

Small island biogeography in the Gulf of California: lizards, the subsidized island biogeography hypothesis, and the small island effect

K. Barrett^{1*}, D. A. Wait¹ and W. B. Anderson² ¹*Department of Biology, Southwest Missouri State University, Springfield, MO, USA and* ²*Biology Department, Drury University, Springfield, MO, USA*

Abstract

Aim We used insular lizard communities to test the predictions of two hypotheses that attempt to explain patterns of species richness on small islands. We first address the subsidized island biogeography (SIB) hypothesis, which predicts that spatial subsidies may cause insular species richness to deviate from species–area predictions, especially on small islands. Next, we examine the small island effect (SIE), which suggests small islands may not fit the traditional log-linear species–area curve.

Location Islands with arthropodivorous lizard communities throughout the Gulf of California.

Methods To evaluate the SIB hypothesis, we first identified subsidized and unsubsidized islands based on surrogate measures of allochthonous productivity (i.e. island size and bird presence). Subsequently, we created species–area curves from previously published lizard species richness and island area data. We used the residuals and slopes from these analyses to compare species richness on subsidized and unsubsidized islands. To test for an SIE, we used breakpoint regression to model the relationship between lizard species richness and island area. We compared results from this model to results from the log-linear regression model.

Results Subsidized islands had a lower slope than unsubsidized islands, and the difference between these groups was significant when small islands were defined as < 1 km². In addition to comparing slopes, we tested for differences in the magnitude of the residuals (from the species–area regression of all islands) for subsidized vs. unsubsidized islands. We found no significant patterns in the residual values for small vs. large islands, or between islands with and without seabirds. The SIE was found to be a slightly better predictor of lizard species richness than the traditional log-linear model.

Main conclusions Predictions of the SIB hypothesis were partially supported by the data. The absence of a significant SIE may be a result of spatial subsidies as explained by the SIB hypothesis and data presented here. We conclude by suggesting potential scenarios to test for interactions between these two small island hypotheses. Future studies considering factors affecting species richness should examine the possible role of spatial subsidies, an SIE, or a synergistic effect of the two in data sets with small islands.

Keywords

Lizards, spatial subsidies, small island effect, species–area curve, species richness, subsidized island biogeography.

*Correspondence: K. Barrett, Department of Biological Sciences, 331 Funchess Hall, Auburn University, Auburn, AL 36849-5414, USA.
E-mail: barrerk@auburn.edu

INTRODUCTION

Schoener (1976) states 'one of community ecology's few laws' is the positive log-linear relationship between species richness and the size of an island or habitat fragment (Williams, 1943; MacArthur & Wilson, 1967; Wilcox, 1980). Since the publication of MacArthur & Wilson's (1967) *The Theory of Island Biogeography*, numerous authors have offered supplemental hypotheses and/or critiques to the theory (MacArthur *et al.*, 1972; Murphy, 1983a; He & Legendre, 1996; Connor *et al.*, 2000; Anderson & Wait, 2001; Lomolino & Weiser, 2001). So much of the research on species–area relationships supports the idea that species richness increases with island area that Lomolino (2000) has suggested it might be 'more expedient to report the few exceptions'. Here, we examine two hypotheses, subsidized island biogeography (SIB; Anderson & Wait, 2001) and the small island effect (SIE; Preston, 1962; Lomolino, 2000), which both predict that species–area relationships on small islands may vary from species–area relationships on larger islands in a given system. We used lizard species richness data from sixty islands in the Gulf of California to examine these hypotheses.

The SIB hypothesis (Anderson & Wait, 2001) predicts that spatial subsidies (resources within the system derived from outside that system) may alter the species richness of subsidized islands such that island area alone is not a sufficient predictor of species richness. Exactly how spatial subsidies alter species richness depends upon the degree to which the total productivity of the island is augmented by the subsidies (Anderson & Wait, 2001). For example, islands receiving small to moderate amounts of subsidized material may have greater species richness than would be predicted solely by area (Fig. 1, area A). These islands would fall on the ascending side of the hypothesized unimodal curve of productivity and species richness (Rosenzweig, 1995; Mittelbach *et al.*, 2001). Islands receiving large amounts of subsidized material (i.e. those on the descending side of the unimodal curve) may have fewer species than the species–area curve would predict (Fig. 1, area B).

