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A GENERAL EXPLANATION FOR INSULAR BODY SIZE TRENDS IN TERRESTRIAL VERTEBRATES¹

TED J. CASE

Department of Biological Sciences, Purdue University, West Lafayette, Indiana 47907

Abstract. The insular body size trends for different vertebrate families are compared. Certain groups such as lagomorphs, bats, artiodactyls, elephants, foxes, raccoons, snakes, and teiid and lacertid lizards are habitually represented by relatively smaller forms on islands. On the other hand, cricetid rodents, iguanid lizards, tortoises, and bears often have races with larger body sizes on islands. Contrary to conventional niche theoretic concepts, in many instances knowledge of the body sizes of some of these animals' insular and mainland competitors does not help explain the difference in that species body size in the 2 places. To account for these divergent size changes I examine optimum body size models that use as the optimization criterion the net energy gained by an organism over a given time period. These models predict that increases in the mean amount of available food should lead to evolutionary increases in body size, but only if body size is not tightly constrained by additional physical or biotic factors: such additional factors might be important if a change in body size alters an animal's effectiveness in finding or handling preferred food items or increases competition with its neighbors.

Next, using arguments derived from simple non-age-structured 2 species predator-prey models, the availability of food for a given consumer species at equilibrium is compared in theoretical island and mainland situations. Because islands usually contain fewer competitors and the insular physical environment is often more moderate, food availability for colonists is initially expected to be high. On the other hand, as the population grows resources will become depleted. Further, the loss of many predator species on islands may allow consumer densities to increase to such an extent that at equilibrium food may become relatively more limiting for consumers on islands than on the mainland. Whether the supply to demand ratio (S:D) of consumers for their food is ultimately greater or lower will depend on the relative magnitude of these various factors. Within this framework, a necessary condition for island S:D ratios to be greater than on the mainland is that the consumers maintain individual feeding territories. For animals whose body sizes are not tightly bound within narrow limits by physical or competitive restraints, an increase in S:D should lead to an evolutionary increase in body size. Accordingly, a good association is found between the presence or absence of territoriality and the direction of the insular body size shift in a number of different vertebrate groups. Yet there are exceptions which fall into 2 categories: First, if a species' mainland predators preferentially take larger individuals, selection favoring small size may override selection based on optimizing energy input. Such may have been the case for the now extinct mainland relatives of certain giant relictual insular reptiles. Secondly, an animal's body size may be tightly constrained by physical or competitive factors. The body size of island foxes, rattlesnakes, and some lizards appears to be primarily adjusted to the competitive milieu along typical niche theoretic lines. That is, body size may be predicted quite well from knowing the size class of competitors which are absent from an island or from differences in the species' prey-size distribution between island and mainland sites.

Key words: *Biogeography; body size; evolution; Gulf of California islands; islands; lizards; mammals; predator-prey; reptiles.*

INTRODUCTION

Ecologists have long recognized the unique opportunity that islands offer in allowing them to decipher the variables influencing niche packing patterns (Crowell 1962, MacArthur and Wilson 1967, Diamond 1970a, 1970b). Perhaps, it is not as well appreciated that islands can serve as natural experiments to test theoretical predictions about the evolution of life-history attributes such as body size, sexual dimorphism, growth rate, clutch size, and age-specific patterns of survivorship and reproductive effort. One such attempt was made by Cody (1966) who anticipated the reduction in clutch size exhibited by many higher latitude island birds. Because islands usually have fewer species in any particular genera selection for

distinctive isolating mechanisms may be relaxed. Mayr (1942) invoked this argument to account for the occasional loss of conspicuous male morphological characteristics in island birds.

Without any strong theoretical basis, naturalists have often recorded the tendency for different vertebrates to evolve either larger or smaller body sizes on islands (e.g., Mertens 1934, Hesse et al. 1937). I propose a new hypothesis which seems to account for a large number of these insular size shifts in reptiles and mammals.

EMPIRICAL INSULAR SIZE TRENDS

First, it is necessary to establish the nature and validity of insular size trends among various vertebrate groups. Foster (1963, 1964) made an extensive effort to quantify these trends for mammals, and found a clear tendency for rodents (mostly cricetids and microtines) to be large on islands, and artiodactyls, carnivores and

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lagomorphs to be small. Insectivores are as likely to decrease in size as not and too few island residents were considered among marsupials to make any generalization. Additional examples not tabulated by Foster substantiate most of his proposed trends. Cowan and Guiguet (1965) document the sizes of many mammals living on islands off British Columbia. Small races of blacktail deer (*Odocoillus hemionus*) and reindeer (*Rangifer dawsoni*) exist on several of the islands. Large races of the deer mouse (*Peromyscus maniculatus*) also exist on most of these islands. A relatively large race of the ground squirrel (*Citellus*) occurs on Espiritu Santo and large races of woodrats in the *Neotoma lepida* group occur on this and 7 other islands off Baja California (San Jose, San Francisco, Cedros, Todos Santos, San Martin, Danzante and San Marcos; Goldman 1910, Burt 1932). A small deer occurs on Cedros Island (Merriam 1898) and a small race of *Lepus* exists on Margarita Island off Venezuela (Miller 1889). Small races of the rabbit *Sylvilagus cumanicus*, exist on Testugos, Margarita, Curacao and Aruba Islands (Hummelinck 1940). Additional records for insular carnivores cast doubt on the validity of Foster's generalization for carnivores. His data were based on only 15 observations, 8 of which were for different populations of island foxes and 3 records for island raccoons. Additional data for foxes and raccoons support a general tendency for insular small size. Small red foxes occur on Anticosti in the St. Lawrence Gulf (Cameron 1958). Raccoons on islands off British Columbia are relatively small as are raccoons on the Key Vaca Islands and the Ten Thousand Islands off Florida, and off Barbados Island in the Lesser Antilles (Goldman 1950). But other carnivore genera, including *Martes*, *Ursus*, and *Mustela*, increase in body size on some islands off British Columbia. Skunks and lynx appear indistinguishable in size from mainland relatives on these same islands (Cowan and Guiguet 1965). Spotted skunks (*Spilogale putorius*) definitely do not decrease in size on the Channel Islands off California (Grinnell et al. 1937). The large races of brown bears on the Kodiak Islands off Alaska are well known (Burt and Grossenheider 1952).

Foster did not discuss the clear tendency for insular elephants to be dwarfs; most of the evidence comes from fossil records of now extinct forms (Stock 1935, Hooijer 1951). Also, both suborders of bats (Megachiroptera and Microchiroptera) have insular forms which are smaller than mainland relatives about 3 times as frequently as the reverse size trend (Krzanowski 1967).

A voluminous literature dealing with insular size changes in reptiles exists (e.g., Carlquist 1965) but there is no published tally of the direction of size changes for various orders comparable to the analysis of Foster (1963, 1964) for mammals. Mertens' (1934) monograph probably comes the closest to filling our present needs.

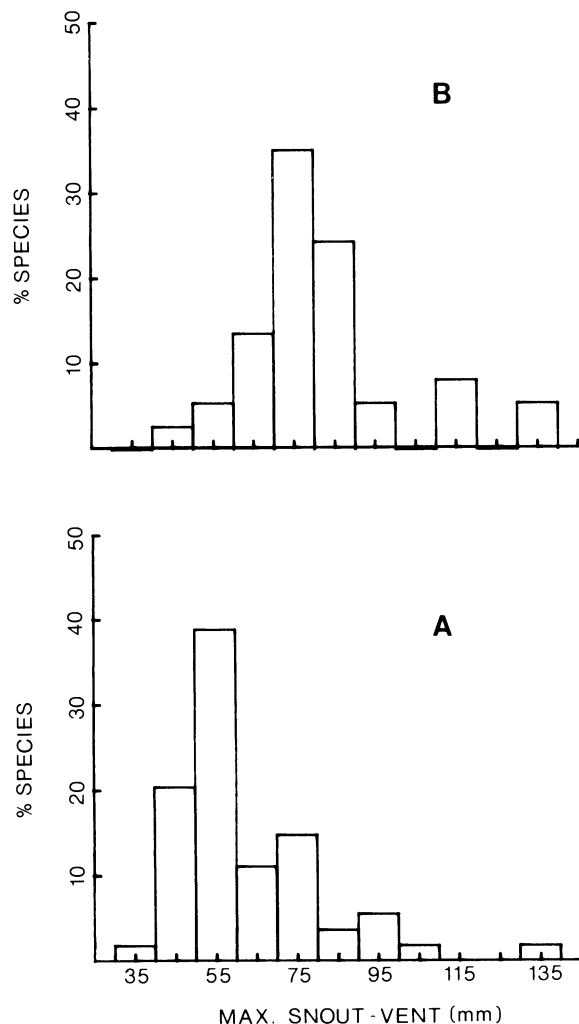


FIG. 1. Frequency of *Anolis* species of various body sizes. Body size is measured as the maximum snout-vent length recorded for individuals of a given species and is represented in 10 mm intervals. a) Frequency histogram for anoles of Southern Mexico, Central America and Northern South America. b) Frequency histogram for anoles inhabiting the Lesser Antilles. See text for sources of data.

