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MEASURING THE ALLEE EFFECT: POSITIVE DENSITY DEPENDENCE IN SMALL MAMMALS

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Abstract. Positive density dependence (the Allee effect) has numerous implications for the dynamics, distribution, and conservation of populations, but has been considered difficult to measure because it should occur only at small population sizes. Theories of density-dependent habitat selection provide a simple solution. Allee effects produce erratic habitat selection where individuals that initially pack into the better habitat flow rapidly into the poorer one at a threshold density. The instability creates a hiatus or “hole” in abundance along habitat isodars (graphs of density assuming ideal habitat selection). The presence of an Allee effect can be detected easily by calculating the exact probabilities of the observed frequency of data points in the hiatus area with that expected if fitness is positively density dependent at low density. Tests of the theory using rodents occupying mesic and xeric habitats in Canada’s Rocky Mountains reveal a clear example of the Allee effect in red-backed voles, and hint at a similar effect in deer mice. The tests suggest that populations of small mammals may frequently reach low densities where positive density dependence in fitness may play a significant role in population persistence.

Key words: *Alberta, Canada; voles and deer mice; Allee effect in two rodent species; Allee effect, measuring; Clethrionomys; conservation; density dependence in two habitats; density dependence, positive vs. negative; habitat, high vs. low quality; habitat selection, effect on population dynamics; isodars, contrasts between two species; Peromyscus; population density.*

INTRODUCTION

The continuing reduction and fragmentation of natural populations by human activities highlights an urgent need to measure the effects of low population density on the persistence, fitness, and associated recovery of small populations. Three kinds of effects are especially crucial. (1) Small populations are subject to stochastic processes of birth and survival that can threaten their persistence (e.g., Gotelli 1998). (2) Lower threshold densities or sizes may exist below which population processes, such as the ability to find mates, are sufficiently altered that populations decline to extinction (e.g., Myers et al. 1995, Veit and Lewis 1996, Grevstad 1999). (3) Population growth at low density (or size) may increase with increased density (or population size [Courchamp et al. 1999, Stephens et al. 1999, Stephens and Sutherland 1999]). All three processes have, at various times, been called examples of the Allee effect (Allee 1931) that has received increasing, and long-overdue, attention (Courchamp et al.

1999, Stephens et al. 1999, Stephens and Sutherland 1999, Berek et al. 2001, Keitt et al. 2001); strictly speaking, the term “Allee effect” should be reserved for the situation where the fitness of an individual increases with conspecific density or population size (Stephens et al. 1999).

While most ecologists readily acknowledge the potential importance of Allee effects on population dynamics, few explicit examples exist (Sæther et al. 1996, Kuussaari et al. 1998) because it is extraordinarily difficult to measure population growth rates or mean fitness in any population, let alone in those that exist at low density. Yet Allee effects have long been known to create “erratic changes” in habitat distribution (Fretwell and Lucas 1970, Fretwell 1972) that should serve as a signature for positive density dependence.

I begin by demonstrating how one can determine patterns of abundance from ideal habitat selection, then develop a simple graphical theory that illustrates the instability in habitat selection caused by the Allee effect. I show how the Allee effect creates a hiatus (an absence of data points) at low density in graphs of density between pairs of habitats assuming ideal habitat selection (isodars). I document how the hiatus and its

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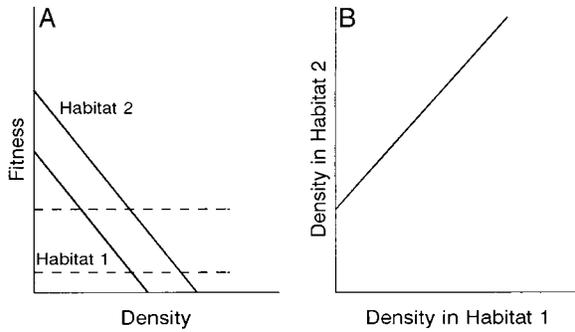


FIG. 1. An illustration of how ideal habitat selection produces linear isodars. (A) Fitness declines with density in two habitats. Intersections with horizontal dashed lines define the densities in each habitat when the expected fitness is the same in both. (B) The ideal densities plotted as the isodar, the line along which the expected fitness is identical in each habitat.

associated Allee effect can be detected by exact-probabilities tests, then apply the technique on two populations of small mammals living in mesic and xeric habitats in western Canada. The isodars reveal an Allee effect. I conclude with a critique of the method, and a brief discussion illustrating how one can test the theory by experiment.

