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DIFFERENTIAL DIAGNOSTICS OF ISLAND RODENT POPULATIONS

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Abstract. The cause of increased densities, survival, and body size and decreased reproductive output of rodents isolated on islands was explored by constructing a series of models. Qualitative methods of signed digraphs and time averaging were used to examine the correlation pattern among resource level, population density, individual body size, reproductive output, and predation. Data collected from two species of rodents in Massachusetts were compared with the models. The models suggest that the explanation for characteristics exhibited by island rodent populations lies in the structure of the interrelations among the variables included in the model. Specifically, patterns on islands may be accounted for if the differences between locations are due to differences originating at the predation level when predators are present and at the density level in the absence of predators. The most likely pathway for such an effect is "predation reduces density, density reduces reproductive effort, and reproductive effort reduces body size". While the conclusions are specific to rodent populations, the method has broader application and provides the first step toward developing a diagnostic key to population dynamics..

Introduction

Populations of rodents isolated on islands often show morphological, demographic, and behavioral differences when compared to mainland populations (e.g., Foster 1964, Tamarin 1978, Gliwicz 1980, Williamson 1981, Lomolino 1985, Stamps and Buechner 1985). These differences include higher and more stable densities, better survival, increased body size, and reduced dispersal, reproductive output, and aggression. Population density is predicted to vary along gradients of island isolation and size (Adler *et al.* 1986, Adler and Wilson 1989). Increasing isolation may increase density by limiting dispersal and thereby creating a 'fence effect' (e.g., Tamarin 1978). Densities may increase with isolation until the probability of successful dispersal is negligible. The effect of isolation is offset by increasing island area as an island approaches the realm of a mainland (MacArthur 1972, Adler *et al.* 1986). This area effect is less direct and may be due to increases in the diversity of habitats, competitors, or predators.

Differences in habitat diversity alone are apparently not sufficient to account for increased densities on islands (e.g., Tamarin 1978). In rodent communities comprised of only a few morphologically and trophically divergent species, competitive effects may also not be sufficiently powerful to account fully for increased island densities; in such communities, predation may play a more focal role, although the mechanism remains obscure. In this paper, we construct a series of models to examine mechanisms by which predation might affect rodent populations and contribute to demographic differences among island and mainland populations.

Our attempt here is to integrate more fully the plausible explanations for population-level characteristics into patterns of interaction that might explain the entire suite of island rodent population characteristics, the observed patterns on different islands, and more generally the structure of population dynamics in rodents. The phenomena to be explained in relation to islands are shown in Table 1. We approach their explanation with two kinds of models, signed digraphs and time averaging (Levins 1974, 1975, Puccia and Levins 1985). Signed digraphs apply strictly to the differences among the equilibrium levels of different populations and, with some modification, to average values. This method therefore assumes that the variables are at equilibrium or at a moving equilibrium. Time averaging is applicable to temporal patterns of populations as well as to average spatial differences and does not assume that the system is in equilibrium. This method examines average values, variability, and covariance. Fortunately, the predictions of the two approaches are almost identical. We also illustrate the utility of the approach as a step toward constructing diagnostic keys for population dynamics.

Table 1. Characteristics of island rodents to be explained in this paper.

Trait	Pattern on islands
Population density	Higher
Individual body size	Greater
Reproductive output	Reduced, either through lower proportion of individuals breeding, greater age at sexual maturity, smaller litter sizes, or shortened breeding seasons
Survival rate	Higher

Theory and methods

Signed digraphs

With signed digraphs, we want to predict the changes in the equilibrium values of each variable in the system due to a change in parameters. Variables are included because they are direct objects of interest, because they have been observed and are to be accounted for, or because their role is speculative and we want to determine their impact. We have deliberately chosen variables at the individual level (fecundity and body size) as well as at the population level (population densities of predators and their prey and abundance of food) because we see explanation as residing not in only one level but in the interactions within and among levels (e.g., Akçakaya 1992). Only those variables are included that appear to act directly on other variables of the system.

The edges of the graph are the interactions between variables; they are identified only by sign since the direction of impact is much more accessible than the mathematical form of that impact. In mathematical terms, the sign of the link from X_j to X_i is $\partial(dX_i/dt)/\partial X_j$ taken at equilibrium, i.e., the familiar alphas of two-species models. These signs are usually obvious from the proposed biology; for example, the direct impact of food is to increase consumer density, but the direct effect of consumer density is to decrease the food supply. There may be other effects as well, by way of other variables and links.

