

BODY SIZE AND ISLAND PEROMYSCUS:
A PATTERN AND A HYPOTHESIS

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Abstract: The deermouse, Peromyscus maniculatus, occurs on most of the islands of coastal British Columbia, and when it forms insular races they are almost invariably larger in body size than their nearest mainland relatives. When $\ln(\text{mean body length})$ is regressed against $\ln(\text{island area})$ and $\ln(\text{distance from the mainland})$ for samples of islands from two areas of coastal British Columbia, a significant negative correlation of area and body length, independent of distance, is found in one sample and suggested in the other. Such a relationship suggests that one or more ecological correlates of island area produce selection pressure for large body size as area decreases. Such correlates include low or reduced interspecific competition and predation, possibly more stable climates, and greater frustration of dispersal on small than on large islands. These factors tend, other things being equal, to produce higher densities and higher levels of intraspecific competition on small islands relative to large islands and the mainland. If increased intraspecific competition on an island decreases juvenile survivorship but affects adult survivorship relatively little, then selection should favor individuals that live longer and possibly produce smaller litters; selection for large body size is interpreted here as part of an adaptation for greater survivorship potential in this selective mileu. On the other hand, if higher intraspecific competition on an island decreases juvenile and adult survivorship by similar proportions, or retards growth to full adult size in all individuals, then breeding at a smaller body size is selectively advantageous. These two results of intraspecific competition I term the juvenile/adult survivorship (J/A) hypothesis of insular body size evolution. Certain predictions arising from this hypothesis are discussed.

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INTRODUCTION

The Pacific coast of British Columbia, Canada, is dotted with hundreds of islands that vary in area and distance from the mainland. Most of these islands harbor populations of the deermouse, Peromyscus maniculatus, that show varying degrees of morphological distinction from one another and from the mainland population (McCabe and Cowan 1945, Cowan and Guiguet 1965). Such a natural system of isolated replicate populations is of great interest to the evolutionary biologist. Varying degrees of taxonomic affinity and divergence, of interfertility and sterility, and of allelic differentiation would be expected even in the absence of natural selection as a result of random mutation and genetic drift. Indeed, these islands are rich in P. maniculatus populations showing subspecies-level morphological variation. Still more fascinating, however, is the tendency for the most restricted and isolated of these populations to be larger in body size than their nearest mainland relative. Specifically, of the 15 races of British Columbian P. maniculatus described as confined to one or a few small islands (Cowan and Guiguet 1965) one race is smaller, two races about equal, and twelve races larger in body size than their nearest mainland relative. This conforms to the strong tendency toward large body size noted by Foster (1964, 1965) and others (e.g. Berry 1964, Berry et al. 1978 for Mus; Corbet 1964, Zimmerman 1950 for Clethrionomys; Delaney and Healy 1967, Felten and Storch 1971, Berry 1975 for Apodemus) in island races of mice as a rule. Such a pattern suggests one of two possible explanations; either the large-bodied

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TABLE 1: Data on body size, island size, and island isolation (distance from the mainland) for Peromyscus maniculatus populations used in the present analyses. See text for further explanation.

Sample 1

#	Subspecies	Island	N	Body Length (mm)	S.D.	Island Area (ha)	Distance from Mainland (km)
1	<u>macrorhinus</u>	Pitt	20	100.9	2.7	143601	0.5
2	"	Banks	13	103.6	4.9	106391	26.3
3	"	Porcher	8	101.4	2.4	70284	8.4
4	"	McCauley	5	105.8	2.7	27838	15.8
5	"	Campania	11	104.4	6.8	16538	23.1
6	"	Aristazabal	16	100.3	5.1	42446	39.9
7	"	Princess Royal	9	100.9	7.4	260466	1.1
8	"	Swindle	5	106.2	5.4	30594	15.8
9	"	Yeo	13	103.9	3.2	9250	0.3
10	"	Calvert	60	97.4	5.5	30319	5.8
11	<u>rubriventer</u>	Chatfield	4	107.8	5.6	4438	1.3
12	"	Campbell	10	102.9	4.3	14063	9.3
13	"	Dufferin	5	107.8	4.7	4250	2.3
14	"	Horsfall	11	104.2	4.2	5000	5.0
15	"	Athlone (Smythe)	16	104.6	6.9	4125	3.5
16	"	Townsend	6	108.3	3.9	188	12.4
17	"	Hunter	13	106.2	4.4	33351	6.3
18	<u>maritimus</u>	Moore	8	109.6	3.6	250	65.3
19	<u>cancrivorus</u>	Table	19	93.4	3.6	188	2.4
20	<u>pluvialis</u>	Goose	23	105.7	5.7	1813	36.2

