

COMMENTARY

A model for species distributions along a gradient: lizards as study systems

Un modelo para la distribución de especies a lo largo de un gradiente:
lagartijas como sistemas de estudio

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ABSTRACT

Terborgh (1971) proposed a model for zonation patterns of animal species along environmental gradients, which was subsequently applied to altitudinal gradients of species replacements of birds and mammals in tropical biomes. Three major factors were invoked to account for the zonation patterns detected: autecological responses, habitat discontinuities, and interspecific interactions (mainly competition). Here, we expand and generalize Terborgh's model to include ectothermic vertebrates, whose thermal requirements may impose severe constraints to physiological performance (including reproduction). Based on our experience, we propose that our modified model may be applied to understand distributional patterns of lizards along the environmental gradient provided by the tall Andean ranges, by formalizing explicit hypothesis testing.

Key words: Zonation, gradient, altitude, species replacement, ectotherms.

RESUMEN

Terborgh (1971) propuso un modelo para los patrones de zonación de especies animales a través de gradientes ambientales, el cual fue posteriormente aplicado a gradientes altitudinales de reemplazos de especies de aves y mamíferos en biomas tropicales. Tres factores principales se propusieron para explicar los patrones de zonación detectados: respuestas autecológicas, discontinuidades de hábitat, e interacciones interespecíficas (principalmente competencia). Aquí expandimos y generalizamos el modelo de Terborgh para incluir a los vertebrados ectotérmicos, cuyos requerimientos térmicos pueden imponer severas restricciones a su desempeño fisiológico (incluida la reproducción). Basados en nuestra experiencia, proponemos que el modelo modificado puede aplicarse para entender los patrones de distribución de lagartijas a través de gradientes ambientales provistos por la alta cordillera andina, mediante la formalización explícita de pruebas de hipótesis.

Palabras clave: Zonación, gradiente, altitud, reemplazo de especies, ectotermos.

INTRODUCTION

Ecologists trying to understand species distribution patterns often focus on island biogeography (e.g., MacArthur & Wilson 1967, Gilpin & Diamond 1982, Case 1983b), peninsular effects (e.g., Gilpin 1981, Busack & Hedges 1984), latitudinal trends in species diversity (e.g., Kiestler 1971, Meserve & Glanz 1978, Schall & Pianka 1978, Meserve

et al. 1991, Stevens 1989), and altitudinal zonation (e.g., Terborgh 1971, 1977, Pearson & Ralph 1978, Patterson et al. 1989, Stevens 1992).

According to Terborgh (1971), zonation patterns along environmental gradients (e.g., Durrant 1946, Connell 1961a, 1961b, Miller 1964, Beals 1969, Diamond 1970, 1973, Dayton 1971, Fuentes & Jaksic 1980, Hairston 1980a, 1980b, Marquet et al. 1989)

are explained by several causal factors: (1) Animals differ in their responses, and hence their abundances and distributions, due to changing environmental conditions along a gradient; (2) Habitat discontinuities produce distribution breaks; and/or (3) interspecific interactions (particularly competitive exclusion) explain distribution limits.

Most research in this area has been at two contrasting levels of complexity: large-scale correlational analyses of species-rich taxa (e.g., Whittaker & Neiring 1965, Terborgh 1971, 1977, Terborgh & Weske 1975), or simpler situations in which narrow zones of sympatry exist between as few as two species (e.g., Brown 1971, Heller 1971, Heller & Gates 1971, Heller & Poulson 1972, Schluter 1982).

