COENOSES 4 (2): 69-72, 1989

INSULAR DISTRIBUTIONS OF VOLES AND SHREWS: THE RESCUE EFFECT AND IMPLICATIONS FOR SPECIES CO-OCCURRENCE PATTERNS

G.H. Adler, Department of Population Sciences, Harvard School of Public Health, 665 Huntington Avenue, Boston, MA 02115
and
M.L. Wilson, Departments of Population Sciences and Tropical Public Health, Harvard School of Public Health, 665 Huntington Avenue, Boston, MA 02115, (Present address: Institut Pasteur, BP 220, Dakar, Senegal)

Keywords: *Blarina brevicauda*, Co-occurrence patterns, Island biogeography, Loop analysis, *Microtus pennsylvanicus*, Population-level interactions, Small mammals

Abstract. Distributional and numerical relationships between the meadow vole *(Microtus pennsylvanicus)* and the short-tailed shrew *(Blarina brevicauda)* on Massachusetts islands were analyzed and found to be inconsistent with previous studies. Population-level interactions between these two species both with and without other variables were qualitatively modeled in order to reconcile inconsistencies. Changes in levels of immigration of *M. pennsylvanicus* to islands can change expectations of coexistence from negative to positive. This rescue effect was apparently powerful enough to alter expected correlations between *M. pennsylvanicus* and *B. brevicauda* on Massachusetts islands.

Introduction

Factors which influence insular co-occurrence patterns currently are receiving considerable study and intense scrutiny (e.g., Connor and Simberloff 1984; Gilpin and Diamond 1984). Most studies have concentrated on competition between closely related taxa, although a few have examined the effects that other interactions might have on insular co-occurrence patterns (reviewed by Harvey 1983). One such interaction is predation. For instance, Lomolino (1984) presented an interesting hypothesis to explain the distributional and numerical patterns of *Microtus pennsylvanicus* (the meadow vole) and *Blarina brevicauda* (the short-tailed shrew) on islands in the St. Lawrence River. He observed that *B. brevicauda* were restricted to islands located near large land masses or to large distant islands, whereas *M. pennsylvanicus*, though more widely distributed than *B. brevicauda*, were more abundant on more distant islands. Vole and shrew densities on islands also were correlated negatively. Experimental introductions of *B. brevicauda* onto small islands inhabited only by *M. pennsylvanicus* reduced the density of the latter. These observations, Lomolino argued, were explained by immigrant selection of the more vagile *M. pennsylvanicus* on the distant islands and its exclusion by the predatory *B. brevicauda* on the less isolated islands.

In a previous study of small mammal distributional patterns on Massachusetts islands, the presence of *B. brevicauda* on 16 of 33 islands surveyed was correlated negatively with isolation (Adler and Wilson 1985), in accordance with Lomolino's observation. In contrast to *B. brevicauda, M. pennsylvanicus* was nearly ubiquitous, being distributed on 32 of 33 islands surveyed. Indeed, we found both species coexisting on tiny (0.1 ha) hummocks in coastal salt marsh. In the present paper, we examine the numerical relationships between *B. brevicauda* and *M. pennsylvanicus* in this study area. We also model the interactions to show how inconsistencies between Lomolino's study and our study can be reconciled and understood within the same theoretical framework.

Materials and methods

Small mammals were sampled by live-trapping on 23 islands located in coastal Essex County, Massachusetts (U.S.A.) in both June and November 1983. Some islands were connected to the mainland by salt marsh at low tide but were isolated completely at high tide (see Adler et al. 1986 for details of these islands). One to three traplines were established along the entire longitudinal axis of each island. Islands of less than 0.6 ha contained only one trapline, whereas larger islands were sampled with two or three traplines spaced approximately 30 m apart. Trap stations within a trapline were located 7.6 m apart. One Longworth live-trap was set at each trap station for two consecutive nights and checked the following mornings. By design, the number of trapnights was highly correlated with island area ($r=0.91$, $P<0.0001$).