Anderson & Wait (2001) suggest the SIB hypothesis may be used to explain species richness on small islands when these islands have species–area slopes that deviate significantly from species–area slopes that include larger islands. We offer an empirical test of the SIB hypothesis using arthropodivorous lizards on desert islands in the Gulf of California. Arthropodivorous lizards are known to consume the arthropods that occur in high densities as a result of marine subsidies to the islands (Polis & Hurd, 1996a; Barrett, 2002). These desert islands provided an ideal system because increases in productivity from marine-derived resources are conspicuous because of low terrestrial primary productivity (Anderson & Polis, 1999). Because of the greater diversity of resources brought onto the islands by marine subsidies (Polis & Hurd, 1996a), these resources may support a greater variety of consumers. In addition, a greater density of lizards (Polis &

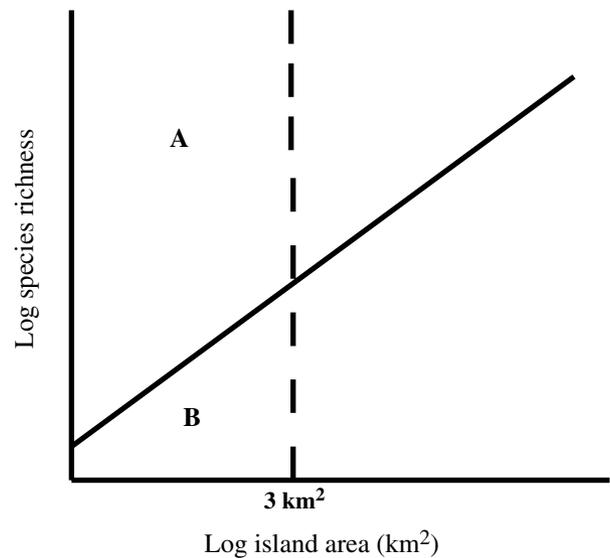


Figure 1 The subsidized island biogeography hypothesis. Anderson & Wait (2001) proposed islands $< 3 \text{ km}^2$ are impacted by spatial subsidies in a manner that may alter species richness. On islands that are moderately subsidized, species richness may be higher than predicted by the species–area curve (region A); however, when spatial subsidies greatly increase productivity species richness may fall below values predicted by area alone (region B). Adapted from Anderson & Wait (2001).

Hurd, 1996b) suggests that extinction rates may decrease in the presence of subsidies, thereby allowing species to persist longer on subsidized islands than would be possible without spatial subsidies. Therefore, as predicted by the SIB hypothesis, we predict that species richness of lizards will be greater on small islands and/or islands with seabirds than that predicted by log–log regressions of species richness and island area. We test the SIB hypothesis by comparing data derived from the linear regression analyses of small islands and islands with seabirds (subsidized islands) to large islands and islands without seabirds (relatively unsubsidized islands).

In addition to evaluating the SIB hypothesis, we also consider the potential impacts of the SIE (Preston, 1962; Lomolino, 2000; Lomolino & Weiser, 2001). The SIE refers to the presence of two distinct patterns in the species–area relationship. For islands greater than some critical minimum, species richness increases linearly with area as described by traditional log–log models; however, below that minimum, species richness varies independently of island or fragment area (Lomolino, 2000). For islands subject to the SIE, species richness is most likely to be determined by inter-island differences in habitat characteristics such as exposure to storms or other stochastic events (Niering, 1963; Losos, 1998), or possibly the availability of subsidized materials from the ocean. We test for a possible SIE for islands in the Gulf of California by using a breakpoint regression model (Lomolino & Weiser, 2001).

METHODS

Data collection

We used the most recently published data to determine the species richness of completely or partially arthropodivorous lizards on islands in the Gulf of California (Grismer, 2002). We amended species richness numbers for four islands (Isla Bota, Isla Cerraja, Isla Flecha, and Isla Pata) near the Bahía de los Angeles region where we discovered *Phyllodactylus nocticolus* Murphy (1983b). Grismer's (2002) checklist does not list this species as inhabiting these islands. We omitted herbivorous lizards (*Sauromalus* spp.) from the analysis because strictly herbivorous lizards are presumably not impacted by spatial subsidies in the same manner as arthropodivorous lizards. We assume that *Sauromalus* spp. do not consume the arthropods that increase in density with marine subsidies (Sylber, 1988). Arthropodivorous lizards (thirteen genera; fifty-one species) inhabit sixty-eight islands in the Gulf; however, we were only able to obtain estimates of island area for sixty of the islands.

