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Reciprocating dispersal by habitat-selecting white-footed mice

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Theories of dispersal driven by density-dependent habitat selection demonstrate that putative examples of source–sink dynamics and balanced dispersal may also be explained by a more general pattern of bi-directional, reciprocating dispersal. Analyses of 19 years of data on dispersal by white-footed mice confirm the theory. Fitness of territorial white-footed mice living in an agricultural mosaic is higher in forest habitat than it is in either edge or fencerows. Density-dependent habitat selection theory predicts that if net emigration by mice flows from the forest to forest-edge during periods of population growth, animals should subsequently move from the edge to forest during population decline. The pattern of mouse dispersal varies between seasons as populations wax and wane in abundance. Mice tend, as predicted, to move from high-density forest habitat into low-density edge during periods of population increase, and from the low-density edge into high-density forest during periods of population decline. Over all years combined, dispersal by white-footed mice was balanced. Each habitat tended to gain as many dispersing individuals as it lost. The results support a conditional dispersal strategy linked to density-dependent habitat selection, but also suggest the possibility of multiple coexisting strategies.

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Two perspectives dominate the contemporary literature on dispersal. According to the source–sink model (Anderson 1970, Holt 1984, 1985, Shmida and Ellner 1984, Pulliam 1988, Pulliam and Danielson 1991), emigrating individuals are imagined to move directionally from source habitats ($r > 0$) to nearby sinks ($r < 0$). The alternative balanced dispersal model (McPeek and Holt 1992) imagines that the propensity to disperse is contingent on habitat. An evolutionarily stable dispersal strategy emerges when the total number of individuals emigrating out of a habitat is balanced by an equivalent number of individuals that immigrate. Each theory is supported by data (Doncaster et al. 1997, Diffendorer 1998, Lin and Batzli 2001).

Theories of habitat selection point to a third and inclusive alternative. If dispersal is contingent on the density-dependent quality of alternative habitats, if populations fluctuate through time, and if individuals choose habitats in a way that maximizes their Darwinian fitness, dispersal will reciprocate between habitats (Morris et al. 2004). When emigrants flow from habitat A to habitat B during periods of population increase, net movement will be in the opposite direction during periods of population decline. Whether the net flux of individuals is balanced, or is biased toward one habitat over another, depends on the relative magnitudes of fitness in the different habitats, the rate of decline in fitness with increasing density, and the degree and pattern of stochastic influences on population regulation. The pattern of reciprocating dispersal is general, however, and occurs whether individuals are free to occupy the habitat of their choice (Fretwell and Lucas 1970), or whether dominant individuals interfere with habitat selection (Morris et al. 2004). We call this

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habitat-contingent strategy the “reciprocating dispersal model.”

We test the theory with time-series on net movement and population dynamics of white-footed mice (*Peromyscus leucopus*). The white-footed mouse is an appropriate species for tests of habitat-dependent dispersal theory because it occupies a wide variety of habitats, its seasonal dynamics are well documented, and it is known to be a density-dependent habitat selector (Morris 1989, 1991a, Halama and Dueser 1994).

We begin with a review of the requisite natural history of white-footed mice to yield testable predictions of reciprocating dispersal. We use 19 years of data on demography, population dynamics and habitat selection to describe general patterns of white-footed mouse dispersal and to test the reciprocating-dispersal theory. The data confirm the theory. We conclude by assessing alternative interpretations of our data and the possibility that reciprocating dispersal driven by habitat selection is but one of several dispersal strategies employed by white-footed mice.

Methods

Natural history and field design

White-footed mice (*Peromyscus leucopus*) are common nocturnal North American rodents that occupy a variety of successional forest habitats in the north-eastern part of their geographical range. *Peromyscus* readily live and reproduce in artificial wooden nest boxes in the largely agricultural landscape of extreme southern Canada and adjacent states of the USA (Nicholson 1941, Howard 1949, Goundie and Vessey 1986, Morris 1986, 1989, 1992a, 1998). Territorial females reproduce from April through June, often take a hiatus from reproduction during the hottest months of the temperate summer, and resume breeding from late August through October (Morris 1986, 1989). Recruitment is relatively high from spring-born litters, and is much lower for litters produced in autumn (Morris 1986, 1992a). Most white-footed mice live only a few months, and their populations fluctuate from seasonal lows at the end of winter to highs following the recruitment of autumn-born offspring in October and November (Terman 1968, Morris 1996a). Populations are regulated by both habitat selection and seasonally-lagged density dependence (Morris 1996a).