One kind of link that is not always obvious is the loop from a variable to itself, the presence or absence of self-damping. Since the definition of this link is the same as for other links, we can return to the original equation when in doubt. If a variable is the product of some other variables rather than self- reproducing, its equation would be of the form

$$dX/dt=P-f(X,Y,Z...)$$

where P, the rate of production, does not include X. F(X) might simply be rX. In any case,

$$(dX/dt)/\partial X=-\partial f/\partial X.$$

If removal (use, mortality, emigration) increases with numbers, then there is a self-damping link. However, if the variable is self-reproducing, with an equation of the form

$$dX/dt=Xf(Y,Z,...),$$

then $\partial(dX/dt)/\partial X=f(Y,Z...)$, which is zero at equilibrium. Thus, simple self-reproduction is not self-damped, but if direct density-dependent regulation occurs, then

$$(dX/dt)/\partial X=X\partial f(X,Y,Z...)/\partial X,$$

which is negative whenever increased density reduces the rate of growth of the population. This negative relationship could occur if emigration or mortality increase with density or if reproduction decreases.

Immigration to a local population also has the effect of contributing to self-damping. Assume a simple self-reproducing population as before, but add an immigration term:

$$dX/dt=Xf(Y,/Z...)+m.$$

Then $\partial(dX/dt)\partial X=f(Y,Z...)$, but since this equation is evaluated at equilibrium, when $dX/dt=0$,