Sample 2

21	<u>isolatus</u>	Pine	3	117.0	5.2	43	14.2
22	"	Nigei	35	103.2	5.1	6000	1.9
23	<u>balaclavae</u>	Balaclava	31	98.1	4.5	1463	5.6
24	"	Hope	44	98.1	3.6	3625	2.3
25	<u>saxamans</u>	Bell	43	105.7	3.5	135	5.3
26	"	Duncan	14	105.6	2.8	68	5.8
27	"	Hurst	18	104.6	3.5	388	4.0
28	<u>doylei</u>	Doyle	15	105.1	3.2	50	4.5
29	<u>carli</u>	Cox	18	104.1	3.8	1063	10.0
30	"	Lanz	18	104.1	4.2	875	16.3
31	<u>triangularis</u>	Triangle	14	110.8	3.0	188	46.0
32	<u>sartinensis</u>	Sartine	12	117.8	3.0	25	33.3
33	<u>beresfordi</u>	Beresford	11	109.5	4.6	11	24.0
*			*				*

racess of mice are the remnants of a once widespread large-bodied race, or they have evolved large size independently as a result of selective forces intrinsic to the ecology of island populations. Where neighboring island and mainland mouse populations have been compared (Berry 1964, 1975; Berry et al. 1978; Corbet 1964; Foster 1965) large and random morphological differences between closely related island populations suggest that each one evolves independently of the others, refuting the relict hypothesis. Size increase in these island mice appears to be a parallel trend in otherwise evolutionarily divergent populations.

The purpose of this paper is to determine the relationship of mean body length to island area and distance from the mainland in two sets of ecologically similar

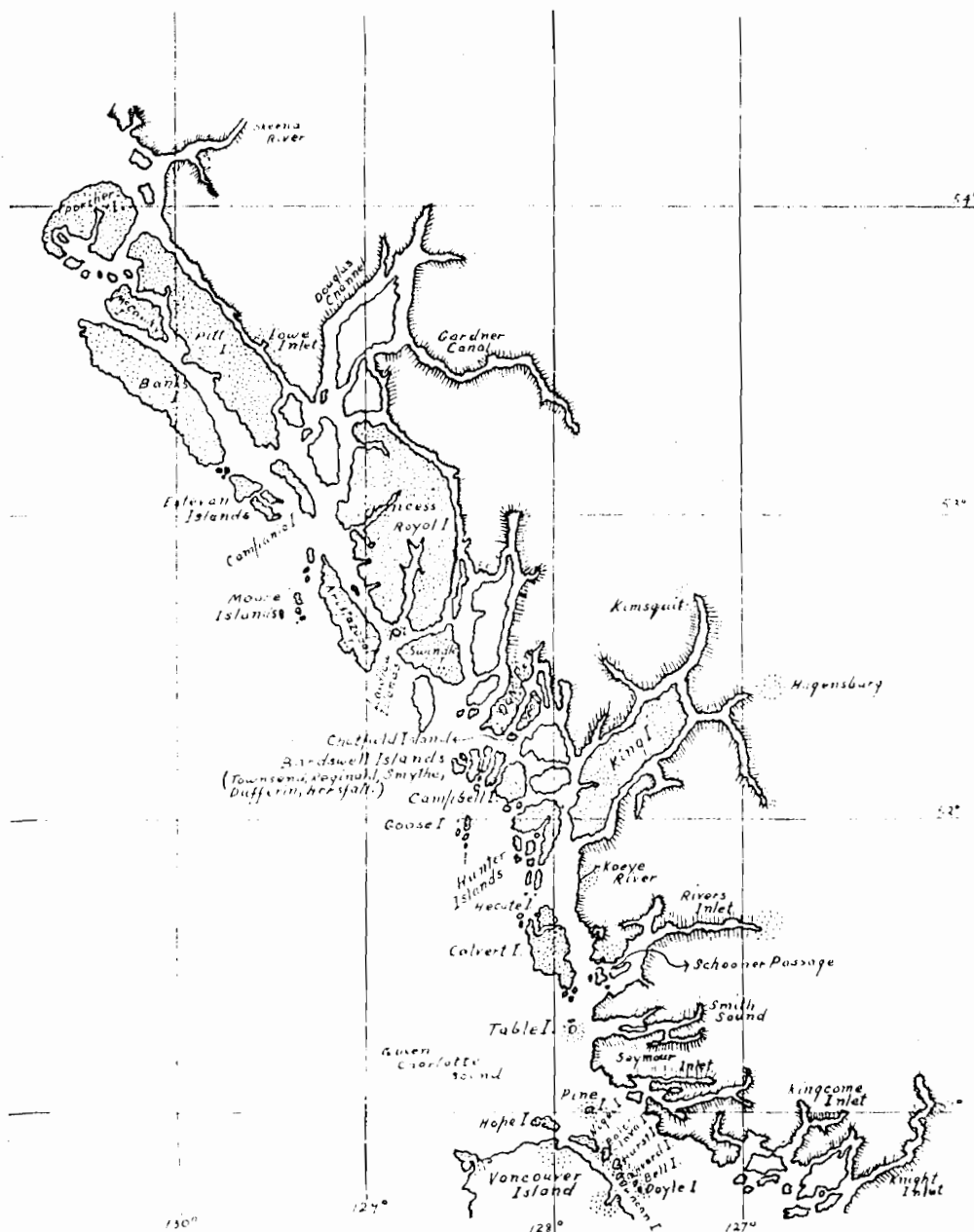


Figure 1. Map of coastal British Columbia taken from McCabe and Cowan (1945).

islands on the west coast of British Columbia, and to explore the evolutionary significance thereof.