We analyzed numerical relationships of *B. brevicauda* and *M. pennsylvanicus* on these intensively sampled islands (Table 1). In order to reduce variance associated with sampling error, we included in the analysis only those islands which were sampled for at least 40 trapnights (five of the 23 intensively sampled islands did not meet this criterion). Such a sampling scheme

Table 1. Physical characteristics of 18 intensively surveyed islands used to examine relationships between relative abundance (DENSITY, measured as the number of individuals captured per 100 trapnights) of *Blarina brevicauda* and *Microtus pennsylvanicus*. Island characteristics are area (total island area in ha), length (total island length in m measured parallel to the mainland (target area of Dueser and Brown 1980)), and shortest linear distance in m to the mainland. Islands designated with a single letter are unnamed. A + designates islands which are isolated permanently from the mainland.

Island	Area	Length	Distance to mainland	Trapnights	Density	
					Blarina	Microtus
A	0.5	72	24	40	5.0	5.0
D	0.7	121	64	48	2.1	2.1
Eagle	9.1	459	24	232	2.2	1.7
F	0.3	89	169	40	5.0	12.5
G	0.3	89	153	48	4.2	0.0
I	0.6	105	282	48	0.0	4.2
J	0.7	97	32	49	4.1	2.0
K	1.4	161	16	76	2.6	3.9
L	0.3	105	86	56	7.1	8.9
Pine	3.3	250	81	152	1.3	3.3
Patterson	1.1	105	298	116	2.6	6.9
O	0.6	56	97	116	2.6	11.2
P	0.3	105	555	48	0.0	10.4+
Smith's	0.8	121	354	80	0.0	11.3+
Nut	2.8	241	402	80	0.0	1.3
Pod	3.0	258	547	156	2.6	3.2
Dean's	2.3	241	918	96	0.0	12.5+
Dilly's	1.4	233	1046	88	0.0	9.1+

should be adequate since as few as 10 trapnights were sufficient to reveal both species on small islands.

Relative abundances of both *B. brevicauda* and *M. pennsylvanicus* on each island were calculated as the total number of individuals captured per 100 trapnights in the June and November samples combined. Relationships between relative abundances of both species and eight variables describing island size, isolation, and physiognomy (area, length, distance to the mainland, distance to the nearest body of land, distance to the nearest larger body of land, the number of sides of the island continually surrounded by open water (maximum = 4), number of major habitat types (maximum = 4), and number of soil types) were examined using Pearson correlation analysis and multiple linear regression analysis ($N = 18$ in all correlations and regressions). Area, length, and the three distance measures were $\log_{10}$ transformed.

In order to explore possible population-level interactions that might explain our results, we utilized Levins' technique of loop analysis for qualitative study of complex systems (Levins 1975; Puccia and Levins 1985). This method produces predictions of correlations among strongly inter-connected populations and permits examination of multiple causal effects under the assumption of dynamic stability for populations in equilibrium or near a moving equilibrium. This method of analysis requires only that the direction of a change in a variable be known rather than the direction and magnitude of change. Finerty (1980) applied loop analysis to the search for factors which may be responsible for population cycles in small mammals, including *M. pennsylvanicus*.

We began this analysis by constructing the simplest model where *B. brevicauda* and *M. pennsylvanicus* were the only variables in the system. We modified this model to include immature *M. pennsylvanicus* as prey of *B. brevicauda* (see Lomolino 1984). Thus, there was no direct link between *B. brevicauda* and adult *M. pennsylvanicus*. More complex loop models of hypothetical interactions among *B. brevicauda*, *M. pennsylvanicus*, common resources, and predators then were constructed and compared for their predictions.