We used island size and seabird presence/absence as surrogate measures of productivity. Polis & Hurd (1996a) have shown that secondary productivity is greater on islands with seabirds, and is negatively correlated with island size, because smaller islands have proportionately more area exposed to the ocean. We attributed seabird presence to islands where seabirds are known to consistently roost or nest. We obtained island area data primarily from Murphy *et al.* (2002); however, island area for Isla El Pardo was absent from this source and was obtained from Due (1992). We determined seabird presence or absence from Felger & Lowe (1976), Sanchez-Piñero & Polis (2000), and L.L. Grismer (pers. comm.). We used the most recent source when data from different sources concerning a single island were not consistent.

Data analysis

To test for the effects of spatial subsidies from the marine system on terrestrial arthropodivorous lizard species richness, we used data obtained from linear regression analyses. These data were used to compare subsidized islands to islands where subsidies are proportionately less important. Anderson & Wait (2001) proposed that small islands most affected by spatial subsidies were those < 3 km². Consequently, we used this cutoff ($n = 40$ islands) for our analysis of the effects of tidal subsidies; however, we repeated all analyses using a cutoff value of 1, 2, 4 and 5 km² ($n = 29, 38, 41$ and 44 islands respectively). We also used an additional cutoff value of 0.25 km² obtained from the SIE breakpoint analysis ($n = 18$). Except for tests with statistically significant results, we only report data from the 3 km² cutoff suggested by Anderson & Wait (2001) and the SIE breakpoint cutoff. Our analysis of the effect of subsidies via seabirds included nineteen islands known to support roosting or nesting seabird colonies.

We plotted the log of lizard species richness against the log of island area for all islands with lizards in the Gulf, and then calculated the residuals for each data point

resulting from a least-squares linear regression. To determine if spatial subsidies altered the variance in species richness as predicted by area, we used a two-sample *t*-test to compare the absolute value of the residuals from subsidized islands to those from unsubsidized islands. We then used a chi-square analysis to determine if the frequency of subsidized islands with species richness values above the regression line for all islands was greater or less than expected by chance. We also tested for a difference between the slopes of the regression lines created by the linear regressions of the two groups (i.e. subsidized and unsubsidized islands) using an analysis of covariance (ANCOVA). For the ANCOVA the predictor variables used in the general linear model were island area, subsidy presence/absence (as defined by island size or seabird presence), and an interaction term. Island area was used as a covariate.

We re-examined the species–area relationships using a breakpoint regression model (Lomolino & Weiser, 2001) to determine if an SIE better explained the variance among species distributions on these islands than a least-squares linear regression model. We performed the breakpoint regression using an Excel macro (Microsoft Corporation, Redmond, WA, USA) developed by Lomolino & Weiser (2001). An SIE is detected by incrementing the trial breakpoint (the point below which species richness varies independent of island area) by 0.01 each iteration. Breakpoint regression analysis models the relationship between species richness and area below the SIE with a slope of zero, and above the SIE with a linear regression line of best fit. After performing the breakpoint regression, we used the breakpoint value as the cutoff value to reanalyse the small vs. large island data sets. We performed all statistical tests in Minitab (Minitab, Inc., State College, PA, USA) and we considered *P*-values < 0.05 to be significant.

RESULTS

When all islands with arthropodivorous lizards in the Gulf of California were analysed together, log island area was a significant predictor of log species richness ($r^2 = 0.58$, $P < 0.005$), and the regression line had a slope (z) of 0.20. A *t*-test between the absolute values of the residuals resulting from this regression revealed no significant difference in the magnitude of the variance generated for large vs. small islands at the 3-km² cutoff ($P = 0.22$). Similarly, for small islands there was no significant difference between the predicted frequency of islands containing greater species richness than expected (50%) and the observed frequency (48%; chi-square, $P > 0.05$). When small (< 3 km²) and large (> 3 km²) islands were analysed separately, log area was a significant predictor of log species richness ($P = 0.04$); however, it was not a significant predictor of log species richness for large islands ($P = 0.06$). The slope for the linear regression of small islands was not significantly different from the slope of large islands ($P = 0.54$). When the same analyses were repeated with a small island cutoff of 1 km², we found a significant difference between the slope of the regression lines for small and large islands ($P = 0.05$, Fig. 2a).