Since 1981, DWM and his assistants have monitored white-footed mouse density and life history in nest boxes placed at approximately 30-m intervals along oak-covered (*Quercus* spp.) fencerows (36 boxes from 1981–1984, 40 boxes thereafter), along the margin of a small (1.5 ha) and adjacent large (20 ha) oak-dominated woodlot (28 boxes), and in a 30-m grid within the woods (15 boxes in the small woodlot, 50 in the larger one). White-footed mice are the only common nocturnal rodents on the 40-ha study site (Fig. 1). Boxes were checked three times each reproductive season at approximately monthly intervals (except autumn 1982 [no checks], spring and autumn 1983, and autumn 1984, 1985 [two checks each]), and all mice eight days of age and older were individually marked. At times the boxes have been checked at monthly intervals outside of the main seasons of reproduction, but not in all years.

Adult mice in boxes located in forest habitat live longer and produce more recruits than do adults living in fencerows (Morris 1989, 1991a, 1996a). The fitness of mice in the edge is intermediate to that of the other two habitats, a result corroborated with estimates of habitat quality based on foraging behaviour (Morris and Davidson 2000). The rank order of habitats in terms of mouse fitness is: forest > edge > fencerows. The density of mice living in forest and edge habitats tends to be greater than that of mice living in fencerows (Morris 1996a). Habitat selection depends on density, and is consistent with the ideal despotic distribution (Morris 1991a, Halama and Dueser 1994). Fitness distributions inferred from isodars suggest that the decline of fitness with density between forest and edge habitats is linear, and that the decline is more rapid in the edge than in the forest (illustrated below).

According to the reciprocating-dispersal model, individuals will tend to emigrate from habitats where they have the greatest impact on fitness and will accumulate as immigrants in habitats where their per capita impact is lower. Individuals are likely to disperse more or less continuously through time (but with a clear temporal component in populations with dramatic cohort effects), and in both directions. But as populations increase and

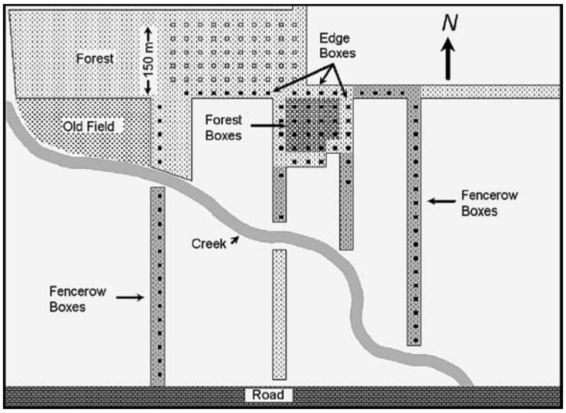


Fig. 1. Schematic illustrating the placement of nest boxes for white-footed mice in a 40-ha study site in southern Ontario. Clear areas are agricultural fields. Stippling represents tree cover in forest and along fencerows. Diamonds correspond to an old field without trees. Circular stipples outline the boxes classified as “forest habitat”. Filled squares represent boxes used in the study, open squares represent other nearby boxes. Distance between boxes is 30 m, otherwise the scale is approximate.

decrease in size, such as in the number of white-footed mice living in seasonal environments, the net flow of individuals between habitats should alternate (reciprocate) with the fluctuating dynamics. Thus, if dispersal is biased seasonally toward the low fitness fencerow and edge habitats during the spring–autumn population increase, dispersal should be biased toward the high-fitness forest habitat during the winter decline.