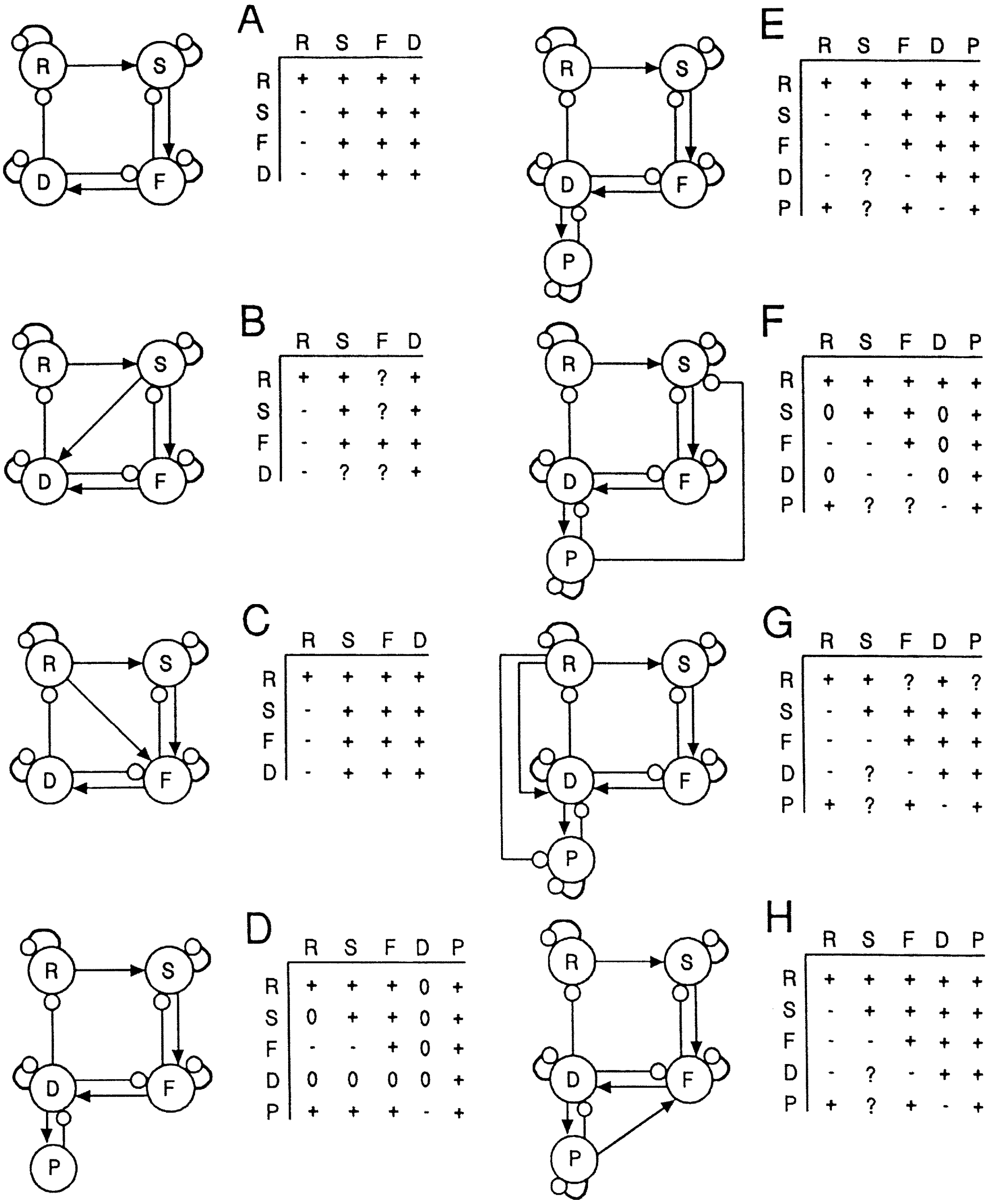
$$f(Y,Z...)=-m/X.$$

Thus, the self-damping attributed to immigration is the proportion of the population that is made up of new immigrants. Random emigration, which is simply proportional to density, does not contribute to self-damping. Finally, we note that a variable may be self-regulating by way of other variables such as the food supply. If these other variables are included in the diagram, then no additional self-damping is needed for the model. However, if the other variables are not included, then there would be a self-damping term. Thus, the presence or absence of self-damping is not a simple fact of nature but rather depends on the model.

Digraph development

What follows is a preliminary foray into the systematizing of dynamic characteristics of populations with the aim of accounting for the suite of characteristics observed in island rodent populations. Our strategy is to present an array of models with a common core structure but differing in some links or variables. For each model, we find the direction of change in the equilibrium level of a variable in response to an input entering the system via each of the variables. For a model with n variables, there will be n^2 predicted outcomes, each indicated by a +, -, or 0. There will also be $n(n-1)/2$ correlations among the variables. We work with the signs of these correlations if they differ from zero.

We include the following 15 links in the models (Fig. 1). Links 1 through 8 appear in the simplest model (Fig. 1A) and comprise the core structure of the remaining seven models.



A

	R	S	F	D
R	+	+	+	+
S	-	+	+	+
F	-	+	+	+
D	-	+	+	+

B

	R	S	F	D
R	+	+	?	+
S	-	+	?	+
F	-	+	+	+
D	-	?	?	+

C

	R	S	F	D
R	+	+	+	+
S	-	+	+	+
F	-	+	+	+
D	-	+	+	+

D

	R	S	F	D	P
R	+	+	+	0	+
S	0	+	+	0	+
F	-	-	+	0	+
D	0	0	0	0	+
P	+	+	+	-	+

E

	R	S	F	D	P
R	+	+	+	+	+
S	-	+	+	+	+
F	-	-	+	+	+
D	-	?	-	+	+
P	+	?	+	-	+

F

	R	S	F	D	P
R	+	+	+	+	+
S	0	+	+	0	+
F	-	-	+	0	+
D	0	-	-	0	+
P	+	?	?	-	+

G

	R	S	F	D	P
R	+	+	?	+	?
S	-	+	+	+	+
F	-	-	+	+	+
D	-	?	-	+	+
P	+	?	+	-	+

H

	R	S	F	D	P
R	+	+	+	+	+
S	-	+	+	+	+
F	-	-	+	+	+
D	-	?	-	+	+
P	+	?	+	-	+

Figure 1. Signed digraphs and predicted responses to inputs through each node. Direct effects are either positive (arrowhead) or negative (small circle). In the tables accompanying the digraphs, each row shows the direction of response of the variables to input entering the system by way of the designated variable. Each column shows the full range of responses of the designated variable to all inputs. A. Core model with food resource (R), body size (S), reproductive effort or fecundity (F), and population density (D). B. Body size increases density directly by increasing survivorship in extreme conditions. C. Reproductive effort is increased by resource abundance. D. A predator that is not self-damped is added. E. The predator is self-damped due to its own density-dependence, immigration from outside the target population's area, or exploitation of an alternative resource that is not included in the graph. F. The predator reduces body size either by producing a younger population or by selective predation. G. Food resource reduces predation and therefore increases density because it reduces the search time for food, during which animals are vulnerable to predators. H. Predation increases fecundity by culling weaker animals.

1. *Density reduces the food supply.* That is, animals eat their food. Although this statement seems obvious, it is also possible that cropping by a herbivore stimulates new growth and actually increases the food supply.

2. *Abundant food increases the body size of adults.* Captured energy and nutrients may be used for growth, bodily storage, or reproduction, but usually all three occur (although in different proportions in different kinds of animals).

3. *Large body size increases fecundity.* This increase will be the case only when animals are mature and in breeding condition but is a reasonable hypothesis.

4. *Fecundity increases density, i.e., more reproduction produces more individuals.*

5. *Fecundity reduces body size.* This reduction may come about directly insofar as fecundity is expressed in litter size since animals from larger litters tend to be smaller. If fecundity is expressed mainly by the proportion of pregnant adult females, but with litter size invariant, then fecundity may affect body size by reducing the food supply since gestation and lactation increase the demand for food per adult. If such is the case, then we would introduce a negative path from fecundity to food resource.