Results

Relative abundance of *B. brevicauda* was correlated negatively with $\log_{10}$ of distance to the mainland ($r = -0.56$, $P = 0.0149$), $\log_{10}$ of distance to the nearest body of land ($r = -0.63$, $P = 0.0053$), $\log_{10}$ of distance to the nearest larger body of land ($r = -0.50$, $P = 0.0340$), and the number of sides of an island continually surrounded by water ($r = -0.67$, $P = 0.0022$). A stepwise regression of relative *B. brevicauda* abundance versus island variables included only the number of sides of an island continually surrounded by water ($\beta = -1.50$). Relative abundance of *M. pennsylvanicus* was correlated positively with $\log_{10}$ of distance to the nearest body of land ($r = 0.65$, $P = 0.0037$). A stepwise regression of relative *M. pennsylvanicus* abundance versus the island variables and relative *B. brevicauda* abundance included $\log_{10}$ of distance to the nearest body of land ($\beta = 5.84$, $t = 4.89$, $P = 0.0002$) and $\log_{10}$ of island area ($\beta = -4.96$, $t = 3.21$, $P = 0.0058$). Correlations between relative *B. brevicauda* or *M. pennsylvanicus* abundances and island variables with observations of zero abundance eliminated similarly showed no negative relationships between *B. brevicauda* and *M. pennsylvanicus*. Similar results were obtained by separate analysis of the June and November samples and by analysis only of islands sampled with more than 50 or more than 100 trapnights.

Mean *M. pennsylvanicus* abundance on islands where *B. brevicauda* was absent was 8.1 ($N = 6$), whereas islands where *B. brevicauda* was present had a mean *M. pennsylvanicus* density of 5.1 ($N = 12$). This relationship, however, could have been due to the greater isolation of the islands without *B. brevicauda*. Those islands permanently isolated from the mainland by standing salt water had a mean *M. pennsylvanicus* density of 10.8 ($N = 4$), whereas those islands not isolated permanently had a mean *M. pennsylvanicus* density of 3.7 ($N = 14$).

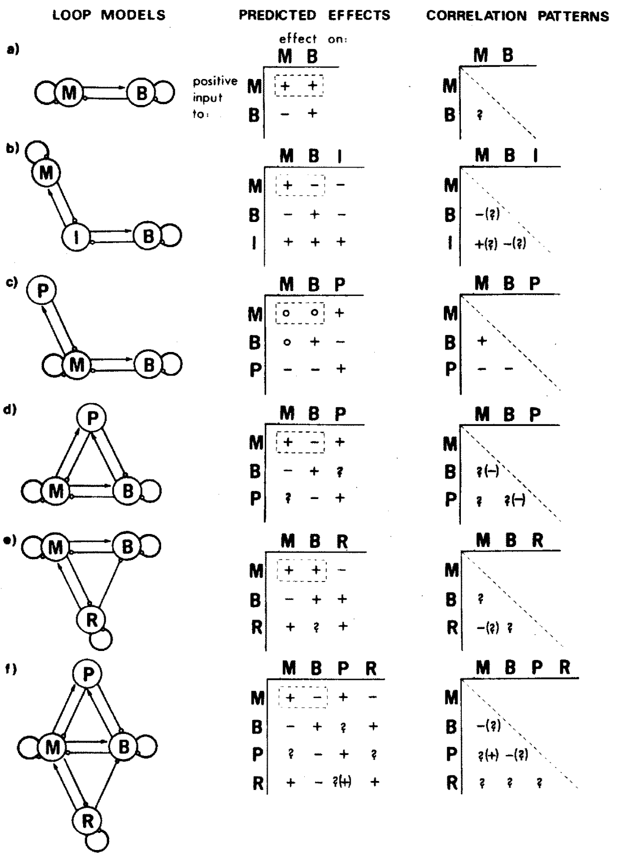

Fig. 1. Hypothetical interactions among populations of *Blarina brevicauda* (B), *Microtus pennsylvanicus* (M), and other organisms shown in six models (a-f, left column), predicted effects of positive inputs to each variable (center column), and associated equilibrium correlation matrices (right column). Other variables include immature *M. pennsylvanicus* (I), a predator (P), and a resource utilized by *M. pennsylvanicus* that inhibits *B. brevicauda* (e.g., habitat degredation). Direct effects are either positive (arrowhead), negative (small circle), or nonexistent (no symbol). Equilibrium correlation is either positive (+), negative (—), or uncertain (?), and where ambiguous the weaker prediction is shown parenthetically.