Abundance of ideal-free habitat selectors

Imagine a density-dependent habitat-selecting species where individuals choose between two equal-sized habitats to maximize individual fitness, where individuals are free to occupy either habitat that they choose, and where continuous population growth in each habitat can be described by the Verhulst-Pearl logistic equation such that $r_2 > r_1$; $K_2 > K_1$ (r is the maximum intrinsic rate of population increase in habitat i , and K is carrying capacity). Then,

$$\frac{1}{N_1} \frac{dN_1}{dt} = r_1 - r_1 \frac{N_1}{K_1} \quad \text{and} \quad \frac{1}{N_2} \frac{dN_2}{dt} = r_2 - r_2 \frac{N_2}{K_2} \quad (1)$$

define the per capita population growth rates in each habitat where N is population size (and, conveniently, also population density in the equal-sized habitats). With ideal-free habitat selection,

$$\frac{1}{N_1} \frac{dN_1}{dt} = \frac{1}{N_2} \frac{dN_2}{dt}$$

Following substitution,

$$N_2 = \frac{K_2(r_2 - r_1)}{r_2} + \left(\frac{r_1}{r_2}\right)\left(\frac{K_2}{K_1}\right)N_1 \quad (2)$$

defines the linear habitat isodar (Morris 1988), the set of densities assuming ideal habitat selection where the expected fitness of individuals is equal in each habitat. The isodar, when habitat selection is based on individual fitness, is the solution in density space to the evolutionarily stable strategy of habitat selection (Morris et al. 2001).

I illustrate the isodar in Fig. 1; later, I contrast this figure with those corresponding to Allee effects. At low population size all individuals should occupy only habitat 2. As population size increases individuals can gain equal fitness in each habitat, and both should be occupied. The data move farther out on the linear isodar with every additional increase in population size.

Erratic habitat selection

Fig. 2 uses piecewise linear fitness functions to illustrate instability caused by positive density depen-

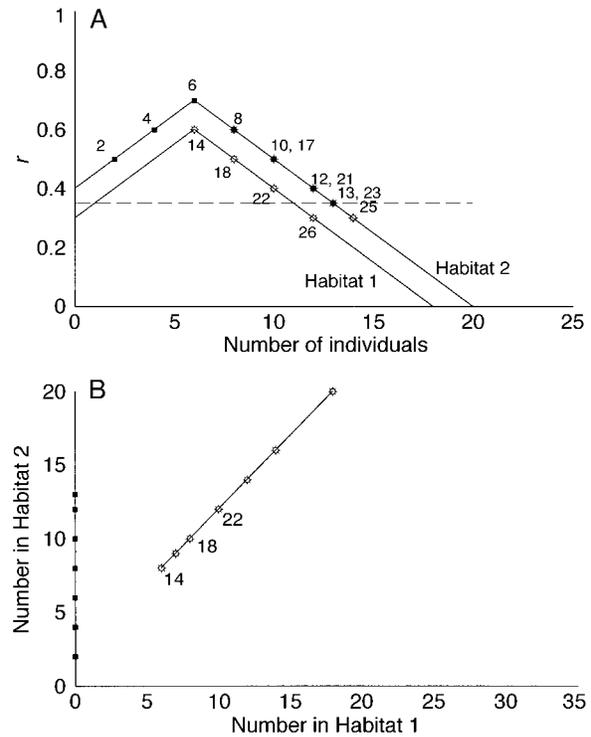


FIG. 2. An illustration of how positive density dependence in fitness at low population sizes (the Allee effect) destabilizes habitat selection. Numbers correspond to the order of habitat occupation by successive individuals; a subset of individuals is illustrated. (A) Ideal-habitat selectors will occupy habitat 2 until their fitness is equal to that in habitat 1 at low density (one individual, dashed horizontal line) even though the fitness in the two habitats is equal at a higher density in habitat 1 (eight individuals in habitat 2). The 14th individual improves its fitness by migrating to habitat 1 and is followed by successive individuals from habitat 2, all of whose fitness increases in habitat 1. (B) The ideal “Allee” isodar has a hiatus in density near the origin caused by the directional movement of individuals “following” the first individual that moves to habitat 1.