Testing reciprocating dispersal

We tested the reciprocating-dispersal theory in white-footed mice by first selecting for analysis only those animals where it was possible to detect dispersal (individuals observed two or more times in nest boxes). The data include all animals captured between the spring of 1981 and autumn 1999. We restricted our analyses to the fencerows, edge, and small woodlot which represent the set of habitats used consistently in previous analyses of habitat selection and life-history evolution in this system. We intend to "save" the data from the large woodlot for future tests of more refined, or post hoc, hypotheses.

We recorded the season and habitat of 'first' and 'final' capture of each animal. Some animals, no doubt, lived in forest boxes while exploiting the edge (and vice versa), but our emphasis on animals occupying nest boxes identified their 'resident' habitat. An individual was deemed to have dispersed if the habitats of first and final capture were different. The procedure classified an animal that moved to another habitat, and subsequently returned to its original habitat, as a non-dispersing individual. Though habitat switching may represent two or more dispersal events, it might also represent exploratory behaviour that could bias our analyses if we used those data. We acknowledge that our estimate may include a few habitat-switching individuals (animals that perished before we encountered their return to their original habitat). Our approach will, nevertheless, reduce the possible mis-classification of dispersing animals and should generally yield a minimum estimate of the number of dispersing rodents that is consistent among habitats.

We used loglinear models to determine potential impacts of sex, habitat, season, and age-class on rodent dispersal. We also used the loglinear analysis to search for two- and three-way interactions in the proportion of animals dispersing among habitat, sex, and age-classes. Barring any interactions, we lumped data for both sexes and age-classes in further analyses. Individuals captured first as immatures (eyes closed), juveniles, or sub-adults (based on pelage) were classified as young animals; all others were classified as adults.

We searched for balanced versus directional dispersal by calculating per capita rates of dispersal, and by using goodness-of-fit tests that contrasted the total number of animals entering a habitat with the total number leaving it between reproductive (spring through early autumn) and non-reproductive (late-autumn and winter) seasons. The test was designed to evaluate the assertion that, in the absence of knowledge about reciprocating dispersal, migration could appear either balanced or driven by source–sink dynamics. Similar approaches have been used by others to differentiate between source–sink and balanced dispersal (Diffendorfer 1998). We then repeated the analysis in different seasons to search for the seasonal bias in emigration predicted by reciprocating-dispersal theory.

We complemented the seasonal test for reciprocating dispersal with two subsequent loglinear analyses that assessed whether or not the overall pattern of rodent dispersal varied with habitat and season. The first (three-way) analysis tested whether the number of dispersing versus philopatric individuals varied among habitats and between seasons. A significant three-way interaction would support the reciprocating-dispersal model's prediction that the pattern of dispersal has both a habitat and seasonal bias. The second (four-way) analysis tested whether or not the number of rodents observed in a habitat depended on the identity of the first or final habitat they were captured in, as well as the season of first versus final capture. Each of the 36 cells ($3 \times 3 \times 2 \times 2$) in the analysis was the sum of the number of rodents in a habitat that either originated from, or were last captured in, habitat i during season j. A significant four-way interaction would demonstrate that the pattern of rodent movements between habitats differed between seasons (reciprocating dispersal).

The various analyses used only those animals whose first and final captures corresponded to the seasons included in the analysis. Otherwise, the sample of animals in each analysis varied with the combinations of variables, habitats, and missing values (eg. animals that escaped during handling).

We completed our analyses by calculating habitat isodars (graphs of density in pairs of habitats that emerge from ideal habitat selection) for each pair of habitats (Morris 1996a), and by plotting long-term trends in population dynamics. These final analyses had two purposes, (1) to ensure that the patterns of population density in different habitats corresponded with the underlying theory of reciprocating dispersal (i.e. density-dependent habitat selection, Morris et al. 2004), and (2) to assess whether any pattern of reciprocating dispersal by the rodents corresponded with changes in population size. Specifically, we wished to assess whether isodars confirm that the underlying fitness functions in each habitat diverge from one another. The divergence assumption is implicit in models of reciprocating-dispersal when maximum fitness is similar in different habitats (as in white-footed mice, Morris 1989, 1991a). The predictions of reciprocating-dispersal theory depend on differences between habitats in the rate (and pattern) of decline of fitness with increasing density (Morris et al. 2004).

