1969; Losos 1996). *Anolis* species occurrence is non-random with respect to island area and habitat diversity. All islands host the small anole, *Anolis aeneus* (snout–vent length = 66 mm, body sizes for Grenada: Schoener 1970). The larger anole, *Anolis richardi* (101 mm), is restricted to the largest two islands, which are at opposite extents of the Grenadines. The degree to which sympatric anoles compete for resources is related to niche overlap in body size and perch position due to overlapping insectivorous diets (Schoener & Gorman 1968; Rummel & Roughgarden 1985).

Is the bioenergetic model with competition for Grenada sufficient to predict on which of the Grenadines islands the two lizard species coexist? We calculate the

island-wide abundance of the larger anole, *A. richardi*, predicted by the bioenergetic model with competition for each island. Initially, we calculate the predicted abundance by assuming the same insect abundance on all islands. Subsequently, the influence of incorporating island-specific and empirically measured insect abundance in the model is examined. Analysing discrepancies between the bioenergetic null model predictions and empirical distributions addresses the degree to which additional factors determine patterns of species coexistence in the Grenadines.

## Methods

### THE BIOENERGETIC MODEL

The model assumes an individual anole is an energy-maximizing sit-and-wait predator, the foraging radius of which is limited by lizard density. Details of the basic model are provided by Roughgarden (1997). The model is extended to include temperature dependence by Buckley & Roughgarden (2005). The model is an animal counterpart for the neighbourhood model, in which plants interact with their adjacent neighbours (Pacala & Silander 1985). Essentially, the model balances energetic input from foraging with energetic costs associated with metabolism and reproduction. Lizards are assumed to forage on a linear interval, which simplifies the spatial dynamics and produces model predictions that are comparable to empirical transect counts. The assumption is biologically reasonable because lizards tend to maintain perch positions that limit prey sighting to a linear band.

We model lizards as optimal foragers that maximize the energetic yield per unit time. The foraging energetic yield,  $E(d)$ , of foraging within a radius,  $d$ , is derived as the energetic input less the energetic cost divided by the total foraging time:

$$E(d) = \frac{e_i - e_w t_w(d) - e_p t_p(d)}{t_w(d) + t_p(d)} \quad \text{eqn 1}$$

where  $e_i$  is the energy per insect;  $e_w$  and  $e_p$  are energy per unit time expended waiting and pursuing, respectively; and  $t_w$  and  $t_p$  are time expended waiting and pursuing, respectively. The pursuit and waiting times are a function of prey density,  $a$  (insects  $\text{m}^{-1} \text{s}^{-2}$ ), and lizard velocity,  $v$  ( $\text{m} \text{s}^{-1}$ ) ( $t_w = 1/ad$  and  $t_p = d/v$ ; Roughgarden 1997; Buckley & Roughgarden 2005). The handling time is assumed to be minimal and included in the pursuit time. The energetic cost of handling is accounted for by discounting the energetic content of each insect by the assimilation efficiency (Buckley & Roughgarden 2005). 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.

At low densities, the solitary foraging radius,  $d_s$ , is that which optimizes  $E(d)$ . Density dependence is introduced when crowding forces the territory size to

be less than the energetically optimal  $d$  for solitary anoles, and thus reduces the energetic yield from foraging for each lizard. A specified transect length,  $L$ , is partitioned between  $N$  foragers (Roughgarden 1997). The model of individual foraging energetics is extended to population dynamics by calculating the change in population per unit time (production function) as the product of the population growth rate, based simply on birth minus death, and the population size,  $N$ , as follows:

$$\Delta N = [bE(d) - \lambda]N \quad \text{eqn 2}$$

where  $\lambda$  represents mortality and the reproductive cost of metabolism while not foraging, and  $b$  is the reproductive rate per unit net energetic yield. All density dependence is included in the expression for  $E(d)$ , which can be substituted into the production function. As the foraging energetic yield is dependent on population size,  $N$ , we can explicitly solve for equilibrium population size (carrying capacity,  $K$ , where the population growth rate equals 0,  $bE(d) - \lambda = 0$  and the initial rate of population growth (intrinsic rate of population increase,  $r_0$ ):

$$K = \frac{L(be_i av + \sqrt{(be_i av)^2 - 4av(be_p + \lambda)(be_w + \lambda)})}{2v(be_w + \lambda)} \quad \text{eqn 3}$$