Points of stable density in habitat 2 only are denoted by solid symbols; points corresponding to stable coexistence in both habitats are denoted by sunbursts. Piecewise fitness functions correspond to $r_2 = 0.4 + 0.5(N_2)$ for $0 \leq N_2 \leq 6$, $r_2 = 1 - 0.5(N_2)$ for $6 \leq N_2$ and $r_1 = 0.3 + 0.5(N_1)$ for $0 \leq N_1 \leq 6$, $r_1 = 0.9 - 0.5(N_1)$ for $6 \leq N_1$ in habitats 2 and 1, respectively, where r is the maximum rate of population increase in habitat i and N is the number of individuals occupying that habitat.

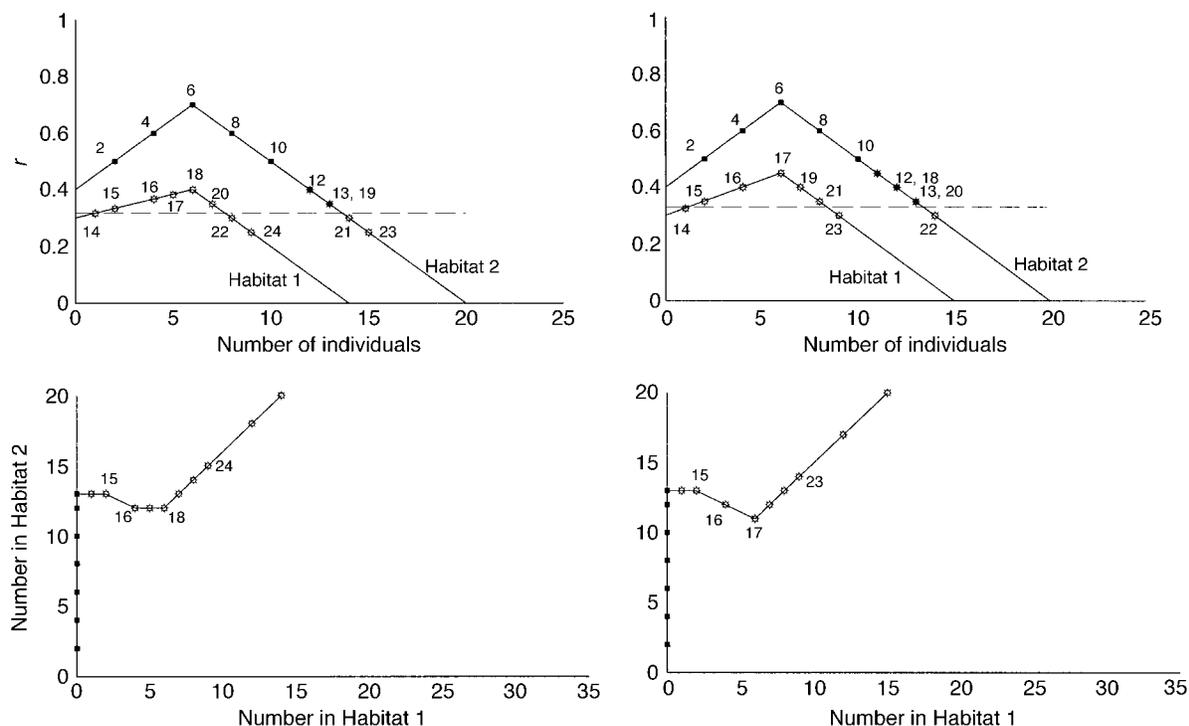


FIG. 3. Two examples illustrating how isodars can attain a “J shape” when the increase phase of fitness in the “worse” habitat has a shallower slope than the decline phase of fitness in the “better” habitat (the ratio of slopes is 1:3 on the left, and 1:2 on the right). Numbers correspond to the order of habitat occupation by successive individuals; a subset of individuals is illustrated.