We calculated population densities as the mean number of different adult mice (standardized by numbers of boxes and nest box checks) that were captured in a given season and habitat. We tested the goodness-of-fit of linear versus quadratic and cubic isodars using the Akaike information criterion (AIC, calculated in SAS Version 8). We rejected a linear fit only if the AIC of more 'complicated' equations was reduced by at least ($2 \times \alpha$) where α is the number of parameters included in the model (Hilborn and Mangel 1997). Final isodar solutions were calculated by geometric-mean regression. Other than the AIC tests, analyses were performed using SPSS (Version 10) and MINITAB (Release 13) software.

Our estimates of population density assume that nest boxes yield unbiased estimates of mouse density. This assumption was verified by an earlier observation that nest-box estimates of mouse density in the forest habitat are highly correlated with those from independent live-trap estimates (Morris 1996a). Our estimates also assume that colonization of, and residency in, nest boxes is similar in the three habitats. We attempted to eliminate any habitat-related bias by standardizing the interspersion of boxes and their microsite locations (Morris 1989). Three lines of evidence support our assumption of no habitat-induced bias. 1) There is no difference in recapture success of mice occupying boxes in the three habitats (Morris 1989). 2) Within a habitat, there are no detectable differences in the quality of different nest-box locations (Morris 1991a). 3) There are no differences in body-size distributions, or parity, of adult females living in boxes in the different habitats (Morris 1992b).

Results

There was no sex or age-dependent pattern of dispersal

Most white-footed mice did not disperse from one habitat to another, more females were captured than males, and most eligible animals were first captured as juveniles (Fig. 2, 1831 animals). There was no significant two-way (LR $\chi^2_3 = 0.33$, $P = 0.95$) or three-way interaction (LR $\chi^2_1 = 0.096$, $P = 0.76$) of the proportion of dispersing animals with habitat, their sex, or their age. We were thus able to pool data across age and sex classes for subsequent analyses focussed on habitat and seasonal differences in dispersal.

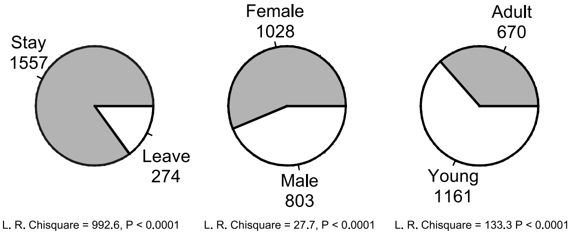


Fig. 2. Approximately 15% of white-footed mice observed on two or more occasions in nest boxes moved from one habitat to another. The sample of potentially dispersing mice included more females than males, and a high proportion of animals captured first as juveniles. There was no significant interaction among sex, age and dispersal.

Per capita dispersal rate was highest in forest and edge habitats

The proportion of mice either staying or dispersing varied among habitats (1826 animals, LR $\chi^2_2 = 95.46$, $P < 0.0001$). Per capita dispersal rate was highest in the forest (highest-quality habitat, 26.7% of 348 eligible animals), it was somewhat lower in the edge (20.3% of 572 animals), and much lower in fencerows (lowest-quality habitat, 7.2% of 906 animals).

When seasons were pooled, dispersal appeared balanced among habitats

A total of 258 different animals dispersed from one habitat to another during spring and autumn periods over the 19-year study period. There was no trend for any single habitat to either accumulate or export an excess of individuals (Table 1, comparison of immigrants versus emigrants by habitat, $\chi^2_1 = 0.11$, $P = 0.74$). A parallel result was obtained when we included animals dispersing in all seasons (274 animals, $\chi^2_1 = 1.21$, $P = 0.27$).