6. *Density reduces fecundity.* This link is one pathway of self- regulation. Its mechanism may be a reduction in either the proportion of adults that breed at any one time or in litter size (e.g., Schaffer and Tamarin 1973). The mechanism may operate uniformly in all populations or it may have been intensified by selection in some populations. In any case, there is a negative input to fecundity.

7. *The food supply, body size, and fecundity are self-damped.* None of these variables is simply self-reproducing.

8. *Density may be self-damped if there are processes at work other than by way of the food supply, predators, or fecundity.* For instance, if high density increases emigration or if territorial exclusion reduces survival at high densities, then density will be treated as self-damped.

9. *Body size might increase density directly (not through fecundity) if large animals survive harsh conditions better than smaller individuals* (Fig. 1B). Similarly, large body size may confer a competitive advantage among conspecifics (Corbet 1961).

10. *Abundant food or rapid growth of the food may have the direct physiological effect of increasing fecundity* (Fig 1C). This effect also could occur if substances in the food supply stimulate the reproductive endocrines of the females (e.g., Negus and Berger 1977, Berger *et al.* 1977, 1981 for *Microtus*).

11. *Predators reduce the density of their prey and are increased by prey density* (Fig. 1D). This link is the straightforward meaning of predation.

12. *The predators may be self-damped if they have their own density regulation, immigrate to the population from outside, or have alternative resources* (Fig. 1E). Highly mobile predators would be more self-damped. Models F through H also include a self-damped predator.

13. *Predation may reduce body size* (Fig. 1F). If predators preferentially utilize larger prey or if growth continues throughout life so that predation produces a younger population that is smaller, then there will be a direct negative link from predators to size.

14. *The food supply may reduce predation if the time spent searching for food is also the time of greatest vulnerability to predators* (Fig. 1G). This effect may turn out to be more operative than the food-to-size link if there is always enough food available, providing the animal searches long enough. If this path is present, then there will also be a direct positive path from food to density because of increased survival.

15. *Predators may increase fecundity* (Fig. 1H). This increase would come about if predation culls weaker animals and leaves a population with a higher reproductive potential and would result in a positive link in the graph from predators to fecundity. This increase could also occur if animals respond to reduced density by increasing their reproductive output (see link 6).

Digraph limitations

The question arises as to whether these models and their links are complete and realistic. Since we do not specify the forms of the equations, the only assumptions that are made about the interactions between variables are their directions and signs. The digraph may be mistaken in that a link is included that is not operative. If removing that link changes the predictions, it would be detected; if it has no effect or only reinforces the effects of other pathways, then it could be detected only by direct observation or by experimentally removing the other links that have the same effect. For example, a direct negative link from fecundity to food supply reduces body size and food level in the same way as the path from fecundity to density to food supply. If there is a predator that is not self-damped, then the path through density will have no effect and the direct fecundity-food path will have an effect. If there is no predator but density is not self-damped, then the fecundity-food path has no effect. Finally, if both density and predator are self- damped, then the fecundity-food path would not be separable from the fecundity-density-food path.

We may also have omitted important variables such as other species. If there are such other variables of importance, they affect the variables of interest only by providing some input to one or another variable of the system. For example, a competitor may remove food, which would impact the system in the same way that other conditions such as weather affect the food supply, or the competitor may compete for space and thereby act as a negative input directly to density. Therefore, for the purposes of this analysis, missing variables provide additional inputs. At first, this conclusion is puzzling; it seems to suggest that even the simplest models are adequate, but when a variable is omitted its reciprocal interaction is lost. An omission not only affects the variables of interest but is also affected by them. Therefore, an input is not an arbitrary forcing function from outside but a part of the dynamics.

The proposed diagrams do not pretend to include everything that affects population dynamics; rather, we claim that all other factors act by way of the identified variables and can be included as inputs to the system through those variables. In general, the simpler the digraph the more boundaries it has over which seemingly arbitrary inputs may enter. As we expand the model, processes are included in the system that are more amenable to analysis. The models we present here are complete in the sense that everything that is omitted can be dealt with as inputs through one or another of the variables.

Determining outcomes

We have an input to a variable whenever a parameter in the equation for that variable is altered. The sign of an input to a variable due to change in parameter C is the sign of $\partial(dX/dt)/\partial C$, that is, the direction in which the parameter affects the rate of change of the variable in whose equation it appears.