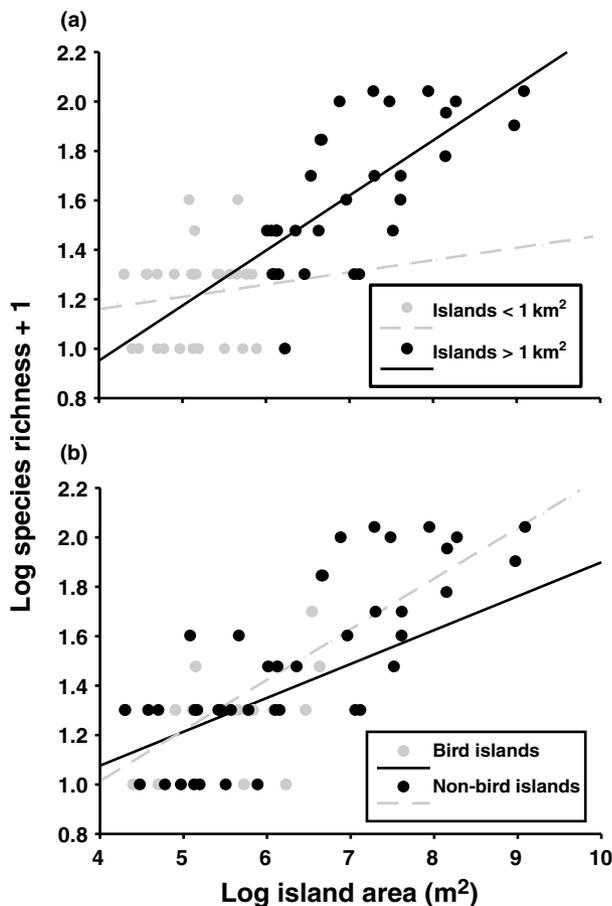


Figure 2 The least-squares linear regression of log lizard species richness vs. log island area for (a) small islands ($z = 0.05$, $r^2 = 0.02$, $P = 0.52$) vs. large islands ($z = 0.22$, $r^2 = 0.47$, $P < 0.005$), and (b) islands with seabirds ($z = 0.11$, $r^2 = 0.19$, $P = 0.06$) and islands without seabirds ($z = 0.21$, $r^2 = 0.62$, $P < 0.005$) in the Gulf of California. The slopes of the two lines were significantly different between small and large islands (ANCOVA; $F = 4.11$, $P = 0.05$), but not between islands with and without seabirds ($F = 1.97$, $P = 0.17$).

The analyses above were repeated for islands receiving subsidies from seabirds vs. islands without seabirds. The variance around the line of best fit resulting from the species–area regression of all islands was not significantly different between islands without seabirds and islands with seabirds (t -test between the absolute value of the residuals, $P = 0.49$). For islands with seabirds, no significant difference existed between the predicted frequency of islands containing greater species richness than expected (50%) and the observed frequency (39%; chi-square, $P > 0.05$). Log island area was a significant predictor of arthropodivorous lizard species richness on islands without seabirds ($r^2 = 0.62$, $P < 0.005$); however, the regression was only marginally significant for islands with seabirds ($r^2 = 0.19$, $P = 0.06$). There was no significant difference between the slopes of these two regressions ($P = 0.38$, Fig. 2b).

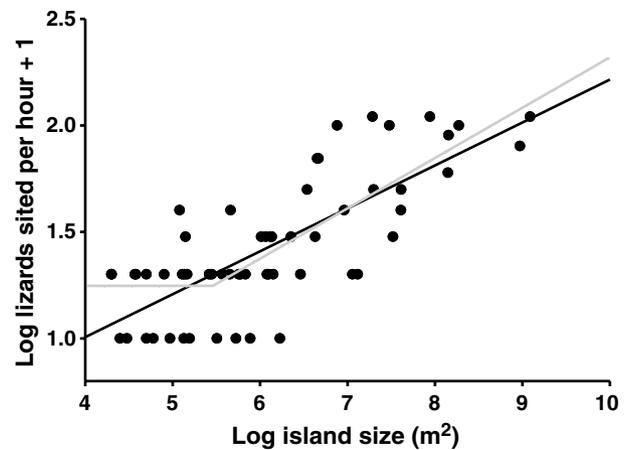


Figure 3 The plot of species richness and island area in log–log space for insular lizards in the Gulf of California showing the least-squares linear (solid, black) and breakpoint (dashed, gray) regression lines. The breakpoint model only explained an additional 3% of the variation compared with the traditional log-linear model ($r^2 = 0.61$ and 0.58 , respectively).