Points of stable density in habitat 2 only are denoted by solid symbols; points corresponding to stable coexistence in both habitats are denoted by sunbursts. Similar J shapes can emerge if the respective slopes of the fitness functions are similar, but the area occupied by individuals in habitat 1 is large relative to that of habitat 2 (immigrating individuals arriving in habitat 1 increase density and fitness there by a small amount; emigrating individuals from habitat 2 decrease density and fitness by a relatively greater amount). Piecewise fitness functions correspond to: (left side) $r_2 = 0.4 + 0.5(N_2)$ for $0 \leq N_2 \leq 6$, $r_2 = 1 - 0.5(N_2)$ for $6 \leq N_2$ and $r_1 = 0.3 + 0.17(N_1)$ for $0 \leq N_1 \leq 6$, $r_1 = 0.7 - 0.5(N_1)$ for $6 \leq N_1$; and (right side) $r_2 = 0.4 + 0.5(N_2)$ for $0 \leq N_2 \leq 6$, $r_2 = 1 - 0.5(N_2)$ for $6 \leq N_2$ and $r_1 = 0.3 + 0.25(N_1)$ for $0 \leq N_1 \leq 6$, $r_1 = 0.75 - 0.5(N_1)$ for $6 \leq N_1$.

dence at low population density (the Allee effect). The figure reflects the theory's assumptions that individuals base habitat selection on individual fitness, and that individuals do not move from one habitat to another as groups (it is possible that a rapid change of habitats by individuals could appear as a coordinated group movement). Again, at low density, only habitat 2 will be occupied (numbers indicate the habitat choices made by different individuals). With increased density, fitness first increases in habitat 2, then decreases until individuals can attain equal fitness in habitat 1 (eight individuals in habitat 2). Any individual that migrates from habitat 2 to habitat 1 will face a reduction in fitness, however, because the fitness in habitat 1 is lower at low density (one individual, dashed line). Thus, individuals will continue to aggregate in habitat 2 (all data points “stack-up” along the ordinate on the isodar plot) until the first migrating individual (14th) can improve its fitness by moving to habitat 1. But now, because of positive density dependence, other migrants can gain even higher fitness, and we anticipate a rapid

flux of individuals flowing from habitat 2 to habitat 1 (eventually equalizing at six individuals in habitat 1 and eight individuals in habitat 2). The end result is an isodar that has data points along its ordinate, and along the isodar at higher densities, but none (or at most, ephemeral points) near the isodar intercept.

If the positive slope in density-dependent fitness in habitat 1 is shallow, compared with a steep negative slope in habitat 2, there may not be enough individuals moving from habitat 2 to quickly eliminate the positive density dependence in habitat 1. Habitat selection will be even more erratic because the increased fitness that remaining individuals attain in the high-quality habitat 2 may exceed the fitness gain of emigrants to habitat 1. Such an effect should be easily detected because increased density in habitat 1 will, in the Allee region, be associated with reduced density in habitat 2 (the isodar will be bifurcated into a “J shape” because it has a negative slope at low density [in what would normally be the hiatus region], Fig. 3). A J-shaped isodar can also emerge when the area of the “worse”