The object of interest in the models then, is the impact on the equilibrium level of each variable in response to inputs entering the community by way of each variable. For the models we construct, the sign of the impact may be found as follows. Multiply the signs of all the links along the path from the variable where the input enters the system to the variable whose change we want to find. Next, erase the path and examine the remaining system. If there are any variables that are not self- damped and are isolated from two-way interaction with the rest of the system when the path is removed, then this path has no effect. Otherwise, the effect of the path has the sign of the product of its links. If there is more than one path from the point of input to the variable studied, the effects of all the paths must be added. If different paths between the same two variables have different signs, then the impact is ambiguous and semi-quantitative arguments may be used.

Time averaging

Survival, an important parameter in the rodent system under consideration, is not a variable in the digraphs. Increased survival in island populations may be a consequence of reduced predation, but since "survival" is studied generally through recapture or resighting, it really means non-removal from that population either by death or emigration. The ratio of young to adults might be inferred from reduced fecundity and higher adult survival. This young/adult ratio is also not a variable of the models. If reproductive effort had been reduced in the past and adult survival increased (as often happens in island populations), then this ratio would be lowered. However, if reproduction and survival both decreased or both increased, then we could not predict the effect on this ratio. Since the ratio of young to adults is a consequence of past reproduction, it does not lead directly to conclusions about current reproductive effort. Nevertheless, with time-averaging this ratio becomes important as a way of finding the correlation between survival and adult density.

With time averaging, we examine the expected covariance between density and survival based on the ratio of young to adults. We use the expectation operator E[.] to average and simplify relationships among these variables. The expectation operator may be applied to any differential equation just as more familiar operators such as logarithms are applied (Puccia and Levins 1985). Time averaging is applicable because the long-term average or expected value of the derivative of a bounded variable is zero (Puccia and Levins 1985), and because the ratio of averages of two variables often differs widely from the average ratio of those variables (Lewontin and Levins 1989).

Empirical testing

Correlation patterns provided by the digraph models were compared with the pattern of Table 1 in order to identify relevant links and pathways. Predictions of the time averaging model were compared with data collected from island and mainland populations of *Peromyscus leucopus* (the white-footed mouse) and *Microtus pennsylvanicus* (the meadow vole) in coastal Massachusetts (Adler 1985, Adler and Wilson 1987, Adler *et al.* 1987, Seamon and Adler, unpublished data). Data were collected by monthly or biweekly livetrapping over a two- to five-year period on grids placed within forest or grassland. Grids consisted of a 7X7 matrix of trap stations spaced at either 7.6 m or 10 m. Each station of the grids was occupied by a single Longworth livetrap, and traps were set for 2 consecutive nights and checked on subsequent mornings each sampling period. All captured rodents were ear- tagged with numbered metal tags, weighed, and sexed, and reproductive condition was noted before release at the point of capture. Ratios of young to adults were calculated for each population. Since both species bred seasonally, we included data collected only during breeding seasons; during nonbreeding periods, the ratio of young to adults was 0. The covariance between density and adult body mass was also calculated for each population to compare with the digraph predictions. We included in this analysis only adult males to eliminate error associated with undetected pregnancies in females. Body mass was represented by either the mean mass of adults in a sampling period or by the mass of the largest individual in a given sampling period.

Results

Signed digraphs

The impact on the equilibrium level of each variable in response to inputs are shown in the tables accompanying the digraphs of Fig. 1. In these tables, we follow the convention that the input is always positive; if the parameter is decreased instead of increased, the signs would be reversed. In some cases, we know the direction of an input. For instance, we may know that food is more available in some locations; the tables then make direct predictions about what we might observe, but in other cases we do not know the signs of all the inputs. The point of interest is whether the impacts on two variables have the same or opposite signs and therefore are predicted to have positive or negative correlations. The models all make either 16 or 25 predictions for the impact of positive inputs, depending upon whether or not there is a predator present.

The different models have both consistent and inconsistent predictions. For example, they all agree that positive inputs to variables R, S, and P increase those variables; that input to R increases S; and that input to P reduces D but increases R. The increase of a variable in response to its own input makes sense but is not universal. If there were positive feedback in the system, then input to a variable could actually result in its decline. In some cases, the predictions are ambiguous because different pathways have opposite signs. For instance, the effect of predation on density is negative in most cases, but when we allow a positive link from predation to fecundity (link 15, Fig. 1H) we have an ambiguity arising since now predation increases density via fecundity while reducing density directly; however, the effect of predation on body size may be positive by the pathway "predation reduces density, increases food supply, increases body size" or negative by the pathway "predation reduces density, increases fecundity, reduces sizes in large litters". The effect of inputs to density on body size are ambiguous in all models with predators except with undamped predators (Fig. 1D, where the impact is zero) and where predators reduce body size directly (Fig. 1F).