The breakpoint regression model provided only a slightly better fit than log–log linear regression ($r^2 = 0.61$, Fig. 3). The breakpoint for the model was 0.25 km^2 . This value included eighteen of the study islands (30%). After the breakpoint was established, we repeated the tests for large vs. small islands using the breakpoint value of 0.25 km^2 as the small island threshold. There was no significant difference between the absolute value of the residuals for large vs. small islands resulting from the linear regression of all islands (t -test, $P = 0.59$). For islands below the breakpoint, no significant difference existed between the predicted frequency of islands containing greater species richness than expected (50%) and the observed frequency (56%; chi-square, $P > 0.05$). Additionally, the slopes of the linear regression lines created by the two groups were not significantly different (ANCOVA, $F = 0.14$, $P = 0.34$).

DISCUSSION

We examined two hypotheses, SIB and the SIE, that provide explanations for species richness patterns on small islands. We used arthropodivorous lizard species richness data from desert islands in the Gulf of California to evaluate these hypotheses. By analysing these data, we provided the first empirical evaluation of the SIB hypothesis. Additionally, we add to the data that has been used by others (Lomolino & Weiser, 2001) to test for an SIE, a concept that has received much attention in the current biogeographical literature (Lomolino, 2000, 2002; Williamson *et al.*, 2001, 2002).

Anderson & Wait (2001) suggest the effects of oceanic spatial subsidies on insular species richness are most likely to be conspicuous on islands $< 3 \text{ km}^2$. Our analyses failed to detect any statistically significant patterns at this island size;

however, we did identify a significant difference between the slopes of large and small islands using a 1-km² cutoff (Fig. 2a). With all analyses the slope of the regression for small islands was lower than for larger islands (causing the slope to primarily pass through region A in Fig. 1). The residuals (resulting from the species–area regression of all islands) for the two groups did not differ consistently from one another in either magnitude or sign (i.e. above or below predicted values).

In addition to using island size as a surrogate measure of productivity via spatial subsidies, we also used the presence of seabirds. The slope of the regression for islands subsidized by seabirds was less than for islands without seabirds (primarily region A, Fig. 1), but this difference was not statistically significant. Analyses on the residuals from the species–area regression revealed no significant differences in magnitude or sign between islands with and without seabirds.

Our use of the breakpoint model to detect a potential SIE revealed only a slight (3%) improvement in the amount of variance in species–area predictions relative to the log-linear model. Lomolino (2000) suggests the SIE may correspond to the range of island sizes where resources are limited to a degree prohibiting the persistence of most populations. In cases such as this, it is possible that a lack of an SIE could be evidence for an effect of spatial subsidies, which may allow populations to persist despite a lack of *in situ* resources (Anderson & Wait, 2001).

We suggest that the significant difference between the slopes of the regressions for islands < 1 km² and those > 1 km² supports a synthesis of the ideas contained within the SIB and SIE hypotheses. While a significant difference between slopes was not found using seabirds as a measure of spatial subsidies, the trend between subsidized and unsubsidized islands was the same. The lack of a clear relationship between island area and species richness that Lomolino (2000) and Lomolino & Weiser (2001) have suggested may very well be due to spatial subsidies. To further test such a hypothesis, one could examine the species richness on small islands with permeable borders (sloping beaches), and compare it with the species richness on otherwise equivalent small islands with impermeable borders (coastal cliffs). If density and species richness are consistently greater on islands with greater permeability to marine inputs by tidal action relative to impermeable islands, then the SIB hypothesis cannot be ruled out as a possible mechanism explaining species richness patterns.

Community interactions can be complex; consequently, there may be factors contributing to the observed patterns for which we have not accounted. We assumed there was no relationship between island age and the ability of a lizard community to indirectly utilize intertidal resources as a result of our numerous observations of lizards foraging in intertidal zones on islands with a variety of geologic histories (Carreño & Helenes, 2002). We also make the assumption that seabirds on these islands are not acting as lizard predators. Our unpublished data on lizard density across many islands in the Gulf with and without seabird populations

suggests seabird presence greatly increases lizard abundance. A high density of consumers resulting from spatial subsidies has been documented in several island studies (Markwell & Daugherty, 2002; Polis & Hurd, 1995; Rose & Polis, 1998; Sanchez-Pinñero & Polis, 2000). Increased consumer density may alter community interactions and result in effects on species richness not predicted by the SIB hypothesis. We were not able to test for all such interactions; thus, while we recognize their potential role in the ecology of insular lizards, here we have only evaluated patterns of species richness as predicted by the SIB and SIE hypotheses. Understanding if increased density can stabilize populations to a degree that eventually increases species richness is important to future island biogeography studies.