Unfortunately, many of the gigantic reptiles Mertens discusses are relict endemic genera and the body size of their extinct mainland ancestors is unknown in most cases. Excluding these species, a clear tendency remains for iguanid lizards and most herbivorous lizards to become large on islands (Mertens 1934, Shaw 1945, Soulé 1966, Rand et al. 1975). Two notable exceptions are the Lesser Antilles *Iguana* and *Ctenosaura hemilopha* in the Gulf of California. Island forms are not significantly larger (or smaller) than mainland races (Lazell 1973, Smith 1972).

Schoener (1969b) documented the fact that anoles on islands in the Lesser Antilles occur sympatrically only when they are of very discrepant body sizes, the implication being that a competitive limiting similarity

TABLE 1. Maximum snout-vent lengths (SVL) of macroteiid species in Central and South America and on islands in the Lesser Antilles. Measurements are in millimetres

Mainland		Lesser Antilles	
Species	SVL (max)	Species (Islands)	SVL (max)
<i>Ameiva ameiva</i>	197	<i>Ameiva ameiva aquilina</i> (Grenada, St. Vincent)	122
<i>A. leptophrys</i>	133	<i>A. a. tobagana</i> (Tobago)	150
<i>A. festiva</i>	144–129	<i>A. vanzoi</i> (St. Lucia)	133
<i>A. quadrilineata</i>	88	<i>A. major</i> (Martinique?)	111
<i>A. undulata</i>	129–138	<i>A. fuscata</i> (Dominica)	155
<i>A. chaitzami</i>	85	<i>A. cineracea</i> (Guadeloupe)	139
<i>Cnemidophorus remniscatus</i>	90–104	<i>A. pluvianotata</i> (Montserrat)	130
		<i>A. griseoidi</i> (Antigua, Barbuda)	112
		<i>A. atrata</i> (Redonda)	104
		<i>A. erythrocephala</i> (Nevis, St. Kitts, St. Eustatius)	125
		<i>A. corvina</i> (Sombrero)	111
		<i>A. pleei</i> (Anquilla, St. Martin, St. Barts)	125
		<i>Cnemidophorus lemniscatus</i> (Trinidad, Tobago)	90–104

exists based on body size. Superimposed on this selective force is, I believe, a more generalized tendency for increase in body size. Because of the rapid evolution in Caribbean anoles it is impossible in most cases to trace extant island forms to mainland progenitors. Though such one-to-one comparisons are excluded, we may still examine overall size changes by comparing the distribution of maximum body sizes for species in the Lesser Antilles and in the adjacent mainland (southeastern Mexico, Central America and northern South America). Figure 1 displays the frequency of *Anolis* species according to their maximum snout-vent length. Data for mainland anoles are drawn from Fitch (1976; only those species which have sample sizes of >20 are considered here). Data for anoles of the Lesser Antilles are based on Lazell (1972).

The 2 most frequently represented body size categories on the mainland are 50 to 60 mm and 40 to 50 mm. On the Lesser Antilles the most frequently represented size categories are 70 to 80 and 80 to 90 mm. Clearly the "average" island anole is larger. Much of this difference stems from the fact that anole species which occur alone on islands tend to be larger than the median size (Schoener 1969b).

In other lizard families, patterns are less clear cut. There appears to be a general tendency for larger body size in island races among the Scincidae, Gekkonidae and Agamidae (Mertens 1934). For example, New Caledonia alone has 7 endemic giant geckos (Müller 1974).

Information is limited for lizards in the families Lacertidae, Teiidae and Varanidae, but (excluding insular relict species) they more often than not decrease in body size on islands (Mertens 1934, Kramer 1946, 1951, Kramer and Mertens 1938). To these examples may be added the recent discoveries of small races of *Ameiva chysolaema* (Teiidae) on Grosse Caye, a small satellite island off Haiti (Schwartz 1973); *Lacerta erhardii* on Hydra off the Peloponnese peninsula; *Lacerta trilineata* on Spetsai off the Peloponnese peninsula (Clark 1967b).

Table 1 compares the maximum snout-vent length of teiid species in the genera *Ameiva* and *Cnemidophorus* for the same 2 areas involved in the anole comparison (Fig. 1). Data for the Lesser Antilles come from Underwood (1962), Baskin and Williams (1966) and Ernest Williams (*personal communication*). Sizes of mainland teiids were drawn from Echternacht (1970, 1971) and Burt (1931). Again, in most cases, the mainland ancestry of the island ameivas is unknown, although many are thought to be related to *Ameiva ameiva* (Baskin and Williams 1966). In the case of the *A. ameiva* subspecies on Grenada, St. Vincent, and Tobago islands this is definitely the case and all of these island races are considerably smaller than mainland *A. ameiva*.

On Cuba there are 17 named subspecies of the endemic *Ameiva auberi*. These range in maximum snout-vent length from 78 to 136 mm (Schwartz 1970). Five of these subspecies are >100 mm. On various satellite islands surrounding Cuba there are an additional 6 endemic subspecies which range in maximum snout-vent length from 76 to 93 mm. That is, none of these satellite islands contains *Ameiva* populations as large as the largest which exist on Cuba itself.

Snakes in general and the Crotalinae in particular are usually smaller on islands. Table 2 gives a number of examples to document this fact but is by no means exhaustive. A notable exception to the trend of insular small size is the large race of *Crotalus mitchelli* on Angel de La Guarda Island in the Gulf of California. Finally, it is well known that the largest extant species of land tortoises are restricted to islands (Hooijer 1951).

Insular size changes in birds are less unequivocal and when they occur are lower in magnitude than those found for most reptiles and mammals (Mayr and Vaurie 1948, Pitelka 1951, Amadon 1953, Bourne 1955, Grant 1965). Part of the ambiguity in the avian literature is due to differences between authors in what parameter they chose to measure. Apparently, birds more often adapt to the insular environment by chang-

TABLE 2. Examples of snake species which are smaller on islands compared to populations living on the adjacent mainland or much larger islands

Species	Island	Reference
<i>Vipera lebetina</i>	Cyclades	Mertens 1934
<i>Bothrops insularis</i>	Guamada	Amaral 1921
<i>Crotalus tortugensis</i>	Tortuga	Klauber 1956
<i>C. exsul</i>	Cedros	Mertens 1934
<i>C. viridis</i>	Coronados	Klauber 1949
<i>C. ruber</i>	Cedros	Klauber 1949
<i>C. atrox</i>	San Pedro Martir	Cliff 1954
<i>C. catalinensis</i>	Santa Catalina	Cliff 1954
<i>C. mitchelli</i>	El Muerto	Klauber 1949
<i>C. molossus</i>	San Esteban	Klauber 1949
<i>C. ruber</i>	San Lorenzo Sur	Radcliffe and Maslin 1975
<i>C. durissus</i>	Aruba	Brongersma 1940
<i>Elaphe quadrivittata</i>	Florida Keys	Mertens 1934
<i>E. quatuorlineata</i>	Ios	Clark 1967a
<i>Masticophis bilineatus</i>	San Esteban	Lowe and Norris 1955
<i>Natrix subminiata</i>	Hainan and Hong Kong	Mertens 1934
<i>Pituophis catenifer</i>	Santa Cruz and Coronado	Klauber 1946, 1949
<i>Dipsas variegata</i>	Trinidad	Peters 1960
<i>Alsophis portoricensis</i>	Mona	Schwartz 1966
<i>Trimeresurus flavoviridis</i>	Loo Choo and Tokara	Fukada 1965

ing the relative size of their tarsi, beaks, or wings than their total body size. The most consistent change birds exhibit on islands is an increase in bill size. In view of the numerous exceptions occurring in the other measurements, no other generalizations can be made. It is possible that by breaking the class Aves into its component orders, a clearer picture of bird insular evolution would emerge.

Like the other biogeographic "rules," these insular size trends are only statistical. The same lizard or rodent species, for example, may be relatively large on some islands but not on others. The same island may support gigantic forms of one lizard or rodent species, yet dwarf races of another (Foster 1963, Mertens 1934). Any theory proposing to account for these insular size trends must also be consistent with their numerous exceptions. Most of the investigators cited above have advanced possible explanations for the particular size trend displayed by the organisms they studied, but as yet, no one has really come to grips with the problem of why overall trends should be so different in different groups.

One common explanation for these size changes goes as follows. Many competing populations of vertebrates partition resources with respect to the size of prey (Cody 1974, Schoener and Gorman 1968). Further, the size of the prey taken and the size of the predator are closely related (Schoener 1969a, Hespeneide 1973). On islands lacking small-sized competitors, an abundance of small prey will be available. To utilize this resource better, the predators should evolve smaller body sizes. There are 2 reasons why this theory by itself is insufficient. First, although many examples exist showing that larger predators take larger prey, there is little evidence except in certain large mammals that the removal of such predators

results in an increase in the level of their prey. Neither is there any evidence that islands supporting large lizards, for example, have generally larger insects. Recent data collected by Rand et al. (1975) on *Anolis agassizi* on Malpelo Island, by Jon Roughgarden and George Gorman (*personal communication*) for *Anoles* on islands in the Caribbean, and by myself (*personal observation*) for lizards on islands in the Gulf of California do not support this hypothesis. Secondly, and perhaps more seriously, herbivorous mammals like elephants, deer, and hares are obviously not partitioning resources on the basis of prey size. Often these species occur on mainlands without any sympatric confamilial competitors, yet they show a reasonably consistent tendency to become small on islands. On the other hand, herbivorous reptiles usually increase in size.