MATERIALS AND METHODS

Data used in this analysis are shown in Table 1. The Peromyscus maniculatus specimens used in this study come from two main sample areas. Sample 1 consists of most of the main islands west of coastal mainland British Columbia from the Kingcome Inlet region to the south to the Skeena River outlet to the north. The prevailing race on the mainland coast is the short-tailed Peromyscus maniculatus macrorhinus, in sympatric association with the long-tailed Peromyscus oreas only at the heads of Loughborough, Kingcome, and Bute Inlets (Cowan and Guiguet 1965). Sample 2 consists of the islands north and west of the northernmost tip of Vancouver Island, namely the Gordon, Goletas, and Scott Island groups. The "mainland" race prevailing on

northern Vancouver Island is P. m. interdictus (Cowan and Guiguet 1965). A map of the greater portion of these areas is shown in Figure 1.

The Peromyscus body-length data presented here were furnished by Dr. I. McT. Cowan of the University of British Columbia, and the specimens have been described by him in a previous analysis (McCabe and Cowan 1945). Only mice having rufous, fully adult pelage and a plainly visible degree of wear on M¹ were used in calculation of mean body lengths. Since Peromyscus has determinate growth (Duffy and Sacher 1976), these means should reflect the body sizes of fully grown adults.

Island areas were calculated by tracing topographic maps with a planimeter and adjusting the resulting value to scale in hectares. Distance of the island from the mainland is the minimum map distance from island periphery to mainland coast, measured in millimeters and adjusted to scale in kilometers. The term "mainland" refers to coastal continental British Columbia for Sample 1, and to Vancouver Island for Sample 2.

A multiple regression of the form

$$\ln(\text{Body Length}) = \ln B_0 + B_1 \ln(\text{Area}) + B_2 \ln(\text{Distance from Mainland})$$

was performed on the data in Samples 1 and 2, respectively, where the B_i are constants. Transformation of the data to logarithms helped to linearize their relationships. Henceforth, any reference to body length, area or distance (from the mainland) with regard to this data set will actually refer to the natural logs of these variables.

RESULTS

The regression coefficients for the analyses of Samples 1 and 2 are given in Table 2, and are discussed in turn below.

Sample 1

Figures 2a and 2b show that the relationships of mean body length to area and distance are generally linear. The Table Island datum (#19) is an exception, showing up as an outlier in Figure 1a with a body length smaller than that of populations from islands of comparable area, and indeed smaller than any other population in the sample. Table 2a shows the multiple-regression statistics for Sample 1. The regression is not significant at the 5% level.

Table 2b shows the same analysis with the Table Island datum omitted from the analysis. This omission is warranted by the unique character of the outlier in other respects than body size. The resident subspecies, P. m. cancrivorus, has a pale-colored pelage unusual for Peromyscus of this region (most island races are dark-colored), and Table Island itself is unusual for islands of this region in its shape and ecology --- plateau-like and rocky, with little easy access to the shoreline and none of the exposed, sandy beaches that island Peromyscus typically inhabit (McCabe and Cowan 1945). The multiple-regression without Table Island is significant at the 0.5% level. The partial F for distance given area is not significant at the 5% level, but the partial F for area given distance is significant at the 0.5% level. Thus, island area is the only significant predictor of body length in this analysis. The coefficients for the regression of body length on area alone are given in Table 2c.

Sample 2

Figures 3a and 3b show that the relationships of body length to island area and distance in this sample are linear. The multiple-regression results are shown in Table 2d. The regression is significant at the 0.1% level. The partial F for distance given area is not significant at the 5% level ($p = 0.09$), and the partial F for area given distance is almost but not quite significant ($p = 0.053$). Although area appears to be a somewhat better predictor of body length than distance, neither independent variable contributes significantly to R^2 given that the other is in the regression. This suggests multicollinearity, and indeed the correlation of

TABLE 2: Regression analyses of island Peromyscus Samples 1 and 2. The Regression coefficients B_0 , B_1 , and B_2 are given for each analysis. The significance level of each regression is shown at right. Significance levels for partial F statistics are shown underneath their corresponding regression coefficients.

Data Set	N	$\ln B_0$	B_1 (Area)	B_2 (Distance)	$R^2\%$	Significance Level
(a) Sample 1 full data	20	4.66 .001	-.0030 n.s.	.0057 n.s.	9.1	n.s.
(b) Sample 1 Table Island datum excluded	19	4.75 .001	-.0109 .005	.0003 n.s.	50.6	.005
(c) Sample 1 Area only	19	4.75 .001	-.0110 .001	-----	50.6	.001
(d) Sample 2	13	4.69 .001	-.0140 n.s.	.0232 n.s.	67.2	.001
(e) Sample 2 Area only	13	4.78 .001	-.0211 .005	-----	56.0	.005

*
area and distance in Sample 2 is fairly high ($r = -0.60$) compared to the correlation of these variables in Sample 1 ($r = -0.27$). Thus, we cannot safely decide which independent variable is the better predictor of body length, or if both have important effects.

Given this difficulty, a regression of body length on island area alone, the results of which are shown in Table 2e, was performed for comparison with the regression of body length on area shown in Table 2c for Sample 1. The slopes and intercepts of both regressions are similar, and suggest that the relationship of body length to area seen in Sample 2 may be a continuation of the same relationship we see between these variables in Sample 1 to the north. However, a Levene's test (described in Van Valen 1978) for equality of residual variances of these two regressions showed that they were significantly different at the 5% level. Therefore, no tests for identity of regression parameters were performed.

The main conclusions to be drawn from these regression analyses are that a) there appears to be a marked correlation of mean body length with island area among the island Peromyscus populations of Sample 1, and that this correlation is independent of the degree of isolation (distance) of the islands from the mainland and its biota; and b) there is some evidence that mean body length varies with island area in Sample 2 in a way similar to that of Sample 1, though in Sample 2 the effects of area and distance cannot be discriminated statistically.