$$r_0 = -\lambda + b \frac{e_i - e_w / ad_s - e_p d_s / v}{1/ad_s + d_s / v} \quad \text{eqn 4}$$

where  $t_f$  is the duration of foraging;  $L = 1000$  m;  $a = 0.037 \pm 0.13$  insects  $\text{m}^{-1} \text{s}^{-1}$  (mean  $\pm$  95% CI);  $b = mt_f$ ,  $\lambda = \mu + m(24 \times 60 \times 60 - t_f)e_w$ . For *A. aeneus*,  $v = 1.33$  m  $\text{s}^{-1}$ ;  $e_p = 0.15$  J  $\text{s}^{-1}$ ;  $e_w = 0.008$  J  $\text{s}^{-1}$ ;  $e_i = 3.53$  J. For *A. richardi*,  $v = 1.51$  m  $\text{s}^{-1}$ ;  $e_p = 0.15$  J  $\text{s}^{-1}$ ;  $e_w = 0.02$  J  $\text{s}^{-1}$ ;  $e_i = 9.78$  J. The daily mortality rate,  $\mu$ , is assumed to be  $1/365$  day $^{-1}$ . The parameter  $m$  is the quantity of eggs produced per joule  $\times$  the probability of surviving to adulthood, and is assumed to be  $1/e \times 0.0001$  eggs  $\text{J}^{-1}$ .

Model parameterizations are detailed by Buckley & Roughgarden (2005). All parameters except  $t_f$  are assumed to remain constant with respect to elevation. Briefly, from lizard length (Schoener 1970), we use empirically well established relations to derive lizard mass (Pough 1980); resting and maximum metabolic rate (Bennett & Dawson 1976; Bennett 1982); maximum sprint speed (Huey & Hertz 1982; Losos 1990; Irschick & Losos 1998); and prey size (Schoener & Gorman 1968). The energetic yield of each prey item,  $e_p$ , is discounted by the capture rate. 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 ( $f = 0.5$ , Roughgarden 1995; Buckley & Roughgarden 2005). We assume that the probability of the insect remaining stationary is distributed exponentially to solve for the capture rate. The influence of small-scale microclimate variation and thermal physiological influences on

processes such as digestion were omitted to maintain model simplicity.

The qualitative predictions of the bioenergetic model are robust to parameterizations other than body size, thermal constraints and prey abundance (Buckley & Roughgarden 2005). The most uncertain model parameter is insect abundance, which we measured empirically (Buckley & Roughgarden 2005). We use the 95% CIs of insect abundance to depict the sensitivity of the model outcomes on Grenada. For the model fitting, we parameterize the model with the lower 95% CI for insect abundance on Grenada, as it yields more empirically realistic abundances. This parameterization does not influence the shape of the abundance trend or relative species abundances. In addition to the insect abundance data we collected for the islands of Petit Bateau and Carriacou, we use data from Roughgarden & Fuentes (1977). The estimation methods were equivalent, with the exception of manufacturer changes in the sticky collecting substance. We determine the abundance of a specified prey size by multiplying the overall insect abundance by the probability density function using an abundance–size relationship for a wet tropical forest (Schoener & Gorman 1968).

Temperature dependence is incorporated by calculating the duration of foraging,  $t_f$ , as the period during which the environmental temperature falls within each lizard's functional temperature range. We used hourly sea-level environmental temperature data during the sampling season (NOAA National Weather Service) and the wet adiabatic lapse rate ( $0.65$  °C/100 m) to derive a temperature trend as a function of elevation and hour. The trend was fitted to 2 years' hourly temperature data collected at sea level on St Lucia, which is just north of the Grenadines. The extremes of the critical temperature range were measured empirically as the temperature at which the lizard is too cold to roll over and the temperature at which the lizard begins to pant (*A. aeneus* = [22.6 °C, 39.2 °C]; *A. richardi* = [22.6 °C, 37.1 °C], Buckley & Roughgarden 2005). This critical temperature range was measured on the island of Grenada and applied to the Grenadines. From the critical temperature range, we derive the temperature at which lizards can run at maximum velocity and the temperature at which it is sufficiently warm to initiate foraging (VanBerkum 1988).