The use of either extremely complex or extremely simple assemblages has limitations for an in-depth understanding of the factors structuring assemblages in general. Perhaps the most influential community-level analyses of terrestrial vertebrate zonation patterns have been performed on the bird faunas of New Guinea and Peru (Terborgh 1971, 1977, Diamond 1972, 1973, 1975, Terborgh & Weske 1975). These studies have asserted that interspecific competition plays the primary role in setting most species' distributional limits. However, they involved many bird species (sometimes > 250 spp.), making it impossible to examine or infer direct interactions among any given species pair. In addition, tropical forest habitats are so vegetationally complex that attempting to correlate the distribution or abundance of any particular bird species to particular vegetational components also suffers from problems of sheer complexity. Thus, while broad assemblage patterns may perhaps be discerned, the direct influence of any of the proposed factors on a given species can be very difficult to determine. Such studies have come under strong criticism (e.g., Connor & Simberloff 1983) for stressing the role of competition while failing to document the actual food and/or microhabitat preference of any of the component species, as well as the failure to demonstrate interference interactions among alleged competitors. (Interestingly, long before competition became a reigning

paradigm in ecology, Rand [1936] studied altitudinal zonation of New Guinea birds and suggested that temperature changes with increasing elevation regulated bird distributions).

At the other end of the spectrum, the work on species pairs (e.g., Brown 1971, Baker 1974, Schluter 1982), while providing detailed knowledge of causal factors, can only hint at how structure might arise in more complex assemblages. Multiple cases of different species combinations are then needed for answering community ecology questions (e.g., Schluter & Grant 1984). A middle ground is well suited to better understand factors that shape assemblages, using a system of moderate complexity and species whose ecologies are readily examined.

We propose that many aspects of the problem of assemblage structure are better addressed in a situation of intermediate complexity, specifically using lizards as the study group. These reptiles have been called "model organisms" for ecological studies (Huey et al. 1983), being easy to study due to their low vagility and ease of observation and capture. In contrast to the inherent problems of previous work, microhabitat selection and availabilities are easily quantified, and diet studies can be performed in a number of ways. Thus, they are excellent subjects for both comparative studies of behavioral (e.g., Stamps 1977, Fox 1978, Carothers 1981, 1983, 1984), population (e.g., Tinkle 1967, Ballinger 1979, Dunham 1980), and community phenomena (e.g., Schoener 1968, 1975, Pianka 1973, 1975, Pacala & Roughgarden 1982, Case 1983a, Roughgarden et al. 1983).

LIZARDS OF THE GENUS *LIOLAEMUS* IN CENTRAL CHILE

The diurnal South American tropidurid genus *Liolaemus* occurs over a wide longitudinal, elevational, and habitat span. Its distribution ranges from the Equator to Tierra del Fuego, from sea level to over 4500 m, and from the cold coastal rain forests of southern Chile to the driest place on Earth, the Atacama Desert (Donoso-Barros 1966). Species differ widely in size, diet, and microhabitats (Donoso-Barros 1966). Zonation among these species in

the central Chilean Cordillera has been noted by other researchers (Hellmich 1934, 1951, Fuentes & Jaksic 1979, Fuentes 1981), and Cody (1970) found zonation among some congeneric bird species in the same region. Several researchers have suggested that members of this genus evolved traits convergent upon those of lizards from several families of lizards in central California (Sage 1973, Fuentes 1976). Thus, the radiation in habitats occupied, niche use, and morphology within this genus is quite striking (e.g., Hurtubia & di Castri 1973). In this fauna, the number of species and habitat complexities are not overwhelming, yet high enough for exploring community-level phenomena. Unlike the North American lizard fauna (Kiestler 1971), species abundances and diversity stay high with increasing elevation. Additionally, all are congeneric, suggesting (e.g., Grant & Abbott 1980) that tests of competition might fruitfully be pursued. We do not try to exorcise or exonerate "the ghost of competition past" (Connell 1980), but rather, we wish to formalize certain questions regarding the limits of present-day distributions.