DISCUSSION

Were we to see a pattern such as shown in Figure 1a, and were the abscissa in this figure to denote latitude, longitude, altitude, or some other geographic spatial ordination, we would conclude that a cline in body size exists among these Peromyscus populations. The fact that the abscissa denotes island area, and that the populations represented are all but totally isolated from one another, suggests something quite different. Body size among these populations appears to vary concomitantly with and as a result of some correlate of island area itself, more or less independently of the effects of isolation from the mainland race.

These results refute, for one thing, the hypothesis of the larger-bodied island

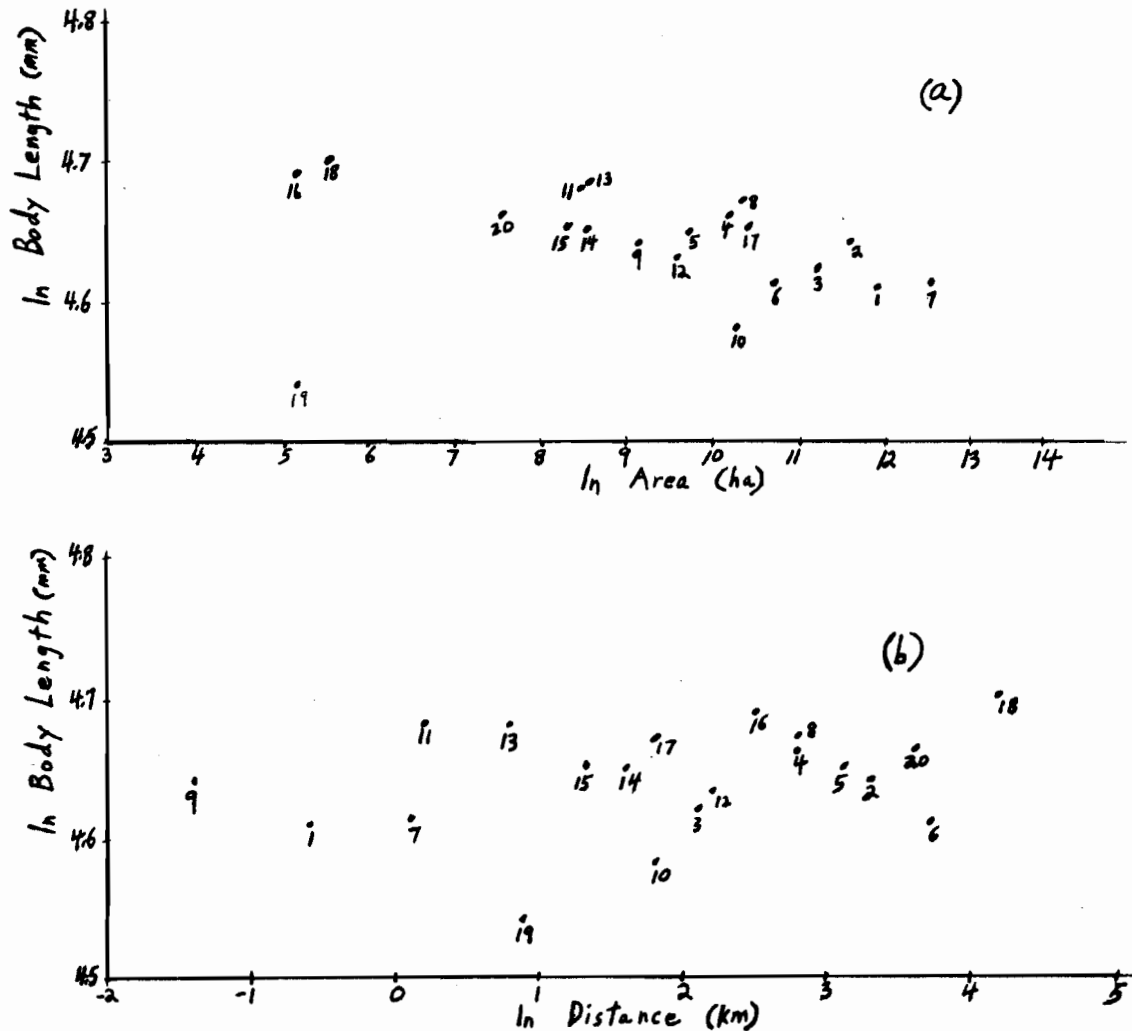


Figure 2. Scatter plots of Body Length vs. Island Area and Distance from the Mainland for Sample 1.

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mouse stocks as having arisen from a single common large-bodied ancestor of once-widespread distribution. The mice appear to have colonized or been stranded on their islands and evolved their differences in body size independently sometime within the approximately 10,000 years since the retreat of the last glaciation made the region habitable for *P. maniculatus* (McCabe and Cowan 1954). This hypothesis has already been refuted by McCabe and Cowan for the populations of Sample 1, since the large-bodied insular subspecies represented there are too distinct in other characters to have arisen from a single ancestral source. However, the concomitant variation of body size with area disproves it on the basis of body-size criteria alone.

The exceptional nature of *P. m. cancrivorus* from Table Island, its small body size, becomes even more exceptional under the hypothesis that small island area somehow selects for large body size of resident mice. Why should tiny Table Island produce a small race of mice? This question will be addressed again further on.