Small islands are often overlooked by many island studies (Brown & Lomolino, 1998); however, studying smaller patches offers an opportunity to gain further insight into the ecological impacts of spatial subsidies on species richness. Additionally, the effects of subsidies via biological transport are likely to be important factors for many island studies (Polis & Hurd, 1995; Sanchez-Pinñero & Polis, 2000). Here, we found evidence that suggest subsidies may alter the slope of species–area regressions. Consequently, we suggest small islands, with their inherently unique features (e.g. greater proportion of border area, more frequent inhabitation by seabirds) receive closer scrutiny in future island studies concerned with patterns of species richness.

ACKNOWLEDGMENTS

We would like to thank Scott Boback, Brian D. Green, Robert W. Murphy, Abigail Sorenson, and an anonymous reviewer for comments on an earlier version of the manuscript. We also thank Mark V. Lomolino for providing the program to test for a small island effect and Lee L. Grismer for helping to identify islands with seabird populations. Doug Aubrey, Kate Heckman, Caleb Hickman, Matt Stone, and Shannon Taylor assisted in the field. Funding was provided by Southwest Missouri State University (Department of Biology, Graduate College, Boritski Scholarship), Sigma Xi, through a Grants-in-Aid of Research, (K.B.) and the Andrew W. Mellon Foundation (W.B.A. and D.A.W.). We thank the Mexican Department of the Environment for a permit to work on the islands (SEMARNAT no. 1448).

REFERENCES

- Anderson, W.B. & Polis, G.A. (1999) Nutrient fluxes from water to land: seabirds affect plant nutrient status on Gulf of California islands. *Oecologia*, **118**, 324–332.
- Anderson, W.B. & Wait, D.A. (2001) Subsidized island biogeography: another new twist on an old theory. *Ecology Letters*, **4**, 289–291.
- Barrett, K. (2002) *The effect of spatial subsidies on the diet, density, and species richness of insular lizards in the Gulf of California*, M.S. Thesis. Southwest Missouri State University, Springfield, MO, USA.