As a final example, on certain islands off British Columbia, *Peromyscus maniculatus* may occur alone or sympatric with *Microtus* or *Clethrionomys*. Regardless of the presence or absence of the other species, all these rodents show a clear tendency to increase in body size compared to mainland forms (Foster 1963, Hall 1938). On the Baja California peninsula, 2 cricetid genera which are particularly common are *Neotoma* and *Peromyscus*. Representative species from each genus usually are broadly sympatric but *Neotoma* species are much larger in body size than *Peromyscus*. When species in these 2 genera occur sympatrically on islands in the Gulf of California, both usually are larger in size than mainland ancestors (Goldman 1910, Burt 1932, Huey 1964, Lawlor 1971). Similarly, the relative size of subspecies of *Apodemus sylvaticus* on various islands off England and Scotland is not strictly related to the presence or absence of other sympatric cricetid rodents (Delany 1961, 1970). *Apodemus sylvaticus* is

largest in size on the islands of Rhum, St. Fair, and St. Kilda. Both *A. sylvaticus* and *Clethrionomys glareolus* are relatively larger than mainland races on the island of Jersey; however, on Mull and Raasay where they are also sympatric, *A. sylvaticus* is not particularly large but *C. glareolus* is (Delany and Bishop 1960, Bishop and Delany 1963, Delany 1970).

The logical development of my explanation for many of these insular size trends is complex so I outline it here. First, optimal body size models are explored and it is predicted that the optimum body size of an animal should be directly related to the availability of its resources. Next, I consider the behavioral attributes of a consumer which influence its abundance and the abundance of its resources at equilibrium in predator-prey systems. Gathering the necessary available information from the literature, I predict for each terrestrial vertebrate group whether the availability of resources on an island is expected to be greater or lower than that in a typical mainland setting. Finally, these 2 arguments are connected by contrasting the empirically observed body size changes for different groups to my predictions.

Of course, simply because an explanation is consistent with known observations does not mean that it is actually operating, or that other explanations could not explain the phenomenon with equal success. Unfortunately, when studying evolutionary events, researchers usually lack the most valuable tool for countering this problem: controlled experiments designed to collect additional data which may distinguish between 1 or another potential hypotheses. Here I examine the success and consistency of my hypothesis in explaining notable exceptions to the usual insular biogeographic rules of body sizes. Indeed, I find that there are examples in which island body size cannot be examined solely on the basis of the general model: in addition it is necessary to invoke either (1) the action of size-selective predators on the mainland which are lacking from the insular fauna, or (2) the more typical niche theoretical concept that there is a limiting similarity between certain competitors based on body size and insular changes in size are best explained on the basis of character displacement.

MODELS OF OPTIMAL BODY SIZE

Most ecologists assume the body size of an organism has evolved to optimize its success within its particular niche. Yet, how do we quantify success? An animal's size may be viewed from 2 different perspectives. First, it represents an evolutionary compromise between maximizing immediate reproductive effort on the one hand and investing assimilated energy into growth to increase survivorship and future reproductive success on the other (Gadgil and Bossert 1970). Secondly, an animal's size may influence, if not determine, the total amount of energy the organism may secure from the environment. A complete model for finding optimal

body sizes should take both these factors into consideration. It is conceivable that although a relatively large size might be the most efficient in a given habitat on the basis of maximizing food harvesting, the rapid growth necessary to achieve this size or the extended period of reproductive immaturity entailed might be decidedly disadvantageous. For age-structured populations the precise criterion of Darwinian fitness is the achieved intrinsic rate of growth, r , for each genotype in the particular environment (Charlesworth 1970, 1973, Roughgarden 1977).

Such a complete model, however, is beyond the scope of this paper. Here I focus on models specifically dealing with the relationship between body size and the ability to secure energy from the environment. I consider the relative fitness of different sized individuals as proportional to the amount of net energy assimilated over a fixed period of time. This energy represents the maximum amount an individual would be able to devote to reproduction. Note however, that in organisms where reproductive expenditure reaches a ceiling independent of body size, this model is only approximate. In these species, any additional energy which might be gained by a slightly larger size would not be channeled into reproduction. Still we might expect that the implied increase in harvesting ability would allow them more time for other activities which, in turn, would confer increased fitness.

Schoener (1969a) and Case (1978b) used this limited criterion for establishing optimal body sizes for solitary consumers. In both models formulae were developed which expressed the expected gain and expenditure of energy per unit time as a function of body size. Both models predict that optimum body sizes should indeed exist based on such considerations. Schoener's model invokes assumptions that larger prey items are more effectively captured by larger predators and small prey by small predators and that there is a log-normal distribution to prey abundance as a function of prey body size. This model is therefore most appropriate for carnivores. Case's model does not involve these assumptions and does not explicitly even consider prey size. This model is more appropriate for herbivores and detritivores for which such assumptions are probably not valid. For my present purposes I am concerned chiefly with establishing how an animal's optimum body size should change with changes in overall food abundance or availability. Both models agree (and reinforce the intuitive notion) that, all other things being equal, increases in food availability will favor larger body sizes.

There are constraints, however, to this relationship. In many species body size will be constrained by physical factors. For example, flight and perching impose physical constraints on a bird's size and form. The body size of geckos and other lizards which have evolved toe pads for vertical movement must not exceed the clinging capacity of their toes. In rodents, the maximum diameter of burrows which will not collapse in a given

soil type may restrict size. For such species, body size will only increase with food abundance up to the point that these other factors become of overriding importance.

Finally, the body size of many predators determines, in part, the size and type of foods they may eat. That is, the total available food for a consumer may itself be a function of its own size. For example, many species guilds avoid intense competition by consuming prey of different sizes. Often such species yield the best examples of character displacement. That is, differences in body size of any guild member in various geographical areas are best accounted for by the presence or absence of other guild members of different body sizes (e.g., Schoener 1969b, Cody 1974, Huey et al. 1974). We infer that there is a limiting similarity to the body sizes of these guild members (Schoener 1974, MacArthur 1972, Hespeneide 1973), the result being that consumer body size can only respond to changes in overall prey abundance to the degree that competition with neighboring competitors on a body size niche gradient does not become too severe.

One consequence of this joint effect of prey abundance and prey body size on optimum body size is that the extent of character displacement may be lower for the smaller members of a guild than for the larger. The loss of a large-sized competitor creates both more food and generally larger sized food, thus favoring a larger optimum body size for the remaining species. Yet, the loss of small-sized competitors does not necessarily favor a smaller body size. Although the prey size distribution may now be shifted or skewed towards smaller sized prey, the total abundance of food will also be greater. If the latter factor is important, it may override selection for small size.

For the many organisms whose competitive coexistence is not based on prey-size differences, changes in overall prey availability may be utmost in explaining body size differences. For example, Case (1976) found a strong correlation between body size and spring rainfall in the herbivorous desert lizard *Sauromalus obesus*. More indirectly, the loss of predators in an area (e.g., on islands) may allow the density of a species to increase, so that its food becomes more limiting. The quantitative exposition of this notion forms the body of the next section.

PREDATOR-PREY MODELS

By now most ecologists have become familiar with the Lotka-Volterra equations and the subsequent refinements added for a more realistic description of predator-prey interactions. I introduce 3 different predator-prey models to illustrate how food availability and body size may change in an insular setting.