Previous research on Caribbean anoles suggests that lizard habitat choice provides at least partial thermoregulation along elevation gradients (Grant & Dunham 1990; Hertz & Huey 1992; Huey, Hertz & Sinervo 2003). Accordingly we assume that, once the environmental temperature falls within the lizard's function temperature range, the lizard behaviourally thermoregulates to the temperature at which it reaches maximum velocity (VanBerkum 1986; Bennett 1990; Irschick & Losos 1998). Resting and maximal metabolic rates are calculated as a function of temperature and mass at this optimal performance temperature (Buckley & Roughgarden 2005). We assume the scale of dispersal relative to

island size prevents intraspecific differences in thermal physiology along the elevation gradient (VanBerkum 1986; Sultan & Spencer 2002).

#### INCORPORATING INTERACTIONS IN THE BIOENERGETIC MODEL

We use Lotka–Volterra approximations to the discrete time-logistic growth equations to simulate competition. The equilibrium abundances,  $N_1$  and  $N_2$ , are found from simultaneously solving two linear equations:

$$N_1 + \beta_{12}N_2 = K_1; \quad \beta_{21}N_1 + N_2 = K_2 \quad \text{eqn 5}$$

where  $K_i$  is the carrying capacity of species  $i$  and  $\beta_{ij}$  is the competition coefficient for the effect of species  $j$  against species  $i$ . The  $K_i$ s are obtained as equilibrium solutions of the single-species production function, parameterized separately for each species. The  $\beta_{ij}$ s are treated as phenomenological coefficients, the values of which are not (yet) known empirically. The implications of various hypothetical values of  $\beta_{ij}$  are explored in the simulations. We solve for equilibrium population sizes ( $N_1$  and  $N_2$ ) in the presence of competition. As the carrying capacity and intrinsic rate of increase varies spatially in our model, we are unable to analyse the dynamics of the competition model to make coexistence predictions for the Grenadines. Rather, we calculate the equilibrium abundance for each pixel given a competition coefficient and sum up the predicted abundance over the pixels.

We examine how varying the form and strength of competition influences the predicted temperature-based abundance patterns. We explore the following forms of competition and combinations thereof: no competition; constant competition; linearly varying competition along the elevation gradient; and competition varying exponentially along the elevation gradient. For each form of competition, we solve for the values of  $\beta_{12}$  and  $\beta_{21}$  that minimize the sum of squares summed over both species along the elevation gradient. For linear competition, we include the approximate maximum elevation predicted by the bioenergetic model (800 m) in the competition coefficient ( $\beta_{12} = c_1 - (c_2/800)x$ , where  $c_1$  and  $c_2$  are constants). The fit of the bioenergetic model with competition to empirical lizard abundance on Grenada was compared with that of the null model (no effects) by ANOVA. The correlation coefficient,  $F$  statistic, and two-tailed  $P$  value are reported for each model. The strengths of the fits are approximate, as several high-elevation sites occur in regions where model outcomes are undefined and could not be included in the sum of squares. These regions are where density dependence ceases but the potential for population growth is  $>0$ . Where lizard performance is low at high elevation, energetic yield,  $E(d)$  is not sufficiently high for the population to reach the equilibrium carrying capacity. All analyses were performed using R (R Foundation for Statistical

Computing). We spatially projected the theoretically predicted and empirical lizard abundances onto the Grenadine Islands in GIS using a 90-m resolution digital elevation model (NASA Shuttle Radar Topography Mission).