Time averaging

The relation of survival to density as determined through time averaging yields the following results. Suppose that the numbers of young and of adults change according to the equations

$$dY/dt=fA-(d+m_1)Y$$

and

$$dA/dt=dY-m_2A$$

where f is fecundity, d is the development rate of the young (the reciprocal of the time to maturation), and m_1 and m_2 are the mortalities of young (Y) and adults (A). Since we have not specified anything about these parameters, the equations as written are complete. We ignore the first equation, in which fecundity and young mortality may depend on density and external conditions. In the second equation, assume only that the age to maturity is constant and that adult mortality can vary for intrinsic or extrinsic reasons.

Taking the expected values of the equation, we get

$$dE[Y]-E[m_2]E[A]-Cov(m_2,A)=0$$

where $E[m_2]$ and $E[A]$ denote expected values of (m_2) and A and $Cov(m_2,A)$ is their covariance. Now divide by $dE[A]$ to get

$$E[Y]/E[A]=E[m_2]/d-Cov(m_2,A/dE[A].$$

Return to the original equation and divide by A. Thus,

$$(dA/dt)/A=dY/A-m_2.$$

Since the left side is the derivative of the natural log of A, as long as A is never zero, its expected value is zero. Thus,

$$E[Y/A]=E[m_2]/d.$$

Comparing the two, we see that if $E[Y/A] > E[Y]/E[A]$, then the covariance of mortality with density is negative and the covariance of adult survival with density is positive. This result will be the case if the external inputs enter the system through predation; a negative correlation of predation with density will result in a positive correlation of survival with density. It is also possible that survival is enhanced by body size increasing the tolerance to weather conditions or intraspecific competition; then there would be positive correlations among size, survival, and density.

Empirical results

The models predict that the positive correlations among density, survival, and body size should prevail both among populations and within populations that vary temporally. In comparing these predictions with the actual field data, the ratio $E[Y/A] > E[Y]/E[A]$ in 42 out of 52 cases, ranging from 57% of populations for *M. pennsylvanicus* males to 95% of populations for *P. leucopus* females (Table 2). Thus, for the majority of cases adult survival is correlated positively with density over time within both island and mainland populations.

The positive temporal correlation of density with body size predicted in the models was examined for *P. leucopus* and *M. pennsylvanicus* across years and populations by calculating covariances of body mass with density. Both species displayed a general trend toward a positive body size-density correlation over time within both island and mainland populations (Table 3). This trend was more evident when entire

Table 2. Average ratios, E[Y/A], and ratios of the averages, E[Y]/E[A], of young and adults in populations of two species of rodents in eastern Massachusetts. Site numbers are our own designations for different study sites. Sites were omitted from analysis if they were sampled for less than 2 years, had very few individuals, or were manipulated (hence the missing site numbers). * indicates island sites where typical island characteristics were strongly evident.

Site Number	Years Sampled	E[Y/A] Males	E[Y/A] Females	E[Y]/E[A] Males	E[Y]/E[A] Females
		Peromyscus leucopus			
3	5	0.53	0.41	0.33	0.30
19	5	0.58	0.29	0.37	0.22
20	5	0.25	0.41	0.15	0.33
21	5	0.15	0.41	0.15	0.34
22	5	0.34	0.28	0.26	0.23
23*	3	0.89	1.38	0.46	0.83
24	3	0.60	1.63	0.63	0.95
30	3	0.17	0.69	0.24	0.67
32	3	0.73	0.73	0.67	0.63
33	3	1.00	0.81	0.59	0.74
34	3	0.39	0.87	0.24	0.62
36	3	0.52	0.27	0.33	0.22
37	3	0.41	0.77	0.37	0.68
38	3	0.54	0.55	0.38	0.42
39	3	0.63	0.48	0.56	0.53
40	2	0.49	1.16	0.33	0.95
41	2	0.31	1.25	0.33	0.77
43	4	0.80	0.40	0.55	0.26
44*	4	0.40	0.37	0.31	0.35
		Microtus pennsylvanicus			
1	4	0.45	0.60	0.50	0.43
3	5	0.06	0.24	0.05	0.16
5*	5	0.28	0.19	0.33	0.21
22	5	0.57	0.55	0.52	0.46
42	4	0.69	0.74	0.61	0.33
43	4	0.12	0.77	0.13	0.54
44*	4	0.68	0.21	0.49	0.23

Table 3. Summary of covariances of body mass (mean and maximum) and density over years and populations for two species of rodents in eastern Massachusetts.