Comparison of results of the loop models demonstrate that interactions with other variables may produce *Blarina-Microtus* coexistence patterns different than those predicted by Lomolino's hypothesis (Fig. 1). Results of loop analysis indicate that *Blarina-Microtus* correlation patterns depend upon the number and effect of other variables which may be operating. The equilibrium correlation pattern (Fig. 1, right column) of models b and f is negative, yet for model c it is positive, and for models a, d, and e it is ambiguous. Thus, even when the direct effects operating between the two species are identical, the influence of other variables may produce different correlation patterns. Loop analysis suggests that there is no single pattern of coexistence between *M. pennsylvanicus* and *B. brevicauda* and that more complex interactions with other variables may alter the two-species dynamic.

Under conditions where variation enters the system through one variable, the predicted effect on abundance patterns of the two species also may differ. On those islands where immigration (positive input) solely by *M. pennsylvanicus* is proposed, loop analysis demonstrates the importance of other variables in predicting the relationship between *B. brevicauda* and *M. pennsylvanicus*. Models a and e of Fig. 1 (center column) suggest a positive correlation between *M. pennsylvanicus* and *B. brevicauda* (results emboldened in dashed boxes) in the presence of positive input, i.e., immigration of *M. pennsylvanicus* from outside the system. Model c suggests that immigration of *M. pennsylvanicus* would result in unchanged density of either *B. brevicauda* or *M. pennsylvanicus*. Finally, models d and f show a negative correlation between the two species where external effects increase *M. pennsylvanicus* abundance. Thus, abundance of *B. brevicauda* may decline with an increase in *M. pennsylvanicus* through the action of predators.

Discussion

Our analysis of the *Blarina-Microtus* relationship on Massachusetts islands suggested no negative effects of *B. brevicauda* on the distribution or abundance of *M. pennsylvanicus*. This conclusion was robust with respect to sampling scheme since analysis of the June and November samples considered separately and combined and analysis including islands with different minimum sampling efforts (40, 50 and 100 trapnights) yielded similar results. However, *B. brevicauda* may have influenced *M. pennsylvanicus* presence or abundance in other ways. For instance, Lomolino (1984) found niche shifts of *M. pennsylvanicus* on islands not occupied by *B. brevicauda*. Although we did not examine habitat use by *M. pennsylvanicus* on the intensively surveyed islands, it is unlikely that *B. brevicauda* substantially affected habitat use by *M. pennsylvanicus* since both species co-occurred on tiny hummocks with only one major habitat type (grassland). Furthermore, Adler (1985) found no effects of fluctuating *B. brevicauda* densities on temporal patterns of habitat use by *M. pennsylvanicus* on two of the extensively surveyed islands (Great Island and Nantucket), as well as at a mainland site.

Loop analysis suggested several mechanisms by which *B. brevicauda* and *M. pennsylvanicus* could coexist on islands. In particular, changes in levels of immigration might change equilibrium expectations of coexistence from negative to positive even if predation intensity or resource use remained constant. Thus, differences in isolation (and therefore probabilities of immigration) between our islands and those in Lomolino's study could have accounted for our differing results.

A lack of correlation between population abundances of two species does not necessarily imply a lack of interaction (Levins and Puccia 1988). Ease of immigration by *M. pennsylvanicus* to islands near the Massachusetts coast may permit coexistence of *B. brevicauda* and *M. pennsylvanicus* on even the smallest of islands (rescue effect, Brown and Kodric-Brown 1977; or compensatory effect, Lomolino 1986). Such less isolated islands may readily be recolonized by *M. pennsylvanicus*, even if *B. brevicauda* cause their local extinction. Indeed, *M. pennsylvanicus* apparently are not permanent residents on some of the less isolated islands we sampled (Adler and Wilson 1985). By contrast, Lomolino's islands appear to be more isolated (by either distance or magnitude of the isolating barrier), and the probability of recolonization after extinction may be much less than on our islands. Thus, Lomolino's hypothesized association between *B. brevicauda* and *M. pennsylvanicus* may not apply to our island system of lesser isolation if rescue effects compensate for any negative effect of *B. brevicauda* on the distribution and abundance of *M. pennsylvanicus*. Furthermore, higher densities of *M. pennsylvanicus* on more isolated islands are consistent with the pattern found for *Peromyscus leucopus* (the white-footed mouse) on these islands (Adler et al. 1986) and may be due to reduced dispersal (Tamarin 1978; Adler et al. 1986).