The *Peromyscus* populations of Sample 2 show a pattern similar to that of Sample 1, except that the separate effects of area and distance on body length cannot be discriminated. The fact that area is a somewhat better predictor of body length than distance, and the similarity of coefficients for the regressions of

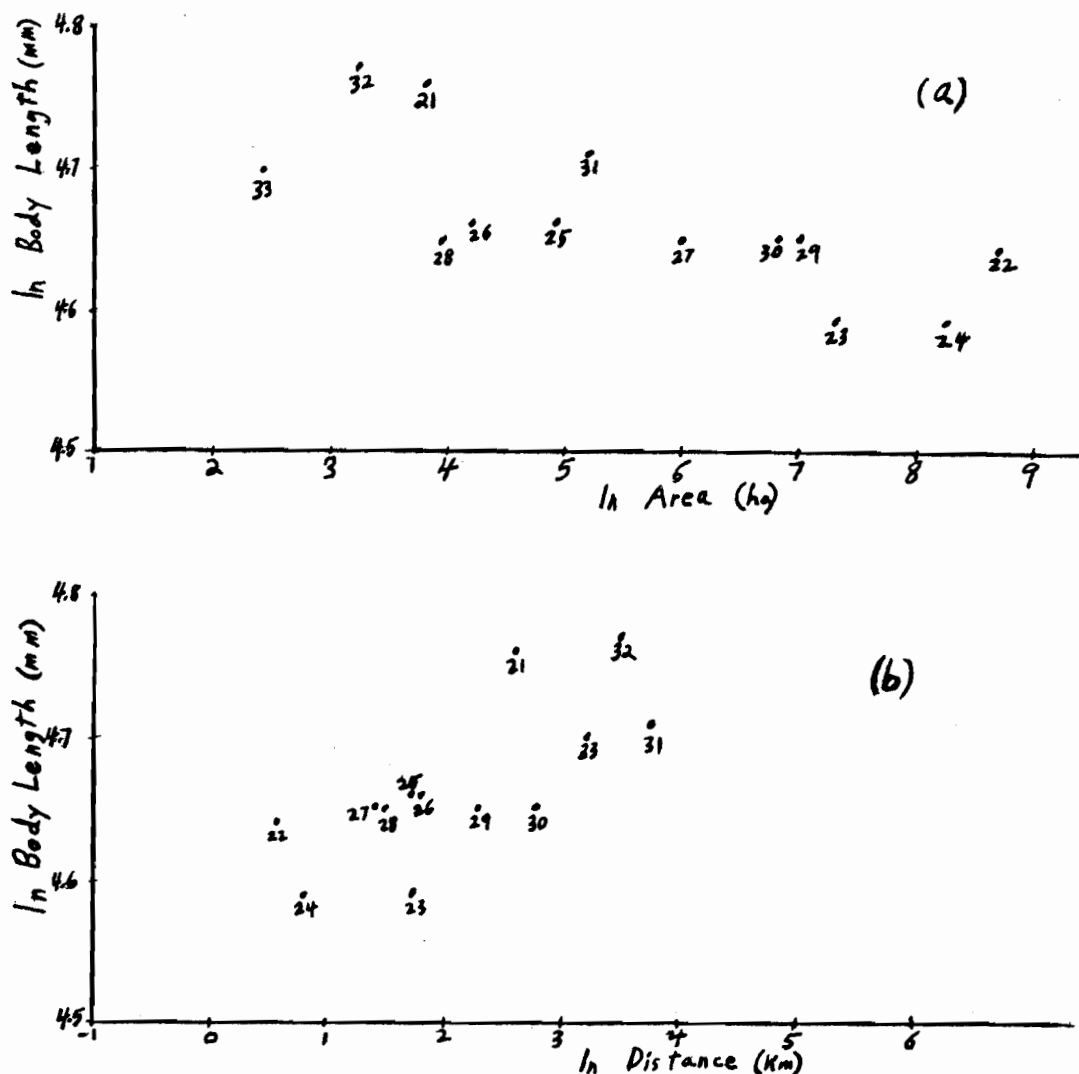


Figure 3. Scatter plots of Body Length vs. Island Area and Distance from the Mainland for Sample 2.

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body length on area in the two samples (Table 2c and 2e), suggest that whatever effects of area on body length are present in Sample 1 may also be working to a similar degree on the populations of Sample 2. The concomitant variation of body length with area and distance tends to refute the hypothesis proposed by Thomas (1971) that the islands of Sample 2 are populated by two distinct types of mice, a small-bodied morph on Balaclava and Hope Islands, and a large-bodied morph on Triangle, Lanz, Hurst, Doyle, and Nigei Islands, the large morph being presumably derived via rafting from populations of the large-bodied P. m. prevostensis on islands to the north. No such distinct size morphs appear in Figure 3.