Model 1:

$$1A) dR/dt = rR(1 - R/K) - WRC/(M + R)$$

$$1B) dC/dt = -dC + WRC/(M + R)$$

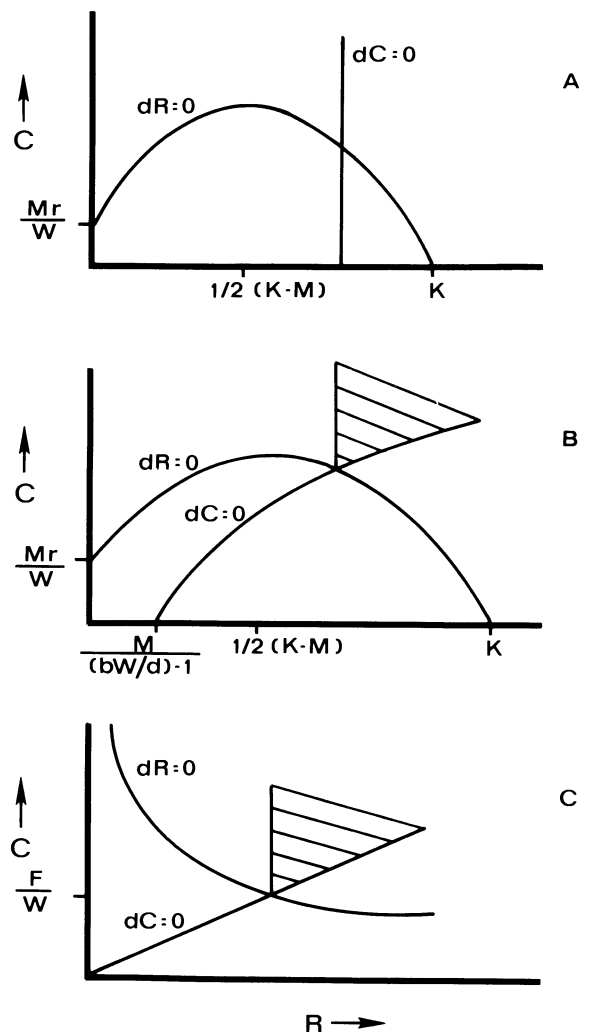


FIG. 2. The zero-isoclines for consumer (C), and resource (R), for the differential equations described in the text. Equations for zero-isoclines are: a) Model 1, $dR = 0$ is $C = \frac{r}{w}(M + R)(1 - R/K)$, $dC = 0$ is $R = Md/(W - d)$; b) Model 2, $dR = 0$ is $C = \frac{r}{w}(M + R)(1 - R/K)$, $dC = 0$ is $C = \left(\frac{WR}{M + R} - d\right)/a$; c) Model 3, $dR = 0$ is $R = F(M + R)/RW$, $dC = 0$ is $C = JR$. If the intersection of the zero-isoclines occurred in the hatched region of each figure (which really extends beyond the figure to infinity), the S:D ratio for the consumers would be greater than at the present equilibrium. If the intersection was stable and to the left of the hatched region, respective S:D ratios would be lower.

Here R represents a unit of resource. The resource grows logistically at a maximum rate r and stops when it reaches a saturation density of K . Resource growth is also limited by consumers, which crop it at a rate proportional to their density and the density of resource. The resource harvesting term $WRC/(M + R)$ describes an increasing function of R which asymptotically approaches W , the maximum rate of harvesting per con-

sumer. M is a constant inversely proportional to the rate that W is reached. The consumer population (C) has a per capita death rate d , and a birth rate proportional to the consumption of resource. The zero-isoclines for this system are depicted in Fig. 2a.

Model 2:

$$2A) \frac{dR}{dt} = rR(1 - R/K) - WRC/(M + R)$$

$$2B) \frac{dC}{dt} = -dC - aC^2 + WRC/(M + R)$$

This model is modified from model 1 in that the consumers interfere with each other at a rate proportional to the square of their abundance (aC^2). The zero-isoclines for this system are depicted in Fig. 2b.

Model 3:

$$3A) \frac{dR}{dt} = F - WRC/(M + R)$$

$$3B) \frac{dC}{dt} = sC(1 - C/JR)$$

In this model, without predation the resource population would grow at a constant rate (F). An example could be fruit falling from trees. Resources are also cropped by consumers as before. The consumers now however grow logistically, with maximum rate s , and a saturation density which is proportional to resource abundance. Hence, J is equal to the number of resource units required to support 1 consumer at equilibrium. The zero-isoclines for this system are depicted in Fig. 2c. A similar resource equation was introduced by MacArthur (1972) and the consumer equation was studied by May (1973) and Tanner (1975).

Model 3 always yields a stable equilibrium point. Models 1 and 2, yield either a stable equilibrium point, where both predator and prey persist at fixed numbers, or a limit cycle surrounding an unstable equilibrium point (May 1973). In the latter instance both species oscillate through time along a characteristic path determined by the parameters of the system. Graphically, stability always results when the 2 isoclines intersect to the right of the prey-isocline's hump. If the intersection occurs to the left of the hump, the equilibrium may still be stable depending upon the value of the other parameters. In particular, a stable equilibrium is favored when the prey's maximum intrinsic growth rate (r) is lower than that of its predator(s) and when the predator has strong intraspecific regulation. Hence, model 2 more easily fulfills these conditions. When these conditions are not fulfilled, limit cycles result. The amplitude of these cycles increases with the extent that the system's parameters deviate from those conferring stability (Tanner 1975). In the next section I explore possible differences in the point of intersection between island and mainland communities and their expected effect on the evolution of body size.

INSULAR-MAINLAND COMPARISONS

Assume for convenience that a stable 3-trophic level subsystem exists on the mainland. For notational purposes, I term its components: resources (R), consumers (C), and predators (P). It is arbitrary at this point

whether this system is imagined as being one of plants, herbivorous ungulates, and mammalian carnivores, or perhaps insects, lizards, and snakes. In any event, I wish to explore the consequences of the insular setting where 1) predators on the consumers are expected to be lost or at least diminished, 2) consumer competitors are fewer, and 3) the climate is more benign.

To keep the model in 2 dimensions I implicitly consider the loss of predators and competitors by their assumed effect on the parameters of the 2 species system. A loss of predators decreases the consumer's death rate (d in models 1 and 2) or increases its effective saturation density (proportional to J in model 3), and/or increases the maximum growth rate (s in model 3). Graphically, this amounts to shifting the consumer isocline to the left and/or upward. On islands the consumers may forage on items and at times and places which on the mainland were either too risky because of predators or energetically unprofitable because of competing species. These considerations, along with an assumed more moderate insular climate, may be envisioned as increasing the growth rate (r) and saturation level (K) of the resources with respect to the particular consumer we focus on: in effect, shifting the resource isocline upward (models 1, 2 and 3) and/or stretching it to the right (models 1 and 2).

Figure 3 depicts 2 contrasting island-mainland situations. On the right, (B), a consumer with limited self-interference and heavy predation on the mainland arrives on an island lacking these predators but expands its niche only slightly, so r and K increase only moderately. Figure 3A depicts a consumer with strong intraspecific interference, a large insular niche expansion, and a small change in mortality. To predict the direction, if any, the consumer's body size is expected to evolve in response to these different changes, we must know how the average availability of food for these 2 hypothetical consumers is changed at the new equilibrium.

Certainly the availability of resources to consumers will be directly related to the abundance of resources at equilibrium (\hat{R}). Yet the supply of resources per consumer will also increase with the productivity of resources at this equilibrium. Of course, at equilibrium the net growth of resources (and consumers) is zero, and the recruitment of resources is just equal to their rate of death. We seek a measure for supply of resources (S) which also incorporates this turnover rate. An appropriate equation is

$$S = \frac{\hat{R} \cdot dR^*}{\hat{R}dt}$$

where $dR^*/\hat{R}dt$ is the per capita recruitment rate of resources at equilibrium (not the growth rate $dR/\hat{R}dt$) (I avoid cancelling \hat{R} in this expression to emphasize its character.) The units of S are resource units (or kilojoules)/time·area while R has units of simply

grams (or kilojoules)/area. The relative demand (D) for resources at equilibrium is simply proportional to the number of consumers (C) times the basic metabolic demands of each consumer (e ; expressed in resource units/consumer/unit time).

$$S/D = \frac{R \cdot dR^*}{Rdt} / C \cdot e$$

This makes S/D dimensionless. Assuming that the consumers have identical physiological and metabolic requirements on islands as on the mainland, we may normalize e to 1.

The calculation of S/D ratios at equilibrium for each of the 3 predator-prey models is presented in the appendix.

Under my assumptions about the expected differences in the insular environment compared to that on the mainland, these calculations indicate that in models 2 and 3, if the island predator-prey equilibrium is graphically located to the right and above the mainland equilibrium, then the S/D ratio will increase (Fig. 2). In these situations, food will generally be more available for the individual consumers, and we expect body size to evolve upward unless it is constrained by other factors in the species' niche. If the island equilibrium point is to the left of the mainland equilibrium, S/D will be lower. Referring back to Fig. 3, one can now see that S/D would be greater on the island than on the mainland in situation A but lower in situation B.

In model 1, which describes consumers without intraspecific interference, the island equilibrium point can never shift to the right of the mainland equilibrium given my 3 assumptions regarding the nature of the insular environment. The S/D ratio can therefore only decrease or stay the same (see appendix). Consumers which obey the general features of this model are therefore expected to be either similar in size to or smaller than mainland individuals.