A MODEL FOR SPECIES DISTRIBUTIONS ALONG A GRADIENT

Terborgh (1971) presented three models to explain distributions, representing the three limiting factors he proposed. He then compared bird distributions against the models to see which one provided the best fit. Our approach (first developed by Carothers 1987) uses three models different from Terborgh's, based upon animal and resource distribution patterns (Fig. 1). Each of our models considers the presence or absence of an additional species. Either a single hypothesis or two alternative hypotheses can explain distributions. When two hypotheses possibly explain a distribution, comparison is made to another transect where resource or species distributions differ in order to test the hypothesis. Terborgh made use of distributions of birds on a separate massif that differed, among other things, in species present (Terborgh & Weske 1975). He viewed this as a "natural experiment" (Diamond 1986) for the test of

competitive interactions in determining distributions, asserting that birds showed elevational expansion of ranges in the absence of parapatric species.

In our model, the resource (R) of a species (X) is plotted as either constant or decreasing with respect to a positive or negative elevational change (Fig. 1). The curve of resource R sets the upper limit on species X. The abundance of species X along the gradient is then plotted. There are three basic patterns (Fig. 1). In each, a new species Y either has an overlapping or parapatric distribution, or is absent. When this second species Y is absent, the limits of X cannot be explained by interspecific competition, predation, or parasitism by Y even when the latter has a demonstrated or suspected effect on X in sympatry. If Y is present, then such competition or predation might be important, a matter then deserving further experimental study.

Pattern I: R is constant while X decreases. With Y absent (Ia), physiological factors are implicated in X's decline. For instance, thermoregulatory constraints reducing individuals' ability to survive may in the end result in the population reaching its minimum viable population size. The trend may be compounded (but not neutralized) by a source-sink dynamics (Pulliam 1988), but see below. If Y appears (Ib), then comparison to other transects along which Y's distribution is different (or if Y is absent) allows tests of the more likely alternative.

Pattern II: R is constant, and X stays constant but declines to zero at a relatively sharply defined border. With Y absent (IIa), sudden physiological thresholds are implicated. For instance, critical temperature for thermoregulation or failure to reproduce. In this case, the physiological stress may be so hard that there is no migration from more benign places (population sources) that allows maintenance of a marginal subpopulation of maladapted individuals (sink population). Lack of a source-sink metapopulation dynamics may not be uncommon among ectothermic vertebrates, given their strong dependence on favorable environmental conditions. If Y appears (IIb), then biotic interactions are implicated (e.g., competition, predation).