Selective Correlates of Island Area

The negative correlation of mean body length with island area seen in this study indicates that one or more correlates of island area may produce selection pressure on body size in these insular populations. Four major ecological correlates of area are likely to have some effect on mouse population dynamics:

a) Low interspecific competition --- As island area decreases, environmental heterogeneity and carrying capacity also decrease, and so the number of species it can support also decreases (Mac Arthur and Wilson 1967). Thus, a species on a small

island may find fewer species that compete with it for food, space, or other resources than it would on a large island or mainland. Of course, the intensity of interspecific competition may still be quite high, as attested by the high incidence of character displacement between island congeners (e.g. island Anolis lizard species studied by Schoener (1969, 1970)) and the higher-level adaptive radiations in island groups such as the Hawaiian and Galapagos. We may say that since competitor species are fewer, the selective effects of interspecific competition are more unidirectional and the adaptive response more unilateral on small than on large islands. Some islands simply have no competitor species, in which case the population is released from the necessity of adapting to them altogether. Thus, the selective effects of interspecific competition on small islands are either simplified or eliminated.

b) Low predation --- The same factors that limit the number of competitor species on a small island limit the number of predator species to an even greater degree, since carrying capacities per unit area are on the average smaller than those for herbivore species (Mac Arthur and Wilson 1967). Thus predators tend to be relatively rare and vulnerable to extinction on islands. Of course, what predator species do exist on a small island may have profound effects on its prey populations. Again, we may say that the selective effects of predation are more unidirectional, and the adaptive response of the prey population more unilateral, on small than on large islands. The effects of predation on evolution are either simplified or eliminated.

c) Climate --- Temperature variation on islands is buffered by the ocean. Mild climates with plentiful rainfall and little seasonal temperature variation are found on many of the islands in this study (Carl, Guiguet, and Hardy 1951, McCabe and Cowan 1945). However, The entire coastal region of British Columbia is mild and moist in climate, so that this factor is probably irrelevant to the present study. Moderation of climate is probably correlated more with distance from the mainland than with island area, though, of course, an island of sufficiently large area is a mainland.

Salinity, a seldom-considered aspect of island mammal ecology, may be an important factor on small islands in which a large proportion of the population must live and gain its sustenance near the shoreline. Small islands frequently exposed to gales and salt spray could conceivably be quite desiccating environments, and so an analog of Bergmann's rule (selection for decreased ratio of body surface to volume and therefore larger body size) may apply. This is consistent with the fact that the largest mouse races of coastal British Columbia are found on small islands with unobstructed exposure to open ocean and westerly gales: islands such as the Scott group (Cox, Lanz, Triangle, and Beresford Islands) in this study, and also the small westerly islands of the Queen Charlotte group which house the large P. m. prevostensis (Cowan and Guiguet 1965).

Aside from the possible effects of salinity on very small islands, we may say that moderate island climates probably tend to increase survival and reproductive success relative to mainland populations as a rule, but that this effect is probably minimal for the islands in this study.

d) Frustrated dispersal --- This term, coined by Lidicker (1975), refers to a populational condition in which motivation to emigrate (e.g. hunger, crowding) exists, but consummation is prevented by barriers or inhibited by the absence of an unfilled dispersal sink (space available for emigration in which at least short-term survival is possible). Since emigration on small islands is restricted by the island perimeter and lack of space for dispersal, the smaller the island area the more frequently is a condition of frustrated dispersal likely to develop. This is illustrated by the fact that restricting dispersal with a mouse-proof fence can greatly increase a mouse population's rate of increase and cause overcrowding even in the presence of normal predation pressures (Krebs, Keller and Tamarin 1969, Boonstra and Krebs 1977, Lidicker 1975).

Three of these four factors, the easing or simplification of competition and

predation pressures and the reduction of climatic variability, probably tend to reduce overall mortality rates in populations living on small as opposed to large islands. Frustration of dispersal, the fourth factor, tends to further enhance the population's rate of increase per unit area by lowering the net outflow of individuals from the population. Thus, we would expect small-island populations to experience (at least before evolution of the original colonist form) frequent high densities and generally more intense levels of intraspecific competition relative to mainland and large-island populations.

Clearly, if intraspecific competition is enhanced on small islands and other population-regulating factors are reduced in importance, this will cause a shift in the emphasis of natural selection in these populations. Life-history parameters are likely to evolve away from the type of the original (presumably mainland-type) colonist. In general, selection for greater efficiency of resource use (K-selection) is expected; a shift away from the strategy of maximal offspring production and toward production of fewer, higher-quality offspring with minimal waste of resources (Mac Arthur and Wilson 1967).

Juvenile/Adult Survivorship and Body Size

The most important difference in selection pressure on small vs. large islands regarding the evolution of body size may be the difference in juvenile survivorship and rates of recruitment into the breeding population. As a population's per capita rate of increase decreases or becomes negative, as in times of population crowding, the selective advantage of short generation time vanishes (Lewontin 1965, Mertz 1970). Murphy (1968) showed by computer simulations that longer lifespan, smaller litter size, and iteroparity is a strategy selectively superior to high litter size and semelparity when juvenile survivorship is low or variable. Thus, if crowding causes lower juvenile survivorship and recruitment rates more frequently on small islands than on large ones, then the population should evolve greater survivorship capability of individuals and fewer or smaller litters per breeding season. Furthermore, if large body size is an adaptation for greater longevity in mice, then large size will be selected for in the small-island milieu. Body size and longevity are correlated among mammals in general and within mammalian orders, though brain size predicts longevity even better (Sacher 1959). Any heritable correlation of body size and longevity should facilitate the evolution of greater body size on islands.

On the other hand, if crowding and subsequent resource depletion on islands decreases the survival rates of adults as well as juveniles, then individuals that take less time and use less energy for growth and development will be at an advantage. An effective way of doing this is to breed at a smaller body size.