It is apparent from Fig. 2 that within the framework of this model a necessary condition for change in the S/D ratio on an island is that the consumers must compete among themselves over food so that the consumer zero-isocline has a positive finite slope near the region of equilibrium. In biological terms this condition translates into a requirement for individual feeding territories or other density dependent forms of intraspecific interference for food or feeding sites. If one mentally shifts each isocline with respect to the other in Fig. 2(b, c) 2 more necessary (but not sufficient) conditions for the new intersection to lie in the zone of higher S/D are revealed. The insular consumer isocline must be higher than on the mainland, implying an increase in consumer survivorship and either resource productivity, as measured by r or F , or constants affecting resource peak abundance (K or J) must also increase so that the resource isoclines shift upward. The combination of both these conditions is therefore nec-

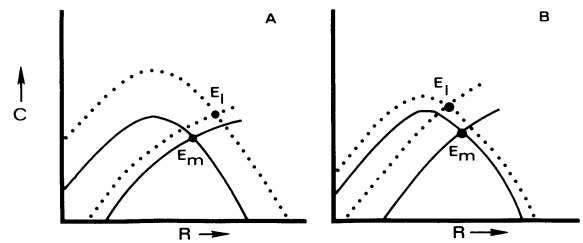


FIG. 3. Comparative consumer-resource systems on islands and mainland; solid lines represent hypothetical zero-isoclines on the mainland and dashed lines are isoclines for the islands. A) In this case, the island intersection E_I occurs above and to the right of the mainland E_M so that the S/D ratio is greater. B) Here, the island intersection falls to the left of the mainland intersection and the S/D ratio is lower.

essary but still not sufficient for S/D to increase. For example, if the consumer isocline shifts upward more than the resource isocline, the new island intersection will fall to the left of the prescribed region, and S/D will be lower than on the mainland (Fig. 3b). The qualitative nature of these conclusions is true for any combination of the particular predator and prey growth equations presented in these models and for a variety of other reasonable equations which I have explored but have not presented here.

Throughout, it has been assumed that the equilibrium on both island and mainland is stable. Frequently, this may not be so (Tanner 1975). Unstable equilibria resulting in limit cycles may occur on an island after the loss of stabilizing higher order predators (Rosenzweig 1973). Situations resembling Fig. 3B approach this state more readily than those depicted in Fig. 3A. If a limit cycle did occur, the S/D ratio would fluctuate periodically along with the resource and consumer densities but the average S/D would certainly decline. The presence of oscillations in food availability has been considered in the optimum body size model of Case (1978b). The result is that the optimum body size is mildly but directly related to the amplitude of these fluctuations. Yet its effect is usually swamped by changes in the mean food availability which declines severely. In any event, it is likely that given stochastic environmental perturbations on an island the limit cycle would eventually hit an axis, and the consumer would go extinct.

TESTING PREDICTIONS

The lower the slope of the consumer's isocline (i.e., the more the consumers squabble with one another) the more likely that the insular setting may result in a higher S/D ratio at the island equilibrium. The explanation for this relationship is intuitive. Because islands lack many of the predators of mainland communities, consumers will probably have greater survivorship at any density. This, in turn, results in higher consumer densities at equilibrium; Gadgil and Solbrig (1972) provide a nice graphical analysis for visualizing this relationship. If all else were equal, the food available per

TABLE 3. Insular body size trends in various terrestrial vertebrate groups and their relationship to territoriality

Group	Size trend ¹	Territoriality ²	Reference ³
Cricetid rodents	↑	++	Eisenberg 1966
Bats ⁴	↓	0+?	Bradbury and Vehren-camp 1976, Wilson 1975
Artiodactyls	↓	0	Eisenberg 1966, Wilson 1975
Lagomorphs	↓	0	Eisenberg 1966, Lechleitner 1958
Foxes	↓	+	Trapp and Halberg 1975
Skunks	↔	0	Eisenberg 1966, Verts 1967
Weasels	↑?	++	Lockie 1966, Grinnell et al. 1937
Raccoons	↓	0	Wilson 1975
Bears	↑	++	Wilson 1975
Elephants	↓	0	Eisenberg 1966, Wilson 1975
Iguanid lizards	↑	++	Carpenter 1967, Brattstrom 1974
Teiid and lacertid lizards	↓	0?	Milstead 1957, Evans 1961
Varanid lizards	↓	0	Pianka 1968, Pfeffer 1959
Snakes	↓	0	Bellairs 1970, Brattstrom 1974
Land tortoises	↑	0	Bellairs 1970, Brattstrom 1974

¹ See text for references to verify these trends.

² The consistency of individual foraging territories in these groups may vary from a high of ++ signifying a strict maintenance of individual territoriality to a low of 0 signifying the absence of such behavior.

³ Most references for territoriality are books or review articles containing the most complete references for the species concerned.

⁴ Social systems are very diverse among bats and those of most species studied by Krzanowski (1967) for insular size changes are unknown. However, most bat species either do not defend foraging territories or defend group foraging territories.

consumer would be lower. But countering this tendency is the expectation that since the island consumers lack competitors as well as predators, they will expand their niches including more items in their diet. Moreover, an insular environment is often more productive because of its more moderate climate. When these latter factors outweigh the trend of higher consumer densities on the islands, resources will be more available on the island and the S:D ratio will increase. When they do not, S:D will decrease or stay the same. Consumers which are territorial for feeding areas will not increase density linearly with increases in food availability. As densities increase on islands because of the loss of predators a greater proportion of their time and energy will be devoted to interference with conspecifics favoring higher island S:D ratios.

Note that not all forms of aggression or territoriality will act in this manner. Aggression over mates or nest-

ing sites will not necessarily prevent food resources from being overexploited; neither will large communally shared feeding territories. Moreover, nearly all animals will display some intraspecific aggression if densities are high enough. What we really desire is an answer to the following question. If the food supply for a particular consumer is supplemented in some manner, will consumer density compensate proportionally within the density range commonly observed? For some organisms, this experiment has actually been performed. In cricetid rodents, the results have been quite consistent. Namely, although survivorship usually increases with food supplementation, density increases mildly or not at all. This was true for *Microtus californicus* (Krebs and DeLong 1965), *Peromyscus polionotus* (Smith 1971), *Peromyscus maniculatus* (Fordham 1971), and *Apodemus sylvaticus* (Flowerdew 1972) but apparently not for *Peromyscus leucopus* (Bendell 1959).

With most other vertebrate groups the answer to our question may only be inferred from behavioral evidence or from the fact that individual home ranges are nonoverlapping.

Table 3 compares the insular body size trend for various vertebrate groups with the extent that these animals defend individual feeding territories. In a number of these groups some species defend feeding territories while others do not. In these instances, I consider only those species which are most closely related to the insular species whose body size has been investigated. For example, pikas defend territories containing caches of vegetation which they have hoarded, yet none of the insular body size data for lagomorphs tabulated by Foster (1963) include these species. Almost all of his data and those presented here concern *Lepus* and *Sylvilagus*, both of which have broadly overlapping home ranges. Likewise, artiodactyls exhibit a broad range of social systems (Geist 1974) but present insular body size trends are almost solely based on species of deer. Bats also display a wide variety of social systems although most species apparently do not defend individual feeding territories. In most cases, the actual social system of the bat species considered by Krzanowski (1967) in his insular body size study are unknown.

Because the presence of self-regulative mechanisms is a necessary but not a sufficient condition for S:D ratios to increase on islands it is remarkable that the association between this 1 attribute and body size trends is so good. One exception is the foxes which are usually smaller on islands although they apparently are territorial. Such a trend is possible within the confines of my model. Returning to the graphical analysis, the S:D ratio will be lower when the insular zero-isoclines intersect to the left of their mainland intersection point. This may occur when the decrease in fox mortality on islands is large compared to the increase in the productivity of their food. Actually, however, this hypothesis

is not supported by the available evidence. This and other more attractive alternatives will be discussed in the next section. Another more striking exception is the land tortoises which lack feeding territories but have large representatives on islands. This too will be accounted for later.

Because lizards are excellent island colonizers and display a wide range of social behavior at both the family and species levels, they make an excellent group to test further the relationship between gigantism and territorial behavior. Unfortunately, few studies provide both the size distribution data and basic observations on the social behavior of these island residents and their mainland relatives to make an adequate comparison. It supports my model that so many of the lizards cited by Mertens (1934) as island dwarfs are in the families Scincidae, Varanidae, Teiidae and Lacertidae, all families which typically lack individual feeding territories. A small race of the nonterritorial *Chamaeleo pardalis* (Chamaeleontidae) exists on Reunion and Nossi-bé islands (Bourgat 1968, 1972). Also, although species of *Lacerta* are usually dwarfs on islands, *Lacerta melisellensis* has a number of relatively large races on islands in the Adriatic (Mertens 1934, Gorman et al. 1975). It would be most interesting to compare the home range behavior of the latter species to the closely related *Lacerta sicula* which typically is small on islands.

APPARENT EXCEPTIONS:

1. SIZE SELECTIVE PREDATION

The most serious contradiction to my model is the land tortoises. I predicted that species lacking territoriality should not display insular gigantism. I show below that this contradiction is more apparent than real, resulting from the extinction of closely related continental forms. But first, it is worthwhile to discuss an additional factor influencing the evolution of body size which is not deduced from my model but appears particularly relevant in the case of land tortoises. Namely, in some prey species predators may differentially select older and/or larger individuals because of the energetic advantage of such a strategy from the predator's point of view (Schoener 1971). For such species, regardless of the S:D ratio there will be strong selection for slow growth and small body size in the prey (Gadgil and Bossert 1970, Brooks and Dodson 1965). If removed from these predators, the body size of such prey is expected to increase to a size more consonant with resource levels and S:D considerations.