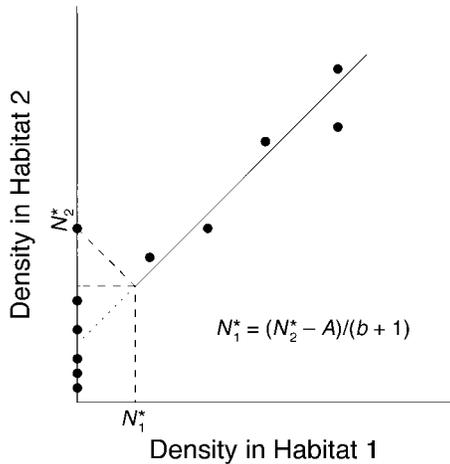


FIG. 4. A hypothetical example of how one can calculate the critical lower density in the secondary habitat corresponding to errors in habitat selection if there was no Allee effect. The kinked dashed line joins the maximum density observed in habitat 2 alone with the equivalent total density on the isodar. An equal proportion of data points should fall between the ordinate and the lower critical density (N_1^*) as lie on the ordinate above the isodar intercept, if the data represent simply errors in habitat assessment along linear fitness functions. The solution for N_1^* corresponds to that given in Eq. 5.

habitat exceeds that of the “better” one. If individuals are in an ideal-free distribution, a doubling in the area of habitat 1 can have the same effect on relative fitness and movement toward habitat 1 as does a shallower positive slope. Habitat 2 would have one half the density as habitat 1, and each emigrating individual would have twice the effect on fitness in habitat 2 as it does in habitat 1. The area effect breaks down at the spatial scale where size of a habitat exceeds the capacity of individuals to attain an ideal-free distribution. Note, however, that even with J-shaped isodars, there is still a hiatus of sorts in the linear extension of the dominant (positively sloped) portion of the isodar.

A hiatus in the isodar at low density could, of course, arise simply by chance in the absence of the Allee effect. Fortunately, it is easy to differentiate between chance and the Allee alternative. Imagine that fitness declines linearly across the entire range of densities, and that individuals err in their optimum habitat choices. At low density individuals may, for example, pack into the better habitat and create data points lying along the ordinate and above the isodar intercept (Fig. 4). A similar proportion of points should dominate the lower portion of the isodar that may, with the Allee effect, be an empty set. To find these points, imagine that the maximum threshold density along the ordinate is given by N_2^* . The equivalent density on the isodar can be found by setting N_2^* equal to total density ($N_1 + N_2$)

$$N_2^* = (N_1 + N_2) = \left[\frac{K_2(r_2 - r_1)}{r_2} + \left(\frac{r_1}{r_2} \right) \left(\frac{K_2}{K_1} \right) N_1 \right] + N_1 \quad (3)$$

from which we can calculate the critical lower density in habitat 1 (N_1^*) as

$$N_1^* = \frac{N_2^* - \left(\frac{K_2(r_2 - r_1)}{r_2} \right)}{\left(\frac{r_1}{r_2} \right) \left(\frac{K_2}{K_1} \right) + 1} \quad (4)$$

which, using Eq. 2, can be generalized to any linear isodar

$$N_2 = A + bN_1 \quad \text{as} \quad N_1^* = \frac{N_2^* - A}{b + 1}. \quad (5)$$

Thus, to test for an Allee effect, one begins by calculating N_1^* . Next, calculate the value of N_2 on the isodar that corresponds to N_1^* , and create a rectangle by drawing vertical and horizontal lines to the axes. If there is no apparent trend toward a J-shaped isodar, count all points in the region $0 < N_1 < N_1^*$. These points would be expected from ideal habitat selection along linear fitness functions, and conversely, represent errors in habitat assessment for populations experiencing Allee effects. If, however, the isodar appears to be J shaped, count only the number of data points within the rectangle for which $0 < N_1 < N_1^*$. Counting points within the rectangle guards against rejecting J-shaped isodars that always imply an Allee effect for ideal-habitat selectors. Finally, contrast the proportion of the counted points out of the total for the entire isodar, with the proportion lying on the ordinate and above the isodar intercept. The proportions should be similar for linear fitness functions, the proportion on the ordinate should be greater with an Allee effect.

Alternatively, if one suspects that the isodar is indeed J shaped, one could use a variety of possible tests to evaluate whether the isodar has negative slope at low density. Often, however, there will be relatively few data points within this region, and it may be necessary to conduct the test (as outlined above) by contrasting the observed and expected proportions of data points.