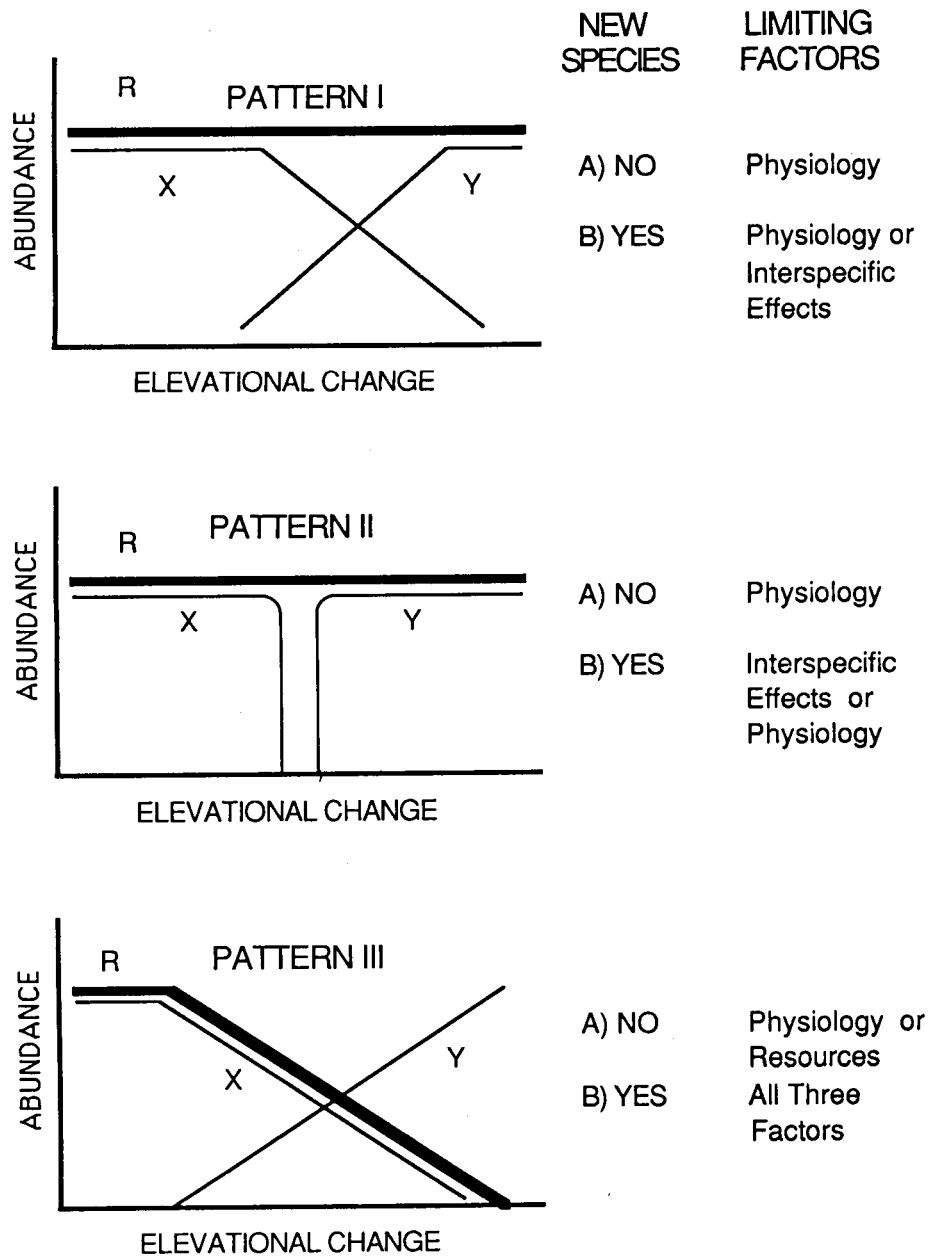


Fig. 1: Graphical representation of possible distributional patterns of resources and species (as a function of growth rates or population densities) with factors influencing them. R = resource, X = study species, Y = possible other affecting species (e.g., predator, parasite, or competitor).

Representación gráfica de los posibles patrones de distribución de recursos y especies (como función de tasas de crecimiento o densidades poblacionales) y los factores que los influyen. R = recurso, X = especie estudiada, Y = posible especie que afecta (e.g., predador, parásito, o competidor).

Pattern III: Both R and X decline. With Y absent (IIIa), physiological constraints or habitat quality can be important. Comparisons to transects with different elevational

gradients will indicate relevance of physiological constraints. When Y is present (IIIb), anything is possible. As before, comparisons to other transects that differ in distributions

of R are needed. Y is not restricted by R although it does use up R to the detriment of X.

Unlike Terborgh's method, ours requires knowledge of each species' resource use, allowing more definitive conclusions to be reached. Also, there are problems with the three factors in Terborgh's model—changes in the physical or biological environment along the gradient, habitat discontinuities, or competitive exclusion. The first two factors are not mutually exclusive (the second is generally a special case of the first), and inter-species interactions other than competition are not considered. Our model uses factors that are unambiguous and more general: (1) physiological limitation resulting only from changing climatological factors along the gradient, (2) changing resource availabilities (generally food or microhabitat), and (3) presence or absence of another species (predators, competitors, or parasites).

We think that the physiological approach is a time-saving starting point (see Bozinovic et al. 1987). When analyses of other data (microhabitat availabilities and congener distributions) are completed, they can be incorporated into the model proposed. At that time one can draw tentative conclusions from the model as to which are the most frequently occurring limitations upon *Liolaemus* distributions. Results from laboratory experiments and natural experiments on differing transects also provide the necessary background for future field experiments and further laboratory experiments to determine most accurately which factors are most important in setting present-day distributional limits. It is noteworthy that much theory exists on the putative factors responsible for species diversity gradients (cf. Stevens 1989, 1992), but little attention has been placed on species' physiology or resource availability. Excessive emphasis on biotic interactions may have blinded us from more obvious and mechanistic explanations.