Presently, giant land tortoises are found only on some islands in the western Indian Ocean and on the Galapagos Islands in the eastern Pacific although their distribution in the Pleistocene was also continental (Hooijer 1951, Brattstrom 1961, Holman 1969). The extant insular species are actually small compared to many of their extinct Pleistocene continental relatives. The hard shell of tortoises probably confers resistance against most potential predators but is useless against

man. In fact, man is strongly implicated in the extinction of land tortoises on the North American continent and on certain islands in the Galapagos (Van Valen 1969, Schmidt and Inger 1957, Hendrickson 1966). The reasons why early man might particularly relish large individuals are obvious, especially in a species where large size enables early hunters to find individuals more easily but does not confer any greater resistance to man's technological hunting techniques. I speculate, therefore, that the S:D ratio for extant tortoises may, in fact, be much smaller on islands than mainlands but the absence of giant tortoises on the continent is due to the presence of man and the concomitant selection for small size which he must have caused.

It should be noted that in other relicts, like the Proboscideans, fossils indicate that insular species were dwarfs compared to contemporaneous continental relatives (Hooijer 1951, Stock 1935).

A number of large insular lizards also may fall in the category of island relicts. Extinct continental relatives of the Komodo dragon (*Varanus komodoensis*), the giant water lizards (family Agamidae, *Hydrosaurus*), and the giant island skinks (*Macroscincus coctaei* and *Corucia zebrata*) may have been as large as or larger than their extant insular representatives (Mertens 1934). *Xantusia riversiana* on the California Channel Islands may also fall in this category (Savage 1967).

It is not valid to explain the large body size of an insular species simply on the basis that that species is a relict of a formerly continental species (cf., Mayr 1952, Cook 1961). Even if it is a relict, the fact remains that selective pressures have allowed large individuals to survive on islands but caused their extinction on the mainland. We are still left with the task of deciphering these differential selective agents. An example from lizards illustrates this point. The genus *Gallotia* [formerly *Lacerta galloti*] is an endemic genus of lacertids inhabiting the Canary Islands. Three extant species exist, 1 of which, *G. simonyi*, has the largest body size (snout-vent length up to 210 mm) of any existing lacertid (Arnold 1973). Fossils from the Pleistocene of the Canary Islands, however, show that earlier related forms were much larger still (up to 600 mm). It has not been possible, as yet, to determine if this older species was a direct ancestor of the present species or if it was displaced by them. In more recent time the entire genus has shown a reduction in range, and the largest species, *G. simonyi*, has been replaced by the generally smaller *G. galloti* on at least 3 islands (Arnold 1973). Hence even among "relict species" body size is evolutionarily adjusted to environmental contingencies or the species will eventually go extinct.

Unfortunately, for most of the reptilian examples I have mentioned there is no solid evidence that their primordial predators preferred larger sized individuals. In the case of the lizards on Jamaica good evidence does exist. Hecht (1951, 1952) found by examining Barn Owl (*Tyto alba*) pellets a clear predilection of these birds to

feed on larger lizard species and on the larger individuals within these species. He attributes the extinction of the largest gecko *Aristelliger titan* to the activities of these predators.

The insular giants *Sauromalus hispidus* and *Sauromalus varius* are herbivorous iguanids inhabiting islands in the Gulf of California. They are probably not relicts but instead insular derivatives of the ancestors of the mainland species *Sauromalus obesus* (Robinson 1972). Additional populations of this genus occur on other islands in the Gulf of California but are not substantially larger in body size than mainland forms (Shaw 1945). Although their present distribution may be confounded by transport by aboriginal man, the gigantic forms are restricted to islands lacking mammalian predators. I have observed that present predation rates as evidenced by tail-break frequencies are from 3 to 10× greater for the mainland species and small-sized island species than for the larger insular species. Whether predation rates increase with body size on the mainland is unknown but suspected.

Anecdotal observations suggest that the body sizes reached by individual marine iguanas have declined on various Galapagos islands since the proliferation of various feral cats and dogs (Schmidt and Inger 1957). The giant rock iguana *Cyclura carinata* inhabits a few small islands in the Caribbean which are relatively predator-free. During the 4 years which Iverson (1977) studied this species, the entire iguana population on 1 study island (>15,000 individuals) was extirpated following the introduction of feral dogs and cats. The effects of the introduction of mongoose on several West Indies islands is probably overstated, but substantial evidence points to a decline in the numbers of *Ameiva* lizards on several islands with the largest individuals being restricted in some cases to small islets which the mongoose has not reached (Baskin and Williams 1966).

Sauromalus and *Amblyrhynchus*, as well as the Galapagos land iguana, *Conolophus*, are exceptions to my model in another way. Although mainland relatives (*Ctenosaura*, *Sauromalus obesus*) display territoriality or some other form of overt aggression over feeding areas, this behavior is greatly relaxed in the insular representatives (Carpenter 1967, 1969). In *S. varius* and *S. hispidus*, the average number of adult individuals inhabiting the same crevices and burrows is 2 or 3. From some crevices I have found as many as 7 individuals of both sexes. I have observed hundreds of *S. obesus* and have never found more than 2 together in the same crevice, and when 2 were found they were never both adult males.

Reduced aggression and territoriality are also evident in some insectivorous island lizards like *Anolis agassizi* on Malpelo Island (Rand et al. 1975) and *Uta palmeri* on San Pedro Martir Island and *Sator angustus* on Santa Cruz Island. In all these cases I have observed that island resource levels are abnormally high. Whenever a species' resources are essentially limitless or indefensi-

ble, territoriality is obviously not profitable. Heavy predation pressure, however, may restrict individuals of such species to feeding areas which are close to refuges. In these instances, if suitable refuges are limiting, territoriality may evolve. On islands where predation is reduced, formerly territorial species are expected to become more tolerant of conspecifics feeding nearby. This lessening of territorial defense may be visualized as shifting the consumer zero-isocline inward and/or upward to a greater extent than that predicted solely on the basis of the removal of predators without a behavioral adjustment by the lizards. The effect is that the S:D ratio will not increase as much as expected at the new island equilibrium but the qualitative direction of size change need not be altered.

This scenario is not applicable to many of the large ungulates. Their larger size and open habitat preclude the use of hiding places for predator defense. In these, predation often seems to act in an opposite direction, forcing them to band together in herds for safety (Wilson 1975). It would be interesting to compare the social structure of insular artiodactyls to that of related mainland species.

In conclusion, considerations of food availability and S:D ratios appear insufficient to explain total insular body size trends. This is particularly evident in many relict reptiles which are insular giants. For these, predators on the mainland may preferentially prey on larger-sized individuals because of their visibility, vulnerability and the greater energy content reward they offer. On islands lacking these predators foraging becomes less risky and food therefore is more readily accessible. Their body size may then approach a size more in tune with optimizing energetic profit.

APPARENT EXCEPTIONS:

2. BODY SIZE CONSTRAINED BY NICHE

Anomalous insular size trends (by my model) may result not only when one interprets relictual populations incorrectly and ignores the effects of size-selective predation, but also if he overlooks those species whose body size is constrained by physical factors, or sensitively adjusted to the prey-size distribution. In these species the optimum consumer body size will be the one most adept at finding and handling the sizes of most available prey. Small deviations from this body size may cause drastic reductions in foraging success regardless of prey abundance. Within this framework a colonist, even though nonterritorial, may increase in body size on an island lacking large-sized competitors since a surplus of large-sized prey will presumably be available. On the other hand, if a territorial species arrives on an island lacking competitors of a smaller body size or for some other reason the island is abundant in smaller-sized prey, then the optimum body size for this species may be smaller than that on the mainland. However, because (1) as we have seen, food will also be more abundant for territorial species at the

island equilibrium and (2) large-sized consumers may harvest both small and large prey while small consumers will have a reduced prey-size breadth (Hespenheide 1973, Wilson 1975), we might expect reductions in body size to be rarer than increases in body size for competitors whose limiting similarity is set by body size differences.

Although the evidence is circumstantial I believe that the nearly universal dwarfism of island foxes may be attributed to such circumstances. First, however, I examine 2 alternative hypotheses for these carnivores.

1) Suppose foxes are small on islands because the decrease in mortality on islands (compared to the mainland) is very great compared to the increase in productivity of food so that the new intersection of predator-prey isoclines lies to the left of the mainland situation much as in Fig. 3B. This hypothesis is not supported by the natural history accounts of the California Channel Island foxes (Grinnell et al. 1937). That is, food is apparently not relatively more limiting on islands than on the mainland. Secondly, foxes experience most of their mortality from disease, starvation and conspecifics (Trapp and Hallberg 1975, Kilgore 1969, Case 1978a), factors which probably only change slightly on islands. Because they experience little predation, foxes will not experience the density release of lower trophic-level consumers.

2) These foxes may represent relict forms of a once smaller continental race (von Bloeker 1967). As discussed earlier, the latter suggestion is by itself immaterial because the fact remains that selective pressures have allowed small-sized individuals to persist on islands but caused their extinction elsewhere. We are still left with the task of uncovering these differential selective agents. The possibility that size-selective predation on foxes is involved is again unattractive for the reasons just discussed.