Fitness functions and their emergent isodars, even in the absence of an Allee effect, need not be linear. Indeed, in the case of preemptive habitat selectors that “select the best available site” (Pulliam 1988, Pulliam and Danielson 1991, Rodenhouse et al. 1997), isodars, reflecting nonlinear negative density dependence, can be dramatically nonlinear (Morris 1994). An Allee effect for preemptive habitat selectors will increase site quality with increases in density at low population size, and individuals should preferentially select sites in one habitat even when otherwise “better” sites exist in alternative habitats. We should, nevertheless, be able to mimic the linear protocol by using the best-fit equation for the empirical nonlinear curve (e.g., Knight 2000) to estimate the critical lower density.

THE ALLEE EFFECT REVEALED

In 1989 my assistants and I live-trapped deer mice (*Peromyscus maniculatus*) and red-backed voles (*Clethrionomys gapperi*) at nine sites contrasting north-facing mesic forest, and south-facing xeric-forest habitats along the front ranges of the Rocky Mountains in Alberta, southern Canada (50°38'–51°05' N, 114°57'–115°12' W; Morris 1996). We estimated rodent density as the mean number of different individuals captured in pairs of 0.16-ha sampling grids (20 pairs overall; these estimates were highly correlated with mark–recapture estimates of rodent density [Morris 1996]). The density-dependent habitat selection of each species was revealed in the respective linear isodars that I calculated with data from three different 72-h sampling periods in early, midsummer, and late summer (20 June–7 July, 1–16 August, and 21 August–26 September, respectively; Morris 1996). Deer mice preferred the xeric habitat, voles preferred the mesic one. In each case, several of the data points on the preferred-habitat's axis exceeded the linear-isodar's intercept (Fig. 5).

I contrasted the proportion of data points expected from negatively sloped fitness–density functions with those expected from the Allee effect. There was no clear pattern of a J-shaped isodar for either species, so I considered all points in the range $0 < N_1 < N_1^*$ (N_1 = density in the least preferred habitat, N_1^* = lower critical density in that habitat) as errors along linear fitness functions. I calculated the exact probabilities associated with the observed proportion of such errors, plus all “worse” cases (Sokal and Rohlf 1995), to test for an Allee effect.

The analysis for the red-backed vole revealed a significant zone of positive density dependence and a concomitant role for the Allee effect in its habitat selection at low density (Fig. 6). There was weak, but suggestive, evidence for a similar zone of positive density dependence in deer mice ($P = 0.07$; Fig. 6). Two of the deer-mouse data points appear to be outliers (Fig. 5) and, if removed, yield a significant Allee effect ($P = 0.01$).

The critical density for deer mice was less than that for red-backed voles (0.76 mice in the mesic habitat compared with 2.04 voles in the xeric habitat) as was the maximum threshold density when the preferred habitat only was occupied (3.5 mice in xeric vs. 5 voles in mesic). The results suggest that, if these deer mice possess an Allee effect, the zone of positive density dependence may be less for deer mice in this pair of habitats than it is for voles.

DISCUSSION

The isodar “test” illustrates that one can, by careful comparison of densities in adjacent habitats, assess whether fitness increases with density at low population sizes (the Allee effect). Applied to the habitat choices of two species of small mammals, the test reveals clear evidence of positive density dependence in voles, and