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LITERATURE CITED

- BAKER SEM (1974) Interspecific aggressive behavior of pocket gophers *Thomomys bottae* and *T. talpoides* (Geomyidae: Rodentia). *Ecology* 55: 671-673.
- BALLINGER RE (1979) Intraspecific variation in demography and life history of the lizard, *Sceloporus jarrovi*, along an altitudinal gradient in southeastern Arizona. *Ecology* 60: 901-909.
- BEALS EW (1969) Vegetation change along altitudinal transects. *Science* 165: 981-985.
- BOZINOVIC F, M ROSENMAN & G RUIZ (1987) Transferencia de calor, convección y gradiente altitudinal. *Archivos de Biología y Medicina Experimentales (Chile)* 20: 85-88.
- BROWN JH (1971) Mechanisms of competitive exclusion between two species of chipmunks. *Ecology* 52: 305-311.
- BUSACK SB & BS HEDGES (1984) Is the peninsular effect a red herring? *American Naturalist* 123: 266-275.
- CAROTHERS JH (1981) Dominance and competition in an herbivorous lizard. *Behavioral Ecology and Sociobiology* 18: 261-266.
- CAROTHERS JH (1983) Size-related activity patterns in an herbivorous lizard. *Oecologia* 57: 103-106.
- CAROTHERS JH (1984) Sexual selection and sexual dimorphism in some herbivorous lizards. *American Naturalist* 124: 244-254.
- CAROTHERS JH (1987) Aspects of the ecology of lizards in the genus *Liolaemus* in the central Chilean cordillera. Doctoral Thesis, University of California, Berkeley, California. ix +151 pp.
- CASE TJ (1983a) Sympatry and size similarity in *Cnemidophorus*. In: Huey RB, ER Pianka & TW Schoener (eds) *Lizard ecology: studies on a model organism*, 297-325. Harvard University Press, Cambridge, Massachusetts.
- CASE TJ (1983b) The reptiles: ecology. In: Case TJ & ML Cody (eds) *Island biogeography in the Sea of Cortez*: 159-208. University of California Press, Berkeley, California.
- CODY ML (1970) Chilean bird distribution. *Ecology* 51: 455-464.
- CONNELL JH (1961a) The effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecological Monographs* 31: 61-104.
- CONNELL JH (1961b) The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42: 710-723.
- CONNELL JH (1980) Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* 35: 131-138.
- CONNOR EF & D SIMBERLOFF (1983) Interspecific competition and species co-occurrence patterns on islands: null models and evaluation of evidence. *Oikos* 41: 455-465.