Six of the 13 examples Foster (1963) tabulated to establish dwarfism of island carnivores come from populations of *Urocyon littoralis* inhabiting 6 of the California Channel Islands. Cody (1974) suggests an explanation for their dwarfism which is based on competition between sympatric carnivores along a body-size gradient. That is, Cody interprets the small size of the island foxes as an expression of the absence of other small-sized carnivores such as raccoons, weasels, kit foxes, and skunks from some islands. This argument has merit. Large potential prey such as rabbits, hares, and large gallinaceous birds are also absent from all islands. The next largest prey items, quail (*Lophortyx californicus*) and ground squirrels (*Spermophilus beecheyi*), are present only on Santa Catalina Island (Grinnell et al. 1937, von Bloeker 1967). Both these species have been recorded in the guts of Santa Catalina Island foxes. Interestingly, this race of fox is the largest of the island subspecies. Elsewhere, as well as on Catalina Island, the island foxes consume berries, fruits, cactus, insects, crabs, and the ubiquitous white-

footed mouse, *Peromyscus maniculatus* (Grinnell et al. 1937, von Bloeker 1967). It is interesting in this regard that on the 2 islands where the omnivorous spotted skunks (*Spilogale putorius*) are also present (Santa Cruz and Santa Rosa Islands) the foxes are again relatively large by island standards (Grinnell et al. 1937).

As mentioned earlier, many other carnivores off the coast of British Columbia and California display no tendency to decrease in size. This includes the omnivorous bears and skunks, and weasels and martens. In fact, except for skunks, these species tend to increase in size. The territoriality of these species is well established (Table 1) and may account for their increase in size. The only other carnivore which consistently decreases in size on islands is the raccoon (*Procyon lotor*). Fittingly, no evidence of territorial behavior has been found in this genus (Wilson 1975).

Rattlesnakes, as well as many other snakes, display a clear trend of smaller body size in island populations (Table 2). This is particularly evident for rattlesnakes on islands in the Gulf of California and off the west coast of the Baja California peninsula (Klauber 1949, 1956). My model predicts that decreases in body size should be accompanied by lower equilibrium densities of the species prey. It is difficult to compare the prey abundance on these islands because of the heterogeneous diet of rattlesnakes. The rattlesnakes in these desert areas subsist primarily on rodents and lizards. The smaller the rattlesnake the greater the proportion of lizards which is consumed. Larger snakes show a greater predilection for rodents (Klauber 1956). During various expeditions to these Gulf of California islands, I and a number of other investigators have trapped rodents. Three of these researchers have kindly allowed me access to their trapping results; further, Case (1975) lists the relative density of diurnal lizards on many of these islands. The relationship between the potential abundance of these prey and the size change of the endemic rattlesnakes is presented in Table 4. Rodents tend to be scarce on certain islands perhaps because of the obvious lack of soil and vegetation (see Felger 1966). Yet lizards (particularly species of small size) may be relatively abundant on these very same islands. Lizard densities on San Pedro Martir Island are 10 to 20× greater than on the mainland. If those continental islands which are only about 13,000 years old are excluded, rattlesnakes are smaller on islands where rodents are scarce but lizards abundant. When the relative abundance of these 2 prey groups is reversed, rattlesnakes are either not different in size or, as in one instance, larger. Lowe's accounts (in Klauber 1949) of the natural history of the dwarf *Crotalus mitchelli* on El Muerto island in the Gulf of California conforms to these predictions. These data suggest that the body size of rattlesnakes may be responding partially to changes in the size distribution of their prey as well as total abundance *per se*.

This hypothesis is compatible with 2 additional ob-

TABLE 4. Relationship between rattlesnake size on islands in the Gulf of California and the abundance of rodents and lizards

Island	Species	Snake body size trend	Trap success all rodents ^a (%)	Rodent trap nights	Lizards ^b sighted/h
Small islands (<10 km²)					
San Pedro Martir	<i>C. atrox</i>	↓	0	300	222, 200
Tortuga	<i>C. tortugensis</i>	↓	15	150	14, 35
San Francisco ^c	<i>C. enyo</i>	↔	9
Large islands (>10 km²)					
Angel de la Guarda	<i>C. mitchelli</i>	↑	31, 12	58, 50	10, 15, 37
	<i>C. ruber</i>	↓			
San Lorenzo Sur	<i>C. ruber</i>	↓	0.1, 4	300, 400	19, 45, 25
San Esteban	<i>C. molossus</i>	↓	3	160	80
San Marcos ^c	<i>C. ruber</i>	↔	1.0	158	Few
Carmen ^c	<i>C. enyo</i>	↔	6, 3	100, 40	15, 21, 27
	<i>C. mitchelli</i>	↔			
Santa Catalina	<i>C. catalinensis</i>	↓	0	40	26
San Jose ^c	<i>C. mitchelli</i>	↔	12	260	8, 44
	<i>C. enyo</i>	?			
	<i>C. ruber</i>	↔			
Espiritu Santo ^c	<i>C. enyo</i>	↔	2	220	11, 21
	<i>C. mitchelli</i>	↔			
Montserrat	<i>C. ruber</i>	↔	4, 8	140, 39	30, 55
Cerralvo	<i>C. enyo</i>	↔	100
	<i>C. mitchelli</i>	↔

^a This information was made available by Kenneth Abbott, Gerald Lieberman, and Timothy Lawlor and is supplemented by my data. Separate values are for different years of collecting between 1970 and 1975. Trap success at 5 mainland Baja California sites for these same periods ranged from 13 to 70%, with a mean value of 30%.

^b From Case (1975) and subsequent unpublished observations. Data were collected during the same periods as that for rodents. Separate values are for different years' observations. Values for 20 Baja California mainland sites ranged from 3 to 37 lizards/h with a mean value of 12.

^c Land-bridge islands.

servations. The first concerns the peculiar reversal of body size displayed by *Crotalus ruber* and *C. mitchelli* on Angel de la Guarda Island (Klauber 1956, Cody 1974). On the mainland *C. ruber* is on the average about twice as heavy as *C. mitchelli*. On this island, *C. ruber* has decreased in size while *C. mitchelli* has increased to the point that the insular *C. ruber* is only about ½ as heavy as the insular *C. mitchelli*. Meristic characters suggest that *C. mitchelli* has diverged more from its mainland progenitors than has *C. ruber*, indicating that *C. mitchelli* arrived on the island first. This particular island is inhabited by lizards weighing as much as 2 kg (*Sauromalus hispidus*) and rodents weighing up to 150 g (*Neotoma lepida*). To use all potential prey items *C. mitchelli* probably evolved a larger body size. As it increased in size, larger prey would be preferred (Schoener 1971). When *C. ruber* arrived, food was probably both more scarce and skewed favoring smaller prey; consequently *C. ruber* decreased in size.

The second example also comes from Klauber (1949). The dwarf rattlesnake *Crotalus viridis caliginis* occurs on South Coronado Island off the northwest coast of Baja California Norte. Its food habits differ from those of the mainland subspecies (*Crotalus viridis helleri*) because it eats primarily lizards rather than mammals. *Crotalus v. caliginis* reaches a size large enough to consume mice but it apparently does not usually include them in its diet even though rodents are relatively abun-

dant on the island. The explanation offered by Klauber seems plausible: namely, the cold and foggy climate of this island forces the heliothermic rattlesnakes to be largely diurnal like the lizards. Hence the optimum rattlesnake size for resource utilization is lower than on the mainland, where rattlesnakes are more crepuscular and nocturnal and thereby encounter rodents more frequently.

The *Cnemidophorus* lizards (family Teiidae) on islands in the Gulf of California provide an excellent example of the complexity of factors which may influence body size. Unlike most insectivorous iguanids which are "sit and wait" predators, lacertids, teiids, and varanids actively search for their prey. This entails roaming over wide areas, and thus these animals usually do not defend set territories (although they have relatively stable home ranges). The effect of this behavior on insular S:D ratios has been discussed earlier. This searching tactic affects the optimal body size in 2 other ways. First, because the amount of energy expended by an animal in vertical movement goes up exponentially with weight rather than to a power <1 as with basal metabolic rate (Taylor et al. 1972), the size of an animal will be constrained when the topography is steep. In fact, these Gulf of California islands are very small and steep, some being essentially vertical cliffs rising from the sea. When an animal's metabolic demand increases with weight raised to a power >1, the optimal body size

is relatively insensitive to changes in food abundance (Case 1978b). Secondly, actively searching lizards like teiids and lacertids usually consume a greater proportion of sedentary prey such as grubs, larvae, and termites compared to more mobile prey such as adult flies, wasps, and adult lepidopterans which are consumed in greater proportion by territorial "sit and wait" feeding lizards (Dixon and Medica 1966, Pianka 1970). The local abundance of nonmobile prey is more easily depressed in spatial patches due to the predator's feeding activities. Consequently, increases in the density and activity of such lizards following the loss of their predators on islands is more likely to result in lower prey levels and a resulting smaller body size than in "sit and wait" lizards whose feeding activities may not greatly affect the local abundance of their prey.