- Brown, J.H. & Lomolino, M.V. (1998) *Biogeography*, 2nd edn. Sinauer Associates Inc, Sunderland, MA, USA.
- Carreño, A.L. & Helenes, J. (2002) Geology and ages of the islands. *A new island biogeography in the Sea of Cortés* (ed. by T.J. Case, M.L. Cody and E. Ezcurra), pp. 14–40. Oxford University Press, Oxford.
- Connor, E.F., Courtney, A.C. & Yoder, J.M. (2000) Individuals–area relationships: the relationship between animal population density and area. *Ecology*, **81**, 734–748.
- Due, A.D. (1992) *Biogeography of scorpions in Baja California, Mexico and an analysis of the insular scorpion fauna in the Gulf of California*, PhD Diss. Vanderbilt University, Nashville.
- Felger, R.S. & Lowe, C.H. (1976) *The island and coastal vegetation and flora of the northern part of the Gulf of California*. Contributions in Science, Natural History Museum of Los Angeles County, Los Angeles, CA, USA.
- Grismer, L.L. (2002) *Amphibians and Reptiles of Baja California*. University of California Press, Berkeley.
- He, F. & Legendre, P. (1996) On species–area relations. *The American Naturalist*, **148**, 719–737.
- Lomolino, M.V. (2000) Ecology's most general, yet protean pattern: the species–area relationship. *Journal of Biogeography*, **27**, 17–26.
- Lomolino, M.V. (2002) '...there are areas too small, and areas too large, to show clear diversity patterns...' R.H. MacArthur (1972: 191). *Journal of Biogeography*, **29**, 555–557.
- Lomolino, M.V. & Weiser, M.D. (2001) Towards a more general species–area relationship: diversity on all islands, great and small. *Journal of Biogeography*, **28**, 431–445.
- Losos, J.B. (1998) Ecological and evolutionary determinants of the species–area relationship in Caribbean anoline lizards. *Evolution on islands* (ed. by P.R. Grant), pp. 210–224. Oxford University Press, Cambridge.
- MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. *Monographs in population biology no. 1*. Princeton University Press, Princeton.
- MacArthur, R.H., Diamond, J.M. & Karr, J.R. (1972) Density compensation in island faunas. *Ecology*, **53**, 330–342.
- Markwell, T.J. & Daugherty, C.H. (2002) Invertebrate and lizard abundance is greater on seabird-inhabited islands than on seabird-free islands in the Marlborough Sounds, New Zealand. *Ecoscience* **9**, 293–299.
- Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B., Willig, M.R., Dodson, S.I. & Gough, L. (2001) What is the observed relationship between species richness and productivity? *Ecology*, **82**, 2381–2396.
- Murphy, R. (1983a) The reptiles: origins and evolution. *Island biogeography in the Sea of Cortez* (ed. by T.J. Case and M.L. Cody), pp. 130–158. University of California Press, Berkeley.
- Murphy, R. (1983b) Paleobiogeography and genetic differentiation of the Baja California herpetofauna. *Occasional Papers, California Academy of Sciences*, **137**, 1–48.
- Murphy, R., Murphy, R.N., Sanchez-Piñero, F., Polis, G.A. & Aalbu, R.L. (2002) New measurements of area and distance for islands in the Sea of Cortes. *A new island biogeography in the Sea of Cortes* (ed. by T.J. Case, M.L. Cody and E. Ezcurra), pp. 447–464. Oxford University Press, Oxford.
- Niering, W.A. (1963) Terrestrial ecology of Kapingamarangi Atoll, Caroline Islands. *Ecological Monographs*, **33**, 131–160.
- Polis, G.A. & Hurd, S.D. (1995) Extraordinarily high spider densities on islands: flow of energy from the marine to terrestrial food webs and the absence of predation. *Proceedings of the National Academy of Science, USA*, **92**, 4382–4386.
- Polis, G.A. & Hurd, S.D. (1996a) Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *The American Naturalist*, **147**, 396–423.
- Polis, G.A. & Hurd, S.D. (1996b) Allochthonous input across habitats, subsidized consumers, and apparent trophic cascades: examples from the ocean-land interface. *Food webs: integration of patterns and dynamics* (ed. by G.A. Polis and K.O. Winemiller), pp. 275–285. Chapman and Hall, New York.
- Preston, F.W. (1962) The canonical distribution of commonness and rarity: part I. *Ecology*, **43**, 185–215.
- Rose, M.D. & Polis, G.A. (1998) The distribution and abundance of coyotes: the effects of allochthonous food subsidies from the sea. *Ecology*, **79**, 998–1007.
- Rosenzweig, M.L. (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge.
- Sanchez-Piñero, F. & Polis, G.A. (2000) Bottom-up dynamics of allochthonous input: direct and indirect effects of seabirds on islands. *Ecology*, **81**, 3117–3132.
- Schoener, T.W. (1976) The species–area relationship within archipelagos: models and evidence from island land birds. *Proceedings of the 16th International Ornithological Congress* (ed. by H.J. Firth and J.H. Calaby), pp. 629–642. Australian Academy of Science, Canberra.
- Sylber, C.K. (1988) Feeding habits of the lizards *Sauromalus varius* and *S. hispidus* in the Gulf of California. *Journal of Herpetology*, **22**, 413–424.
- Wilcox, B.A. (1980) Species number, stability, and equilibrium status of reptile faunas on the California islands. *The California Islands: proceedings of a multidisciplinary symposium* (ed. by D.M. Power), pp. 551–564. Santa Barbara Museum of Natural History, Santa Barbara.
- Williams, C.B. (1943) Area and the number of species. *Nature*, **152**, 264–267.
- Williamson, M., Gaston, K.J. & Lonsdale, W.M. (2001) The species–area relationship does not have an asymptote! *Journal of Biogeography*, **28**, 827–830.
- Williamson, M., Gaston, K.J. & Lonsdale, W.M. (2002) An asymptote is an asymptote and not found in species–area relationships. *Journal of Biogeography*, **29**, 1713.

BIOSKETCHES

Kyle Barrett is a doctoral student at Auburn University. His research interests include the biogeography and food web dynamics of amphibians and reptiles.

D. Alexander Wait is an assistant professor of Biology at Southwest Missouri State University. His research interests include the physiological ecology of plant/animal interactions.

Wendy B. Anderson is an assistant professor of Biology at Drury University. Her interests include the effects of spatial subsidies and boundary permeability on plant and animal community dynamics.