Species	Years			Populations		
	Number of covariances that are:					
	+	-	0	+	-	0
	Mean body mass					
P. leucopus	44	23	0	15	4	0
M. pennsylvanicus	19	12	0	5	2	0
	Maximum body mass					
P. leucopus	47	19	1	16	3	0
M. pennsylvanicus	24	7	0	7	0	0

populations were considered than when populations were subdivided yearly. The correlation became even stronger when body size was expressed as maximum body mass, reaching 100% positive covariances for *M. pennsylvanicus* populations. The field data therefore conform closely with the predictions of the models.

Discussion

We consider four characteristics of island rodent populations (density, body size, fecundity, and survival) and their relationships within the framework of the models.

1. *Population density and body size are positively correlated.* If there is an undamped predator (Fig. 1D), then density does not respond to inputs from food, size, fecundity, or density; none of these links could produce the positive correlation. An input to the predator has an ambiguous response from body size but will give a positive correlation if the pathway D--oF--oS predominates over the pathway D--oR-->S. If P is self-damped (Figs. 1E to 1H), then inputs to R or S would always give the positive correlation, and inputs to D or P could result in positive or negative correlations between size and density.

2. *Density is negatively correlated with fecundity.* This relationship requires that the impact follows the negative link from density toward fecundity. Inputs from R and S would produce positive correlations or none at all. The source of the input could be directly at density from predators or from food to density to fecundity. If there is size-selective predation, then the D-->P--oS-->F pathway (Fig. 1F) would generate a negative correlation between density and fecundity and between density and size.

3. *There is a positive correlation between survival and adult density.* If mortality is due to predation, then a negative correlation between predators and density would have this effect. If survival is favored by body size, then input to S would produce a positive relation between density and survival. However, this pathway S-->D--oF must be stronger than the S-- >F-->D pathway in order to prevent a positive correlation with F. The size-to-density effect would respond to inputs to R or S. The pathways that start from below, reaching P through D (Figs. 1D to 1H), all generate a positive correlation between D and P and therefore a negative correlation of D with predation-induced mortality.

These models show that four major features of island rodent populations may be accounted for jointly if the differences between locations are due to differences originating at the predation level when predators are present and at the density level in the absence of predators. The relevant pathway is "predation reduces density, density reduces reproductive effort, reproductive effort reduces body size". Differences in food supply or genetic changes for body size or for fecundity would produce discordant results. We do not imply these changes do not occur, only that they do not account for the observed pattern. Thus, while initial changes in body size may not be genetically determined, selection over time may favor large body size (Corbet 1961). The model assumes a negative pathway from fecundity to body size. This relationship could arise if reduced reproductive effort in larger island animals is expressed as reduced litter size. However, if it is mostly a matter of fewer pregnancies, each of the same size, another pathway must be found. Since gestation and lactation increase the demand for food, there may be a direct negative link from fecundity to food resource. Alternatively, females during these activities may be more vulnerable to predation, which could give a negative correlation of fecundity with body size but would also increase the proportion of males when reproductive effort is high. The models also predict the observed positive correlation of survival with body size and with density. The trend of large body size in populations of microtine rodents approaching peak densities is well documented (e.g., Chitty 1967, Krebs 1978) and, together with the data in Table 3, lends further support for the hypothesized pathway.

The tables of Fig. 1 predict other correlations as well. For instance, density should be correlated negatively with food supply except when there is an undamped predator, and predation should be correlated positively with food supply. This relationship could have a stabilizing effect on populations since the dangers of food shortage and predation occur out of phase with each other. Since most population-level studies lack concurrent data on food supply and predation intensity, these two aspects should become major issues for further research.

In summary, characteristics of island rodents may be interpreted by models that predict the correlation pattern among population and ecological characteristics. The positive density-body size and density-adult survival correlations and the negative correlation between density and fecundity support the hypothesis that the observed differences among the variables of the model are caused by some external parameters that enter the system via density. The external factors that enter the system are not determined by the model but from the biogeography; insularity operates on resident populations through isolation and area limits. The explanation we offer for characteristics of island rodents lies in the structure of the interrelations among resource level, population density, individual body size, reproductive output, and predation, with the intensity or absence of predation serving as a principle differentiating factor.

The specific conclusions we have reached here are intended to apply to insular rodent populations, but the method has broader application and is intended as a step toward developing a diagnostic key to population dynamics. Such a key could not be limited to the population variables themselves, since that approach would treat all members of the population as interchangeable and the driving parameters of fecundity and mortality as arbitrarily determined externalities. An analysis of population dynamics also requires the inclusion of biological properties of individuals such as body size, nutritional status, temperature acclimation, migration probability, and fecundity. Community-level variables such as the descriptors of other populations related by predation, mutualism, competition, or parasitism must also be considered. Thus, population numbers constitute too narrow a base from which to interpret patterns of population dynamics. Larger models, however, that include individual-, population-, and community-level descriptors may provide many predictions for testing. Depending upon study organism, the particular characteristics used in the diagnosis may not be the same, but the method may still be applied.