#### EMPIRICAL METHODS

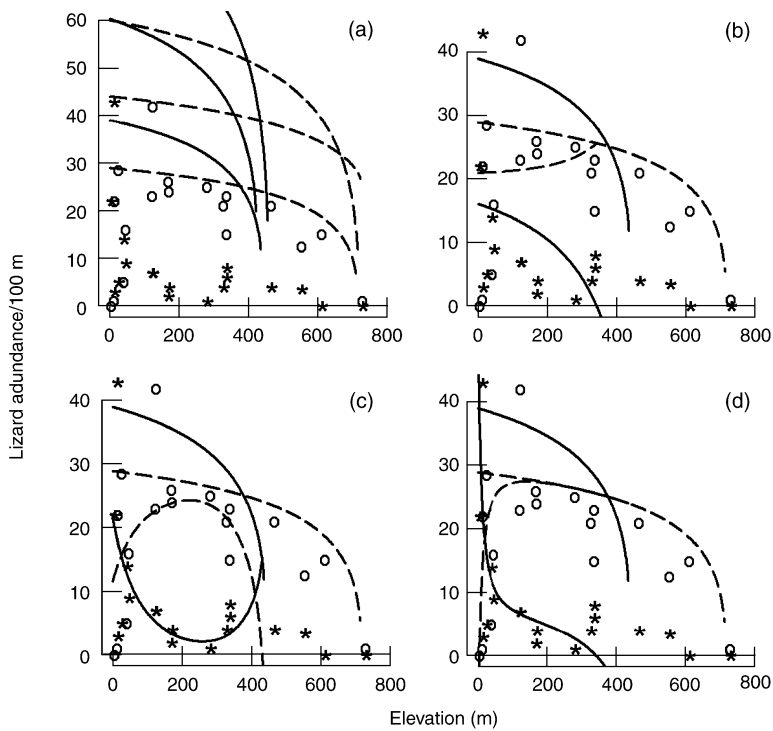
Methods for lizard censuses on Grenada are described in Buckley & Roughgarden (2005) and are analogous to those described below for the Grenadines. We surveyed all Grenadines islands that contained a substantial proportion of undisturbed habitat. On the larger islands, sites were distributed along both windward and leeward elevation gradients. On the smaller islands, lizard abundance was surveyed in lizard habitats near sea level. Observations were conducted in July–August 2004, which is within the wet season. We surveyed during hours of peak anole activity (between 10 : 00 and 16 : 00 h). Anole abundance was estimated by the first author while pacing a linear transect for 2 h. This method allows greater geographical coverage than mark-and-recapture techniques (Diaz 1997). Repeat censuses of sites on other islands in a subsequent year confirmed the robustness (both relative and absolute abundance) of the censusing technique (Buckley & Roughgarden 2005). The  $\approx 100$ -m transect was often along a low-use trail and was chosen to be passable, representative, and to have little or no elevation change. If a substantial distance ( $>100$  m) was traversed in  $<2$  h, an additional transect was surveyed adjacent to the initial transect to maintain constant habitat.

Vegetation was scanned for anoles from the forest floor to canopy within 2 m on each side of the transect. Estimates of abundance differences are conservative, as more time was spent collecting lizard data where lizards were more abundant. Elevation was estimated as the mean of GPS measurements at each end of the transect, and confirmed with digital elevation models. A total of 36 sites were surveyed on 13 islands. The empirically projected lizard densities are linear regressions for islands on which there was a significant decline in abundance with increasing elevation, and the regression accounted for at least 60% of the variation. For the remaining islands, data are means. We spatially projected the theoretical and empirical lizard abundances onto the Grenadine Islands in ARCGIS using a 90-m resolution digital elevation model (NASA Shuttle Radar Topography Mission). Island-wide abundance estimates are derived by summing projected abundance across pixels.

## Results

#### FITTING THE BIOENERGETIC MODEL WITH COMPETITION FOR GRENADA

We applied Lotka–Volterra competition approximations to fit the bioenergetic model with competition for



**Fig. 1.** Empirical data and model outcomes for lizard density (lizards per 100 m) as a function of elevation (m) on Grenada. For the smaller *Anolis aeneus* (species 2): \*, empirical density; solid lines, model outcomes. For the larger *Anolis richardi* (species 1): ○, empirical density; dashed lines, model outcomes. Each graph shows outcomes of the bioenergetic model without competition. Model outcomes for the following forms of competition are depicted as a function of elevation ( $x$ ): (a) no competition; (b) constant competition:  $\beta_{12} = 1.1$ ;  $\beta_{21} = 0.5$ ; (c) linearly varying competition:  $\beta_{12} = 1.5 - (0.7/800)x$ ;  $\beta_{21} = 0.8 + (1.5/800)x$ ; (d) constant/exponentially varying competition:  $\beta_{12} = 1.1$ ;  $\beta_{21} = 0.8e^{-0.018x}$ . For the case of no competition (a), the depicted bioenergetic model outcomes correspond to parameterization with the lower, mean and upper CIs of insect abundance. The range of the y axis is greater in (a).

Grenada. The empirical density patterns (abundance per 100 m) for Grenada diverge from the predictions of the bioenergetic model without competition (*A. aeneus*,  $r^2 = 0.18$ ,  $F_{[1,12]} = 2.15$ ,  $P = 0.2$ ; *A. richardi*,  $r^2 = 0.00$ ,  $F_{[1,12]} = 0.90$ ,  $P = 0.9$ ; Fig. 1a). However, incorporating the species' differential thermal physiologies into the bioenergetic model does lead to successful prediction that the warm-adapted *A. aeneus* will be more abundant at low elevation and cease to persist at lower elevation than *A. richardi*. We examine how competition superimposes on this temperature-associated trend.