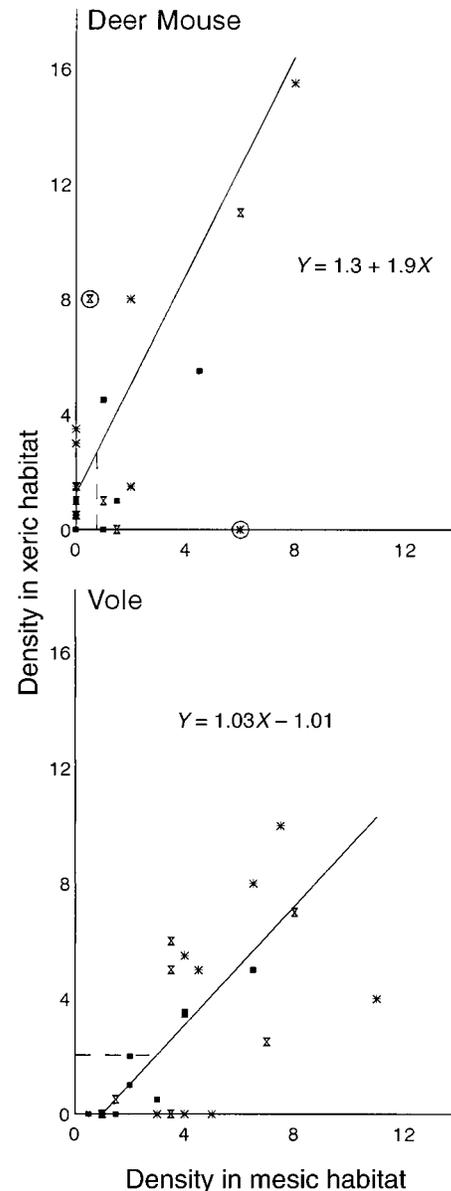


FIG. 5. The isodars, and the lower critical densities (dashed lines) of deer mice and red-backed voles occupying mesic and xeric habitats in the front ranges of the Rocky Mountains of southern Canada. Symbols correspond to different 72-h trapping sessions (session 1, solid squares; session 2, hourglasses; session 3, asterisks). Circled data points highlight “outliers” from the deer-mouse isodar that, if removed, yield a significant Allee effect ($P = 0.01$). Redrawn from Morris (1996: Fig. 4).

hints at a similar Allee effect in deer mice. But the density of each species around its respective isodar was variable, reflecting errors in habitat assessment as well as temporal and spatial differences in the two habitats. The variance can be minimized by reducing the spatial scale of future studies, by selecting pairs of habitats less likely to vary through time, or by reducing the temporal duration of field work.

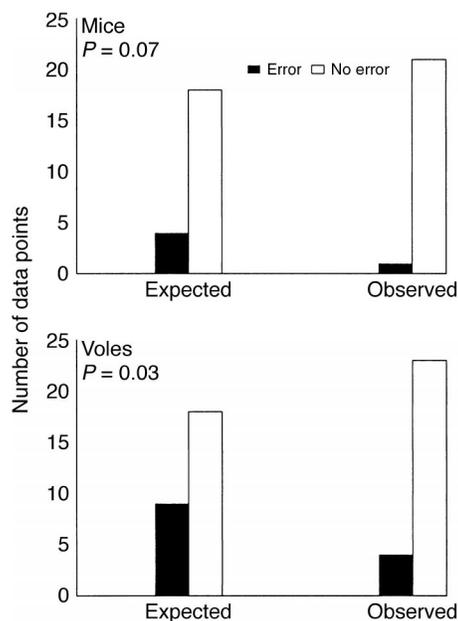


FIG. 6. Expected and observed occupation of two habitats by deer mice and red-backed voles in mesic and xeric habitats in the front ranges of the Rocky Mountains of southern Canada. Statistical significance was assessed by calculating the exact probability of the observed plus all “worse” outcomes. Densities corresponding to “errors” along linear fitness functions are denoted by solid bars; the remaining points are denoted by open bars.

Any attempt to reduce variance must be balanced against the isodar assumption that populations depart frequently from their equilibrium densities. My analyses of deer mice and voles, for example, capitalized on the well-known annual dynamics of the two rodent species. The densities of many other species may fluctuate differently, and over alternative scales of space and time. It is inconceivable, however, that the populations of any species are so precisely regulated, and their environment so stable, that they maintain themselves at constant equilibrium. The clever field ecologist should be able to exploit the variance, measure the isodar, and test for positive density dependence.

The analysis may be complicated if high-quality habitat is rare relative to low-quality habitat. Few individuals may be available to occupy their secondary choice. The increase in fitness in the high-quality habitat as individuals emigrate may exceed the increase in the low-quality one as individuals immigrate. The erratic behavior of habitat selection can be detected easily by its J-shaped isodar.