- DAYTON PK (1971) Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* 41: 351-389.
- DIAMOND JM (1970) Ecological consequences of island colonization by Southwest Pacific birds. I: Types of niche shifts. *Proceedings of the U. S. National Academy of Sciences* 67: 529-536.
- DIAMOND JM (1972) Avifauna of the eastern highlands of New Guinea. *Nuttall Ornithological Club, Cambridge*.
- DIAMOND JM (1973) Distributional ecology of New Guinea birds. *Science* 179: 759-769.
- DIAMOND JM (1975) Assembly of bird communities. In: Cody ML & JM Diamond (eds) *Ecology and evolution of communities*: 342-444. Harvard University Press, Cambridge, Massachusetts. xii + 545 pp.
- DIAMOND JM (1986) Overview: Laboratory experiments, field experiments, and natural experiments. In: Diamond JM & TJ Case (eds) *Community ecology*: 3-23. Harper and Row, New York, New York. xxii + 665 pp.
- DONOSO-BARROS R (1966) *Reptiles de Chile*. Ediciones de la Universidad de Chile, Santiago. cxlvi + 458 pp.
- DUNHAM AE (1980) An experimental study of interspecific competition between the iguanid lizards *Sceloporus merriami* and *Urosaurus ornatus*. *Ecological Monographs* 50: 309-330.
- DURRANT SD (1946) The pocket gophers (genus *Thomomys*) of Utah. *University of Kansas Publications of the Museum of Natural History* 1: 1-82.
- FOX SF (1978) Natural selection on behavioral phenotypes of the lizard *Uta stansburiana*. *Ecology* 59: 834-847.
- FUENTES ER (1976) Ecological convergence of lizard communities in Chile and California. *Ecology* 75: 3-17.
- FUENTES ER (1981) Evolution of lizard niches in mediterranean habitats. In: di Castri F, DW Goodall & RL Specht (eds) *Ecosystems of the world 11: Mediterranean-type shrublands*: 417-444. Elsevier Scientific Publications, Amsterdam. xii + 643 pp.
- FUENTES ER & FM JAKSIC (1979) Lizards and rodents: an explanation for their relative species diversity in Chile. *Archivos de Biología y Medicina Experimentales (Chile)* 12: 179-190.
- FUENTES ER & FM JAKSIC (1980) Ecological species replacement of *Liolaemus* lizards along a habitat gradient. *Oecologia* 46: 45-48.
- GILPIN ME (1981) Peninsular diversity patterns. *American Naturalist* 118: 291-296.
- GILPIN ME & JM DIAMOND (1982) Factors contributing to non-randomness in species co-occurrences on islands. *Oecologia* 52: 75-84.
- GRANT PR & I ABBOTT (1980) Interspecific competition, island biogeography and null hypotheses. *Evolution* 34: 332-341.
- HAIRSTON NG (1980a) Evolution under interspecific competition: field experiments on terrestrial salamanders. *Evolution* 34: 332-341.
- HAIRSTON NG (1980b) Species packing in the salamander genus *Desmognathus*: What are the interspecific interactions involved? *American Naturalist* 115: 354-366.
- HELLER HC (1971) Altitudinal zonation of chipmunks (*Eutamias*): interspecific aggression. *Ecology* 52: 312-319.
- HELLER HC & DM GATES (1971) Altitudinal zonation of chipmunks (*Eutamias*): energy budgets. *Ecology* 52: 424-433.
- HELLER HC & TL POULSON (1972) Altitudinal zonation of chipmunks (*Eutamias*): adaptations to aridity and high temperatures. *American Midland Naturalist* 87: 296-313.
- HELLMICH WC (1934) Die Eidechsen Chiles, insbesondere die Gattung *Liolaemus*. *Abhandlungen der Bayerischen Akademie der Wissenschaften* 24: 31-40.
- HELLMICH WC (1951) On ecotypic and autotypic characters, a contribution to the knowledge of the evolution of the genus *Liolaemus* (Iguanidae). *Evolution* 5: 359-369.
- HUEY RB, ER PIANKA & TW SCHOENER (1983) *Lizard ecology: studies on a model organism*. Harvard University Press, Cambridge, Massachusetts. viii + 501 pp.
- HURTUBIA J & F DI CASTRI (1973) Segregation of lizard niches in the mediterranean region of Chile. In: di Castri F & HA Mooney (eds) *Mediterranean-type ecosystems: origin and structure*: 349-360. Springer Verlag, Berlin. xiii + 405 pp.
- KIESTER AR (1971) Species density of North American amphibians and reptiles. *Systematic Zoology* 20: 127-137.
- MACARTHUR RH & EO WILSON (1967) *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey. xi + 203 pp.
- MARQUET, PA, JC ORTIZ, F BOZINOVIC & FM JAKSIC (1989) Ecological aspects of thermoregulation at high altitudes: the case of Andean *Liolaemus* lizards in northern Chile. *Oecologia* 81: 16-20.
- MESERVE PL & WE GLANZ (1978) Geographical ecology of small mammals in the northern Chilean arid zone. *Journal of Biogeography* 5: 135-148.
- MESERVE PL, DA KELT & DR MARTINEZ (1991) Geographical ecology of small mammals in continental Chile Chico, South America. *Journal of Biogeography* 18: 179-187.
- MILLER RS (1964) Ecology and distribution of pocket gophers (Geomysidae) in Colorado. *Ecology* 45: 256-272.
- PACALA S & J ROUGHGARDEN (1982) Resource partitioning and interspecific competition in two two-species insular *Anolis* lizard communities. *Science* 217: 444-446.
- PATTERSON BD, PL MESERVE & BK LANG (1989) Distribution and abundance of small mammals along an elevational transect in temperate rainforests of Chile. *Journal of Mammalogy* 70: 67-78.
- PEARSON OP & CJ RALPH (1978) The diversity and abundance of vertebrates along an altitudinal gradient in Peru. *Memorias del Museo de Historia Natural "Javier Prado" (Perú)* 18: 1-97.
- PIANKA ER (1973) The structure of lizard communities. *Annual Review of Ecology and Systematics* 4: 53-74.
- PIANKA ER (1975) Niche relations of desert lizards. In: Cody ML & JM Diamond (eds) *Ecology and evolution of communities*: 55-83. Harvard University Press, Cambridge, Massachusetts. xii + 545 pp.
- PULLIAM HR (1988) Sources, sinks, and population regulation. *American Naturalist* 132: 652-661.
- RAND AL (1936) Results of the Archbold Expedition Number 12: Altitudinal variation in New Guinea birds. *American Museum Novitates* 890: 1-14.
- ROUGHGARDEN J, J RUMMEL & S PACALA (1983) Experimental evidence of strong present-day competition between the *Anolis* populations of the Anguilla Bank - A preliminary report. In: Rhodin J & K Miyata (eds) *Advances in herpetology and evolutionary biology: essays in honor of Ernest E. Williams*: 499-506. Museum of Comparative Zoology, Cambridge, Massachusetts.
- SAGE RD (1973) Ecological convergence of the lizard faunas of the chaparral communities in Chile and California. In: di Castri F & HA Mooney (eds) *Mediterranean-type ecosystems: Origin and structure*: 339-348. Springer-Verlag, Berlin. xiii + 405 pp.