We first fitted the bioenergetic model with constant competition along the elevation gradient (Fig. 1b). The sum of squares for both species is minimized when  $\beta_{12} = 1.1$  and  $\beta_{21} = 0.5$ . The constant competition coefficients substantially reduce the predicted density of the warm-adapted *A. aeneus* (species 2) along the elevation gradient. The model succeeds in predicting that competition sharply reduces the density of the larger *A. richardi* (species 1) at low elevation. However, constant competition yields a concave increasing density trend for *A. richardi* at low elevation, and a concave declining density trend for *A. aeneus* in contrast to empirical trends. The model fit is fairly poor for both

species (*A. aeneus*,  $r^2 = 0.13$ ,  $F_{[1,12]} = 1.41$ ,  $P = 0.2$ ; *A. richardi*,  $r^2 = 0.02$ ,  $F_{[1,12]} = 0.52$ ,  $P = 0.6$ ).

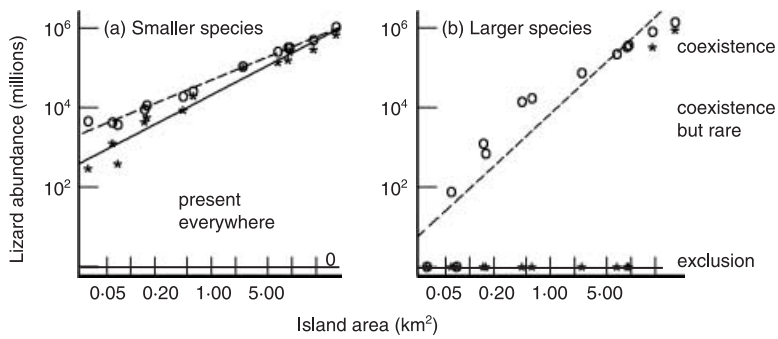
We next fitted the empirical data to the bioenergetic model with linearly varying competition along the elevation gradient (Fig. 1c). The sum of squares for both species is minimized when  $\beta_{12} = 1.5 - (0.7/800)x$  and  $\beta_{21} = 0.8 + (1.5/800)x$ , where  $x$  is elevation (metres). The linearly varying competition succeeds in producing a hump-shaped density trend for the larger *A. richardi* at low elevation, and a convex declining density trend for the smaller *A. aeneus*. However, the linearly varying competition produces strong hump-shaped patterns that do not correspond to empirical trends (*A. aeneus*,  $r^2 = 0.01$ ,  $F_{[1,12]} = 0.18$ ,  $P = 0.7$ ; *A. richardi*,  $r^2 = 0.01$ ,  $F_{[1,12]} = 0.17$ ,  $P = 0.7$ ).

Finally, we examine the implications of exponential changes in competition along the elevation gradient (Fig. 1d). Assuming that the competition coefficient for the larger *A. richardi* remains constant along the elevation gradient, the best fit occurs when  $\beta_{12} = 1.1$  and  $\beta_{21} = 0.8e^{-0.018x}$ , where  $x$  is elevation (*A. aeneus*,  $r^2 = 0.39$ ,  $F_{[1,12]} = 7.68$ ,  $P < 0.02$ ; *A. richardi*,  $r^2 = 0.43$ ,  $F_{[1,12]} = 9.25$ ,  $P < 0.01$ ). Assuming that the competition coefficient for *A. richardi* varies linearly or exponentially along the elevation gradient does not substantially improve the model fit. The steeper-than-linear change in competitive ability reproduces the observed hump-shaped trend for the larger *A. richardi* at low elevation and a convex declining density trend for the smaller *A. aeneus*. This best-fitting model is used as the interactive bioenergetic model for the remainder of the paper.