An additional complication might occur when habitat selection is costly (Morris 1987, 1992). Ideal individuals dispersing from high-quality to low-quality habitat must regain the fitness loss caused by dispersal (Morris 1992). With an Allee effect, dispersal cost will be reduced at low density because individuals can expect to reap a “pyramid” of accruing positive density-depend

ent benefits after they immigrate into the low-quality habitat. The benefits may often balance dispersal costs with little net effect on the isodar. At higher densities, however, the cost of dispersal inflates the isodar intercept (Morris 1992), and thereby reduces our estimate of the critical lower density (Eq. 4).

Source–sink migration (Pulliam 1988) can create similarly intriguing dynamics. Individuals forced from high-quality habitats, and making the best of their misfortune, may settle in habitats with negative fitness. With an Allee effect, the continued arrival of similarly disenfranchised individuals can elevate fitness so that the previously “sink” habitat, at least for a moderate range of densities, has positive recruitment. Though we would require estimates of density-dependent fitness to truly explore source–sink dynamics, the process of an individual occupying the habitat with the highest expectation of fitness corresponds to that for the ideal-free case, and we should be able to use isodars to detect an Allee effect.

The various possible complications that might arise in field tests for Allee effects suggest that it might be productive to first test the theory by experiment. The clever approach used by M. L. Rosenzweig, Z. Abramsky, and A. Subach (Abramsky et al. 1997, Rosenzweig et al. 1997) can serve as a model. The Rosenzweig/Abramsky team used habitat selection by Allenby’s gerbil to test a potentially very common mechanism for Allee effects predicted by nonlinear predation models. Prey species may often attain “safety in numbers” by passively aggregating to spread the risk of predation (Abramsky et al. 1997, Rosenzweig et al. 1997). The Rosenzweig/Abramsky protocol begins by partitioning a single habitat (or homogeneous mix of habitats) in two, then controls population size while allowing the free movement of individuals across the border between the two halves of the split habitat. Individuals should aggregate in one half or the other when their fitness increases with density; they should occupy both halves equally (the isodar, in the absence of an Allee effect has a zero intercept and slope of unity) when fitness declines with density.

Rosenzweig et al. (1997) invented a creative test for positive density dependence by first documenting the linear isodar (Abramsky et al. 1997), then plotting the standardized difference in rodent density between the two halves of the experiment against the mean density (using my symbolism, the standardized difference is given by $[(N_2 - N_1)^2]/\bar{N}$). Along the linear isodar, the densities in each half should be equal, and thus the standardized difference should be approximately zero. The difference should be positive when one or the other habitat has an abundance of individuals (as when a bifurcated isodar has positive slope). The results from Rosenzweig et al. (1997) confirmed the theory, but only when rodents were challenged by predation risk from owl overflights. Otherwise, the competition among rodents exceeded the gain in indirect vigilance (predation

risk was low), and densities were equal in both halves of the experiment. It may be necessary, therefore, when testing for Allee effects by experiment, to also manipulate the suspected mechanism responsible for density-dependent increases in fitness.

The Rosenzweig/Abramsky standardized metric works well in experiments contrasting different sides of a single habitat. Often, in future designs, experimenters may wish to work in two or more habitats. Though the metric could, in principle, be applied to those more complicated designs, the isodar approach I suggest here would appear to be simpler to apply, and to provide a straightforward statistical test for significance.

Density-dependent habitat selection, with or without an Allee effect, should help to buffer populations from the negative effects of low density. As population density declines, only the very best habitats will be occupied. But the process of habitat selection may have limited spatial scale. In deer mice, for example, dispersal appears to be limited to a distance on the order of 140 m (Morris 1992), and even "sub-populations" within a single habitat located at scales exceeding the dispersal distance appear to be regulated independent of habitat selection (Morris 2001). Tests of habitat selection, or uses of habitat selection to detect Allee effects, must ensure that the spatial scale of the study reflects the relevant processes of habitat selection. When the scale is correct, one can use the pattern emerging from adaptive habitat selection to gain crucial insights into positive density dependence and its far-reaching implications to populations, spatial distribution, and the conservation of biodiversity.

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