The loop models of hypothetical multispecies interactions, while certainly not exhaustive, nevertheless illustrate that two species may display different patterns of coexistence depending upon interactions with other variables. Indeed, Lomolino (1986) suggested that compensatory effects should differ among archipelagoes displaying different ranges of island area and isolation. Thus, it is not surprising that our observations differ from those of Lomolino (1984), and in fact support his model of compensatory effects of immigration and extinction and other interactive effects (Lomolino 1986). Our study suggests that the results of seemingly simple coexistence patterns may be misleading if additional variables are not considered and also suggests some specific correlation patterns between *B. brevicauda* and *M. pennsylvanicus* which may not be obvious. Furthermore, conclusions drawn from co-occurrence studies of single island systems may not easily be generalized. A more robust theory of coexistence patterns awaits further study.

Acknowledgements. We thank Michael De Rosa for his assistance with trapping, and we appreciate the cooperation of the Chace family, Robert Eliot, Octavia Hamlin, Cigrid Hart, William Schurcliff, Wesley Tiffney, Jr., and the Trustees of Reservations for granting us permission to trap. Edward Connor, Lawrence Heaney, Mark Lomolino, Charles Puccia, and Thomas Schoener read an earlier draft of the manuscript. Our island work has been supported by NSF grant DEB-8103483 to Robert H. Tamarin, NIH grant AI 19693 to Andrew Spielman, and grants from NSF (BSR-8700130), Sigma Xi, and the Boston University chapter of Sigma Xi to G.H.A.

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. 1985. Small mammals on Massachusetts islands: the use of probability functions in clarifying biogeographic relationships. Oecologia (Berlin) 66: 178-186.

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

Brown, J.H. and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58: 445-449.

Connor, E.F. and D. Simberloff. 1984. Neutral models of species' co-occurrence patterns. In: D.R. Strong, Jr., D. Simberloff, L.G. Abele, and A.B. Thistle (eds.), Ecological Communities: Conceptual Issues and the Evidence, pp. 316-331. Princeton University Press, Princeton.

Dueser, R.D. and W.C. Brown. 1980. Ecological correlates of insular rodent diversity. Ecology 61: 50-56.

Finerty, J.P. 1980. The population ecology of cycles in small mammals. Yale Univ. Press. New Haven, CT, USA.

Gilpin, M.E. and J.M. Diamond. 1984. Are species co-occurrences on islands non-random, and are null hypotheses useful in community ecology? In: D.R. Strong, Jr., D. Simberloff. L.G. Abele, and A.B. Thistle (eds.), Ecological Communities: Conceptual Issues and the Evidence, pp. 297-315. Princeton University Press, Princeton.

Harvey, P.H., R.K. Colwell, J.W. Silvertown and R.M. May. 1983. Null models in ecology. Ann. Rev. Ecol. Syst. 14: 189-211.

Levins, R. 1975. Evolution in communities near equilibrium. In: M.L. Cody and J.M. Diamond (eds.), Ecology and Evolution of Communities. Harvard University Press, Cambridge, MA.

Levins, R. and C.J. Puccia. 1988. The controlling factor in biological communities. Coenoses 3: 149-154.

Lomolino, M.V. 1984. Immigrant selection, predation, and the distributions of *Microtus pennsylvanicus* and *Blarina brevicauda* on islands. Amer. Nat. 123: 468-483.

———. 1986. Mammalian community structure on islands: the importance of immigration, extinction and interactive effects. Biol. J. Linn. Soc., 28: 1-21.

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.

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

Manuscript received: January 1989