I term the mechanisms of size increase and decrease proposed above collectively as the juvenile/adult survivorship, or for brevity J/A, hypothesis of insular body-size evolution. From it we can make a number of predictions:

1. Comparison of large-bodied island vs. small-bodied mainland mouse conspecifics or congeners under identical conditions of high crowding or restricted dispersal should show that individuals of the island stock survive and breed better than individuals of the mainland stock. This has not yet been tested under such controlled conditions. There is evidence that trap samples of P. maniculatus on the smaller Queen Charlotte (Foster 1965) and Gulf Islands (Redfield 1976) of British Columbia consist of relatively old individuals, suggesting low recruitment or greater longevity in these populations. Tamarin (1978) reports that the large-bodied Muskeget Island beach vole, Microtus breweri, has greater survivorship and lower litter size than its mainland relative, M. pennsylvanicus, on live-trapped field grids. However, Sullivan's (1977) live-trap demographic comparison of island vs. mainland P. maniculatus in the Gulf of Georgia, British Columbia, showed survivorship of adults on the islands to be lower than or equal to their survivorship on the mainland. These studies, unfortunately, do not control for differential effects of island and mainland habitats on survivorship, and so tell us little

about survivorship capability as an evolutionary adaptation in these island mice.

2. Mouse populations of similar body size and life-history characteristics should show a decrease in the ratio of juvenile to adult survivorship rates a) in more crowded as opposed to less crowded conditions, b) in conditions of restricted as opposed to unrestricted dispersal, and c) on islands of smaller as opposed to larger area. There is good evidence of competition between juveniles and adults in mouse populations, and of the general competitive superiority of adults. Sadlier (1965), for example, found that P. maniculatus on the mainland show high levels of agonistic behavior during the breeding season. Resident adults in maze experiments were usually extremely antagonistic to intrusive juveniles, which either died or were restricted to small areas of the maze. In the field, Sadlier found that considerable juvenile mortality occurred during the breeding season, and that juvenile survival was much better on an area from which adults had been removed. Such a pattern, upon initial colonization of a small island by this species, could produce greatly reduced juvenile survivorship and recruitment rates. Lidicker (1965) studied confined laboratory populations of four mouse species, and found that the causes of cessation of population growth were reproductive inhibition of all females in Mus musculus, infant mortality and seasonal reproductive inhibition in P. maniculatus and P. truei, and infant mortality alone in Oryzomys palustris. Krebs et al. (1973) report that as densities of naturally cycling Microtus pennsylvanicus populations rise to a peak and subsequently crash to low levels, juvenile survival rates decline much earlier than those of adults, suggesting that the juveniles are more sensitive to competition at high densities than are adults. Millar (1975) decreased the food intake of Peromyscus leucopus breeding in the laboratory and found that females support their offspring primarily through increased food intake, and that shortage of food was reflected primarily in decreased survival and growth rates of the offspring. Young did not appear to be produced at any nutritional risk to the females. Bendell (1959) also found that, in an experimental small-island population of P. leucopus, decreasing food availability decreased juvenile survivorship rates without affecting the survivorship of older age classes.

Strong support for the J/A hypothesis is given by Gliwicz (1980). She analyzes the life-history characteristics of island rodent populations using, as her primary model, a population of the bank vole, Clethrionomys glareolus, from Crab Tree Island in Beldany Lake, Poland, as well as 13 other published examples of confined rodent populations under natural conditions for comparison. Island populations tend to show a greater stability of numbers than "open" or "mainland" populations and regularly reach high densities rarely, if ever, reached on the mainland. Dispersal is reduced: whereas mainland populations contain a substantial fraction of migrants, island mice seldom wander, often settling close to their place of birth. Home ranges of mice on islands are smaller and overlap less, suggesting tighter competition and a more strongly enforced partitioning of resources than in open populations. Most importantly, whereas numbers are regulated primarily through emigration on the mainland, island populations are regulated by low reproduction and early mortality of offspring. Loss of independent individuals is lower on islands, primarily resulting from higher post-juvenile survivorship rates and from low rates of dispersal.

Sullivan's (1977) study noted above shows, interestingly enough, that juvenile survivorship on Samuel Island (206 hectares) is poorer than on Saturna Island (3102 hectares). Since both islands have mice of similar body size, averaging between 22 and 25 grams (see also Redfield 1976), this result supports my prediction for mouse populations on islands of different areas.

These studies indicate a strong tendency for populations of mice to be regulated at times of high density or low resource availability at the expense of juvenile production and survivorship, and suggests that this condition may typify island mouse populations.

3. If greater longevity evolves in island mice, then morphological correlates of longevity should also evolve. Particularly, we may use the relationship

$$L = K E^{2/3} S^{-2/9}$$

where L is maximum lifespan, E is brain weight, S is body weight, and K is a constant (Sacher 1976). This relationship holds among and within mammalian orders, and implies that

$$K' = E/S^{1/3}$$

for a given lifespan, where

$$K' = (L/K)^{3/2} .$$

Therefore, if greater lifespan evolves on islands, then analysis of covariance should show greater age-corrected K' in island than in mainland mouse populations. Among island populations, the correlation of K' with island area should be negative and may produce a better fit than the correlation of body size with area. Though the exact form of K' is not known for within-species variation of lifespan, such an experimental approach could be rewarding.