- SCHALL JJ & ER PIANKA (1978) Geographical trends in numbers of species. *Science* 201: 679-686.
- SCHLUTER D (1982) Distribution of Galapagos ground finches along an altitudinal gradient: the importance of food supply. *Ecology* 63: 1504-1517.
- SCHLUTER D & PR GRANT (1984) Determinants of morphological patterns in communities of Darwin's finches. *American Naturalist* 123: 175-196.
- SCHOENER TW (1968) The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* 49: 819-830.
- SCHOENER TW (1975) Presence and absence of habitat shift in some widespread lizard species. *Ecological Monographs* 45: 233-258.
- STAMPS JA (1977) The relationship between resource use, risk and aggression in a tropical territorial lizard. *Ecology* 58: 349-358.
- STEVENS GC (1989) The latitudinal gradient in geographical range: how so many species coexist in the tropics. *American Naturalist* 133: 240-256.
- STEVENS GC (1992) The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. *American Naturalist* 140: 893-911.
- TERBORGH J (1971) Distribution on environmental gradients: Theory and a preliminary interpretation of distribution patterns in the avifauna of the Cordillera Vilcabamba, Peru. *Ecology* 52: 23-40.
- TERBORGH J (1977) Bird species diversity on an Andean elevational gradient. *Ecology* 58: 1007-1019.
- TERBORGH J & JS WESKE (1975) The role of competition in the distribution of Andean birds. *Ecology* 56: 562-576.
- TINKLE DW (1967) The life and demography of the side-blotched lizard. *Miscellaneous Publications of the Museum of Zoology* 132, University of Michigan, Ann Arbor, Michigan.
- WHITTAKER RH & WA NEIRING (1965) Vegetation of the Santa Catalina mountains, Arizona. II: A gradient analysis of the south slope. *Ecology* 46: 47-89.