Not all these kinds of information are available in all systems. Therefore, the key would not be organized as a morphological key with a fixed branching sequence of decisions. Instead, the key would be in a matrix form in which the investigator could choose the categories appropriate to the study system. The correlation patterns among variables are indicators of the structure of the processes of interest. If the dynamics of a population are driven from below by resource availability, then there is likely to be a positive correlation between resource and consumer; if driven from above by predation, the correlation will be negative (as in Fig. 1, with the relation of predator and density or density and food supply). If there is more than one resource, the one more sensitive to the environment may be correlated positively with the consumer, while the more stable resource will be negatively correlated. In the present study, inferences are drawn from the correlations among observed population density, body size, reproductive effort, and survival. Our models also call attention to correlations that are not available, such as those with food supply or predation. This study is a first attempt at a systematic strategy for designing diagnostic matrices for population dynamics.

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REFERENCES

Adler, G. H. 1985. Habitat selection and species interactions: an experimental analysis with small mammal populations. Oikos 45:380-390.

Adler, G. H. and M. L. Wilson. 1987. Demography of a habitat generalist, the white-footed mouse, in a heterogeneous environment. Ecology 68:1785-1796.

Adler, G. H. and M. L. Wilson. 1989. Insular distributions of voles and shrews: the rescue effect and implications for species cooccurrence patterns. Coenoses 4:69-72.

Adler, G. H., M. L. Wilson, and M. J. DeRosa. 1986. Influence of island area and isolation on population characteristics of *Peromyscus leucopus*. Journal of Mammalogy 67:406-409.

Adler, G. H., M. L. Wilson, and M. J. DeRosa. 1987. Effects of adults on survival and recruitment of *Peromyscus leucopus*. Canadian Journal of Zoology 65:2519-2523.

Akçakaya, H. R. 1992. Population cycles of mammals: evidence for a ratio-dependent predation hypothesis. Ecological Monographs 62:119-142.

Berger, P. J., N. C. Negus, E. H. Sanders and P. D. Gardner. 1981. Chemical triggering of reproduction in *Microtus montanus*. Science 214:69-70.

Berger, P. J., E. H. Sanders, P. D. Gardner and N. C. Negus. 1977. Phenolic plant compounds functioning as reproductive inhibitors in *Microtus montanus*. Science 195:575-577.

Chitty, D. 1967. The natural selection of self-regulating behaviour in animal populations. Proceedings of the Ecological Society of Australia 2:54-78.

Corbet, G. B. 1961. Origin of the insular races of small mammals and the "Lusitanian" fauna. Nature, London 191:1037-1040.

Foster, J. B. 1964. Evolution of mammals on islands. Nature, London 202:234-235.

Gliwicz, J. 1980. Island populations of rodents: their organization and functioning. Biological Review 55:109-138.

Krebs, C. J. 1978. A review of the Chitty Hypothesis of population regulation. Canadian Journal of Zoology 56:2463- 2480.

Levins, R. 1974. Qualitative analysis of partially specified systems. Annals of the New York Academy of Sciences 231:123-138.

Levins, R. 1975. Evolution in communities near equilibrium. Pages 16-50 in M. L. Cody and J. M. Diamond (eds.). Ecology and evolution of communities. Harvard University Press, Cambridge, MA, USA.

Lewontin, R. C. and R. Levins. 1989. On the characterization of density and resource availability. American Naturalist 134:513-524.

Lomolino, M. V. 1985. Body size of mammals on islands: the island rule re-examined. American Naturalist 125:310-316.

MacArthur, R. H. 1972. Geographical ecology. Harper and Row, New York, NY, USA.

Negus, N. C. and P. J. Berger. 1977. Experimental triggering of reproduction in a natural population of *Microtus montanus*. Science 196:230-231.

Puccia, C. J. and R. Levins. 1985. Qualitative modeling of complex systems: an introduction to loop analysis and time averaging. Harvard University Press, Cambridge, MA, USA.

Schaffer, W. M. and R. H. Tamarin. 1973. Changing reproductive rates and population cycles in lemmings and voles. Evolution 27:111-124.

Stamps, J. A. and M. Buechner. 1985. The territorial defense hypothesis and the ecology of insular vertebrates. Quarterly Review of Biology 60:155-181.

Tamarin, R. H. 1978. Dispersal, population regulation, and K-selection in field mice. American Naturalist 112:545-555.

Williamson, M. 1981. Island populations. Oxford University Press, Oxford, UK.

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