4. For any population there must exist a level of competition or resource depletion below which the adult population, as well as the juvenile, also suffers. We can predict that, for any species or population in which competition at high densities significantly lowers adult as well as juvenile survival rates, or inhibits the population en masse from attaining full adult growth, selection will favor individuals that halt growth early, investing the energy once earmarked for growth into reproduction at a smaller body size.

Large mammals might be expected to deplete their food resources to the point of population starvation on islands more often than small mammals for two reasons. The first is that large mammals have larger energy requirements per individual than small mammals, both for growth to adult size and for maintenance of tissues at that size. The addition of one more deer, for example, to an island of size X is a greater strain on island resources than the addition of one more mouse. A dense population of small mammals is equivalent in energy requirements to a sparse population of large mammals (Van Valen 1973a). The second reason is that an island that is a coarse-grained environment to a small mammal may be a fine-grained environment to a large one (see Mac Arthur and Wilson (1967) for definitions of coarse- and fine-grained environments). If so, a population of small mammals on an island would have a greater natural ability to partition food or other resources unequally among its members, a condition that favors, in theory, population stability and a high equilibrium level of food resources (Łomnicki 1978). Large mammals, on the other hand, may be forced into a more equal distribution of their resources among individuals, resulting in a "tragedy of the commons" as densities increase. These differences between small and large mammals, under the J/A hypothesis, may help to explain the "island rule" (Van Valen 1973b) that large mammals tend to evolve small-bodied races on islands and small mammals tend to evolve large-bodied ones. Large mammals probably suffer more strongly from overpopulation and share its burdens more equally among age classes.

Artiodactyls typically form dwarf races on islands (Foster 1965); they also typically deplete their food resources when isolated on islands in the absence of predation. Klein (1965), for example, found that the smaller body size of the black-tailed deer (Odocoileus hemionus) on Coronation than on Warren Island in Alaska is a phenotypic response to general undernourishment of the population resulting, in part, from overgrazing. Coronation Island has no wolves and few human hunters; Warren has both predators. Fenced populations of the roe deer (Capreolus capreolus) in Denmark peaked and crashed like Krebs, Keller, and Tamarin's (1969) fenced vole populations; the population was directly controlled by food supply, which was in turn reduced by the continued presence of the deer (cited but not documented

in Klein and Strandgaard (1972)). This resulted in overbrowsing and forest damage by the deer, high winter mortality from starvation, small body size, and lowered reproductive productivity. The population of dwarf Soay sheep on St. Kilda Island regularly reaches densities too great to survive low winter resource levels, and young and old alike suffer chronic yearly starvation (Milner and Gwynne 1974). The story of chronic overpopulation and starvation of the moose (Alces alces) of Isle Royale in Lake Superior, and subsequent relief from this condition after the arrival of wolves to that island, is well known (Mech 1966). Sondaar (1977) reports that bone beds of an extinct endemic dwarf race of deer on Crete show evidence (osteoporosis) of mass starvation at that location. He suggests overpopulation as a mechanism for the dwarfing of deer, elephants, and hippopotami on islands in the Mediterranean. We may conjecture that universal starvation and pressure for phenotypic decrease in body size is probably accompanied by selection pressure for reproductive maturity at small size as a genotypic adaptation.

The J/A hypothesis agrees with Case's (1978) prediction that territoriality or aggressiveness over food should favor selection for large body size in an island population, whereas lack of such aggressiveness should favor body-size decrease. However, the reasoning behind the prediction is different from Case's in that a) Case postulates an intrinsic increase in fitness with increased body size but I do not, and b) Case predicts that if the ratio of food supply to food demand (S/D) at population equilibrium is greater on the island, then body size should increase, and if S/D is lower on the island then size should decrease. From this he infers his prediction concerning territoriality and insular body-size evolution. The J/A hypothesis predicts that the overall S/D ratio is, for a number of reasons, likely to be lower for island than for mainland populations, and that body size evolves in response not to total population S/D, but to the relative distribution of resources, especially food, between juvenile and adult age classes. Territoriality is predicted to favor selection for large size on islands insofar as it effects a decrease in juvenile survivorship and recruitment while maintaining that of adults relative to the mainland population. The absence of territoriality, on the other hand, is predicted to favor decrease in body size on islands insofar as this implies a relatively equal distribution of the effects of food scarcity among juveniles and adults alike.

The J/A hypothesis would thus predict that Peromyscus maniculatus cancrivorus, the exceptionally small-sized race from Table Island, has evolved small size because food scarcity is greater on this island and because the unusual structure of the island noted by McCabe and Cowan (1945) favors equal distribution of available food between juveniles and adults. Certainly, the lack of sandy beaches and easy access to the shoreline, which is the primary habitat of Peromyscus in the islands of this study, could make Table Island a poorer, less heterogeneous environment relative to other islands. The same explanation may apply to other island animals such as foxes which, though territorial, tend to decrease in size on islands (Case 1978).

The J/A hypothesis may also account for non-linear relationships of body size to island area such as the one described by Heany (1978) for island populations of the tricolored squirrel, Callosciurus prevosti, of southeast Asia. The populations first show an increase in body size as island area decreases, reach a maximum size, and then progressively decrease in size with further area decrease. The point of maximum body size may represent a critical island area at which the various factors affecting juvenile and adult survivorship rates, and the selection pressures on longevity and body size that these produce, balance each other out.

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