#### TESTING THE BIOENERGETIC MODEL WITH COMPETITION FOR THE GRENADINES

Does the bioenergetic model with competition succeed in predicting on which islands two species coexist? We use the interactive bioenergetic model to predict the island-wide equilibrium abundance for the smaller species, *A. aeneus* (Fig. 2a) and the larger *A. richardi* (Fig. 2b). This addresses whether coexistence is enabled when the equilibrium abundance of the larger *A. richardi* exceeds a viable population size. To derive empirical estimates of island-wide abundance, elevation was related to empirically observed lizard abundance for each island. We used digital elevation models to project the relations spatially and sum empirically projected abundances over all pixels on an island. We calculated island-wide abundance both with and without the assumption that lizard density must be above a threshold density in each pixel for the lizards to persist (400 lizards  $\text{km}^{-2}$ , the fourth quartile of maximum predicted densities). Density requirements for local coexistence depressed total abundance somewhat while maintaining a similar relationship to island area.

The bioenergetic model with competition predicts that island-wide equilibrium abundance increases as a power law of island area for both species (*A. aeneus*,



**Fig. 2.** Island-wide abundances of (a) smaller *Anolis aeneus*; (b) larger *Anolis richardi* in the Grenadines Islands. Open symbols and dashed lines, equilibrium abundances predicted by the bioenergetic model with competition ( $\beta_{12} = 1.1$ ;  $\beta_{21} = 0.8e^{-0.018x}$ ). Solid and star symbols and lines, empirical estimates of island-wide abundance. Theoretical abundances are summed over the pixels for each island. Lines depict power-law fits (slopes  $\pm$  SE: *A. aeneus* theoretical,  $0.84 \pm 0.03$ ; *A. aeneus* empirical,  $1.06 \pm 0.07$ ; *A. richardi* theoretical,  $1.88 \pm 0.22$ ). Island size ranges are depicted over which *A. richardi* is predicted to coexist; to be abundant but less so than generally empirically observed; and to be competitively excluded.

$r^2 = 0.97$ ,  $F_{[1,11]} = 891$ ,  $P < 10^{-11}$ ; *A. richardi*,  $r^2 = 0.87$ ,  $F_{[1,11]} = 74.6$ ,  $P < 10^{-5}$ ). The empirically projected island-wide abundances also increase as a power law of island area for *A. aeneus* ( $r^2 = 0.97$ ,  $F_{[1,11]} = 383$ ,  $P < 0.001$ ). The island-wide abundances predicted by the bioenergetic model with competition can be compared with empirical observations. For the smaller lizard, *A. aeneus*, the predicted relationship between island-wide lizard abundance and island area is similar to that observed empirically (Fig. 2a). However, the bioenergetic model with competition overestimates island-wide abundances. This is consistent with the absence of the competitor *A. richardi*. In an ANCOVA, the theoretically predicted and empirically projected abundances are significantly different ( $F_{[1,22]} = 19.9$ ,  $P < 0.001$ ). There is also a significant effect of island area ( $F_{[1,22]} = 517$ ,  $P < 10^{-15}$ ).

The bioenergetic model with competition predicts that the island-wide equilibrium abundance of the larger species will increase as a power law of island area (Fig. 2b). The power-law form is at least partially attributable to using elevation to project abundance. Both maximum elevation and topographical diversity increase as an approximate power law of island area. The model successfully predicts that *A. richardi* will be competitively excluded (predicted island-wide abundances are less than viable population sizes) from the smaller, low-elevation islands. The model additionally successfully predicts high abundance of *A. richardi* on the largest two islands, where coexistence occurs. However, the model predicts that *A. richardi* will be present at high abundance on the mid-sized islands (up to  $\approx 500\,000$  lizards per island). In an ANCOVA, the theoretically predicted and empirically projected island-wide abundances are significantly different ( $F_{[1,22]} = 32.4$ ,  $P < 10^{-5}$ ). There is also a significant effect of island area ( $F_{[1,22]} = 549$ ,  $P < 0.001$ ) and the interaction of island area and the type of data (theoretical/empirical,  $F_{[1,22]} = 28.2$ ,  $P < 10^{-4}$ ).

## Discussion

Our results demonstrate how species interactions superimpose on a systematic response to environmental temperatures to produce novel spatial abundance patterns along elevation gradients. Neither the energetic implications of environmental temperature nor simple forms of competition can account for the abundance patterns singly. However, simulating competition in the bioenergetic model results in the model outcomes matching empirical observations on Grenada. Constant or linearly trending competition is insufficient for the model to produce the empirical patterns. A steeper than linear trend in the competition coefficient is required for the model outcomes to match empirical abundance patterns. Conclusions regarding the specific form of competition are limited due to the potential for ecological noise to drive deviations from the bioenergetic null model. However, our analysis demonstrates that climate and competition interact to determine species distributions.