On certain older islands in the Gulf of California where *Cnemidophorus tigris* is a dwarf, the iguanid side-blotched lizard *Uta* tends to be larger than mainland races (Soulé 1966, Mertens 1934). On San Pedro Martir Island both species are very abundant. The borders of the island are cliffs composed of large boulders covered with bird guano. The top of the island is still rocky but flatter and the rocks are much smaller. Although *Uta* is abundant on both the margins and top of the island, *Cnemidophorus* is scarce on the steeper slopes but nearly as numerous as *Uta* on the upper flatter regions. The stomach contents of both these lizards contain large amounts of fish scraps which are found around the numerous booby and pelican nests, but there is a greater proportion of adult flies and vegetation in *Uta palmeri* stomachs whereas *C. tigris* contains relatively more beetle adults and larvae. Even after adjusting for differences in body size there is relatively more food on the average in stomachs of *Uta* on San Pedro Martir Island than those of *Uta* on the mainland. On the other hand, I observed that the stomachs of the small *Cnemidophorus tigris* on San Pedro Martir Island are less full. This implies that food is relatively more abundant for *Uta* on this island but less abundant for *C. tigris* compared to mainland populations.

Although these results agree with those expected by my model, there are some serious exceptions on other islands in this same chain. First, on a number of islands, neither *Uta stansburiana* nor *C. tigris* are substantially different in size from adjacent mainland populations even though the number of competitor and predator species is substantially reduced. Because the majority of these islands are young (approximately 13,000 years) it might be argued that natural selection has simply not had sufficient time to produce gross morphological differences.

A more serious exception involves insular *Cnemidophorus*. *Cnemidophorus hyperythrus* has an insular subspecies on Monserrate Island which is slightly larger than on the Baja California mainland. Further, a derived insular species *Cnemidophorus ceralbensis* exists on Cerralvo Island which is substan-

tially larger. To account for these discrepancies I feel it is necessary to invoke the argument that the body sizes of *Cnemidophorus* species are influenced, in part, by the presence or absence of congeneric competitors. The evidence for this is as follows. On the east side of the Baja California peninsula there are only 2 sympatric *Cnemidophorus*: *C. tigris* which is a relatively large species and *C. hyperythrus* which is relatively small. I have observed that among these *Cnemidophorus* species the larger lizards tend to eat substantially larger prey than smaller lizards. Habitat overlap, on the other hand, is high between these 2 species. There are 7 islands on which *C. tigris* is significantly smaller than adjacent Baja California populations. All lack *C. hyperythrus*. *Cnemidophorus hyperythrus*, or the endemic derivative, *C. ceralbensis*, occurs without *C. tigris* on only 2 islands. These are the islands of Cerralvo and Monserrate (Robinson 1973) and on both the body size is greater. On the 5 major islands where both *Cnemidophorus* species occur together neither species differs greatly in size from its respective Baja California mainland relatives (Burt 1931).

The importance of body-size as an important niche dimension in this genus is reinforced by a study of the distribution maps for other continental members of the genus. These reveal the relative rarity of sympatric associations between species of similar body size (Zweifel 1959, Duellman and Wellman 1960, Duellman and Zweifel 1962, Stebbins 1966). In the instances where this rule is violated such as south-central New Mexico and the Trans-Pecos region of Texas, similar sized species utilize different habitats but have nearly complete food overlap (Medica 1967, Milstead 1957a, b).

A FURTHER COROLLARY

One prediction generated from this model which is particularly amenable to testing is that insular species displaying gigantism should exist at higher equilibrium resource densities than their mainland relatives. Dwarf island species, on the other hand, should have lower resource levels at their island equilibrium. Unfortunately, there are presently few available data to test this prediction. I have already mentioned the observations on rattlesnakes in the Gulf of California which do not strictly support this prediction because food composition may be equally important. Other data for lizards are more encouraging. San Pedro Martir Island in the Gulf of California supports the largest lizard in the genus *Uta*, *Uta palmeri*. The flies, bees, and other insects on which these lizards feed are also particularly abundant. Furthermore, the lizards feed freely on fish debris around the numerous booby and pelican nests (Soulé 1966, Case 1975). J. Roughgarden and G. Gorman (*personal communication*) found a remarkably good correlation between the body size of insular populations of anoles in the Caribbean and the abundance of insects. The correlation between lizard size and the

average size of available insects was practically nonexistent.

Many of the animals which evolutionarily decrease in body size on islands have been introduced on islands within recent time. These species often display a similar pattern of demographic behavior following these introductions. For example, moose (Mech 1966), deer (Rasmussen 1941, Cameron 1958), reindeer (Scheffer 1951, Klein 1968), and rabbits (Smith and Cheatum 1944, Banks 1965) which have been introduced on islands with few or no predators rapidly increase in numbers and then after seriously overbrowsing plunge precariously close to extinction. Naturally, during this decline, food is scarce. In many of these instances it is doubtful that a stable equilibrium exists, at least on an ecological time scale. On other islands, such as Rhum off Scotland and Hitra off Norway, where introduced red deer (*Cervus elaphus*) have been annually culled by hunters (keeping their zero-isocline from shifting to the left or upward), the population has remained relatively stable (Lowe 1966, Eggeling 1964, Wegge 1975).

Adequate tests of this corollary must await additional data. One indirect method of measuring resource turnover rates for a consumer in a series of areas is by experimentally augmenting these resources and measuring their dissipation rates. These rates along with some knowledge of resource and consumer population levels could be combined to give an appropriate index of the S:D ratio. Attempts to apply this technique to island situations are now underway.

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APPENDIX CALCULATION OF S:D RATIOS FOR PREDATOR-PREY MODELS

Model 1: from eq. 1A,

$$\frac{d\hat{R}^*}{\hat{R}dt} = \frac{W\hat{C}}{M + \hat{R}}$$

From equation 1B,

$$\hat{R} = \frac{d(M + \hat{R})}{W}$$

and therefore, after substituting into eq. 4 (with $e = 1$) and cancelling

$$S/D = \left(\frac{d\hat{R}^*}{\hat{R}dt} \cdot \hat{R}/\hat{C} \right) = d.$$

On an island the consumer's death rate (d) is expected to be equal to or lower than that on the mainland because of the loss of predators. Hence, consumers described by *Model 1* will never have a greater availability of food on islands, and are expected if anything to decrease in body size, based on the lower availability of their food (Fig. 2A).

Model 2: From eq. 2A,

$$\frac{d\hat{R}^*}{\hat{R}dt} = \frac{W\hat{R}\hat{C}}{M + \hat{R}}.$$

From eq. 2B,

$$\hat{R} = \frac{a\hat{C}^2 + d\hat{C}(M + \hat{R})}{W\hat{C}}.$$

Therefore, after substituting into eq. 4

$$S:D = a\hat{C} + d. \quad (A1)$$

In this case, the comparative analysis of S:D is confounded by the inclusion of terms in eq. A1 which are expected to both increase (\hat{C}) and decrease (d) on islands. Fortunately, however, the qualitative solution is transparent.

Divide eq. A1 by a , and express each variable as the difference (Δ) in its values between island and mainland.

$$\frac{1}{a} \Delta(S/D) = \Delta\hat{C} - \Delta d/a.$$

Graphically the change in the height of the consumer isocline at any fixed point along R is exactly $\Delta d/a$, assuming that a , W , and M remain constant from island to mainland setting (to see this, set eq. 2B to zero and solve for C ; see Fig. legend 2). The change in the height of the point of intersection of the 2 isoclines is simply $\Delta\hat{C}$. Whenever $\Delta d/a$ is greater than $\Delta\hat{C}$, the resulting $\Delta(S/D)$ will be negative and the island equilibrium point will necessarily fall in the region above and to the left of the mainland equilibrium (Fig. 2b). Only if the island equilibrium falls in the region above and to the right of the mainland equilibrium (Fig. 2b) will the island S/D be greater.

Model 3: From equation 3A,

$$\frac{d\hat{R}^*}{\hat{R}dt} = \frac{F}{\hat{R}}$$

hence $S:D = F/\hat{C}$.

Since from 3A

$$\hat{C} = \frac{F(M + \hat{R})}{\hat{R} \cdot W}.$$

Then

$$S/D = \frac{\hat{R}R \cdot W}{M + \hat{R}}. \quad (A2)$$

Hence any changes in resource productivity (F) alone will not affect the S:D ratio. Since we assume that M and W are constant, changes in S:D are best interpreted by changes in \hat{R} . Differentiating eq. A2 with respect to \hat{R} ,

$$\frac{\partial(S/D)}{\partial\hat{R}} = \frac{W(M + \hat{R}) - (\hat{R} \cdot W)}{(M + \hat{R})^2}.$$

Because M and W are positive $M + \hat{R}$ will always be greater than \hat{R} and this partial will always be positive. Therefore as \hat{R} increases, so will S:D. Yet, \hat{R} will only increase when the constant J increases. Because we predict the insular environment will be more productive we expect this to occur. Graphically then, the island S:D ratio will increase if the new point of intersection of the zero-isoclines occurs in the region above and to the right of the previous mainland intersection (Fig. 2c).