One limitation with a statistical model of competition is that the species interactions will probably be altered by temperature changes (Davis *et al.* 1998a, 1998b; Fox & Morin 2001). Community changes – including altered competitive dominance (Harte & Shaw 1995; Bertness & Ewanchuk 2002); predation strength (Sanford 1999); food webs (Petchey *et al.* 1999; Voigt *et al.* 2003); and community invasibility (Stachowicz *et al.* 2002) – exacerbate physiological and behavioural responses to temperature change. However, understanding how existing forms of species interactions superimpose on the influences of temperature is an initial step in understanding how temperature and competition interact to govern species distributions.

Spatially projecting the outcomes of the bioenergetic model with competition for the Grenadines examines whether the model can predict patterns of species coexistence. The model successfully predicts that *A. richardi* will be competitively excluded from the smaller, low-elevation islands. However, the model predicts substantial population sizes for *A. richardi* on the mid-sized, one-species islands (up to  $\approx 500\,000$  lizards per island). Are these population sizes viable? Models have found that *Anolis* populations are viable with several thousand individuals (Reed *et al.* 2003), and *Anolis* persist with small populations elsewhere in the Caribbean (Schoener & Schoener 1980; Spiller, Losos & Schoener 1998). However, lizards can reach incredibly high densities (Rodda *et al.* 2001; Rodda & Dean-Bradley 2002). Puerto Rican anoles have been observed at densities of over  $2\text{ m}^{-2}$  (Reagan 1992). The predicted equilibrium abundances correspond to anole densities below those generally observed on Lesser Antilles islands, where densities of  $1\text{ m}^{-1}$  are typical (Roughgarden 1995). Most of the predicted abundance arises from high-elevation areas with high lizard density. Requiring a threshold density when

calculating island-wide abundance did not strongly influence the predicted island abundances.

Can variations in insect abundance account for the absence of the larger lizard on islands where it is predicted to coexist? In the bioenergetic model, increasing insect abundance proportionally increases predicted lizard abundance. Estimated insect abundance varies considerably between the islands and can also be expected to vary seasonally. Roughgarden & Fuentes (1977) found the highest insect abundance on the small islands within the Tobago Cays cluster (Petit Bateau, Jamesby and Petite Tabac). Their estimate of low insect abundance on Union Island, the largest of the single-species islands, yields low predicted lizard abundance. We measured the lowest insect abundance on the largest island, Carriacou (95% CI = 0.009–0.013 insects m<sup>-2</sup>). The high insect abundance on the small islands does not increase the predicted abundances of *A. richardi* on the smallest islands, as *A. richardi* is competitively excluded. On the larger Union Island and Carriacou, the predicted abundances of *A. richardi* are substantially suppressed by empirically measured low insect abundance. Lower insect abundance on larger islands may decrease lizard capacity and prevent coexistence.

Incorporating simple forms of competition into the bioenergetic null model produces the complex abundance patterns observed along the elevation gradient on the two-species islands. Neither the lizards' response to temperature nor simple forms of Lotka–Volterra competition can account for the abundance patterns alone. Applying the bioenergetic model with competition to the Grenadines demonstrates how climate and competition interact to determine lizard distributions and species coexistence. The model successfully predicts coexistence on the largest islands and competitive exclusion on the smallest islands. However, the predicted equilibrium abundances for both species on the mid-sized Grenadines islands are substantial. Why does species coexistence not occur on the mid-sized islands? More detailed island-specific model parameterizations for body size and thermal physiology are required to ensure the suitability of the bioenergetic model as a null model. Previous research suggests that establishment rather than colonization limits species richness (Rand 1969; Losos 1996). Island characteristics not incorporated in the bioenergetic null model, such as area, habitat diversity, resource availability and temporal disturbance patterns, may govern species establishment.

### Acknowledgements

This research was supported by the National Geographical Committee for Research and Exploration, an NSF Predoctoral Grant to L.B.B. and the Center for Evolutionary Studies and Field Studies Program at Stanford University. H. Feinberg, L. Leckie and E. Silva provided field assistance. M. Williams assisted

with the GIS analysis and the Nature Conservancy provided GIS data. We thank the reviewers for extensive comments.

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Received 14 October 2005; revised 13 December 2005;  
accepted 14 December 2005  
Editor: Charles A. Fox