But mice moved out of the forest in spring, and out of the edge in autumn

Dispersal was balanced among the 158 animals captured first in the spring season (Fig. 3, $\chi^2_1 = 2.15$, $P = 0.14$), but there was a trend for animals to disperse out of the forest (6 more emigrants than immigrants) and into the edge habitat (9 more immigrants than emigrants). The pattern

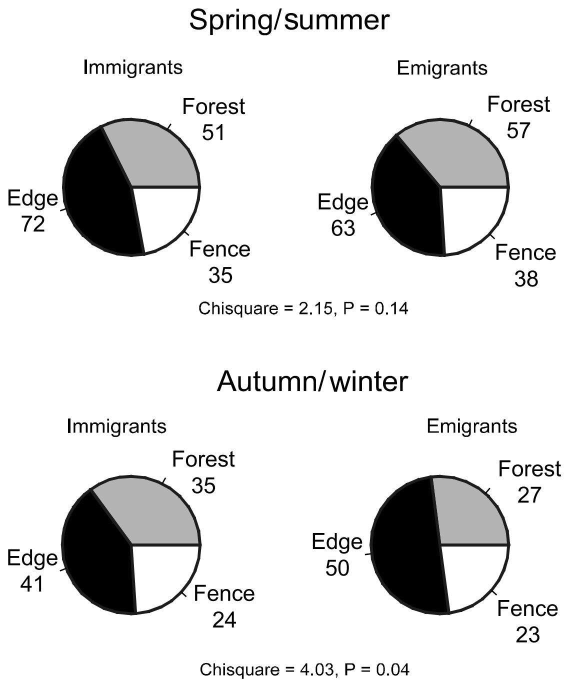
Table 1. Dispersal of white-footed mice appeared balanced when data from forest, edge, and fencerow habitats were pooled across seasons.

Habitat	Emigrants	Immigrants
Forest	84	86
Edge	113	113
Fencerow	61	59

Fig. 3. Though dispersal by white-footed mice was "balanced" during the reproductive season (spring through early autumn), there was a trend for animals to move out of the forest and into the edge. The pattern of dispersal was reversed in late-autumn and winter when dispersal was biased by animals moving from the edge into the forest. "Fence" is short-hand for fencerow habitat.

Habitat	Gain/loss
Forest	-6
Edge	+9
Fence	-3

Habitat	Gain/loss
Forest	+8
Edge	-9
Fence	+1



of dispersal was reversed in autumn when animals moved out of the edge and into the forest habitat (Fig. 3, $\chi^2_1 = 4.03$, $P = 0.04$). The seasonal data support habitat-dependent episodes of reciprocating dispersal.

The results of this analysis were confirmed in a loglinear design that assessed the seasonal pattern of whether individuals tended to stay in their "natal" habitat or disperse to one of the others. White-footed mice moved out of the high-fitness forest habitat from spring to autumn, and out of the edge habitat over winter (Table 2, 1752 animals, three-way interaction between dispersal, season and habitat LR $\chi^2_2 = 7.13$, $P = 0.03$). The dispersal pattern was driven mainly by a high rate of emigration from the forest in spring and summer in comparison to a net flow of immigrants into the forest over winter. The habitat and seasonally dependent pattern of dispersal was retained in a second loglinear analysis that examined the number of rodents whose natal and final habitats were the same (philopatry) or different (dispersal) in the two different seasons (four-way interaction among habitat of first capture, habitat of final capture, season of first capture and season of final capture, 1752 animals, LR $\chi^2_4 = 16.04$, $P = 0.003$).

Despite the highly significant overall pattern, migration into and out of fencerows appeared balanced in each season (Fig. 3). The pattern suggests that the relationship between fitness and density may be different in fencerows than in the other two habitats.

Table 2. Reciprocating dispersal by white-footed mice is directed out of forest habitat during spring and summer, and out of edge habitat in autumn and winter. Data represent the number of animals observed in nest boxes on at least two different occasions.

Seasons	Dispersal strategy	Habitat		
		Forest	Edge	Fencerows
Spring/summer	Stay	116	253	445
	Leave	57	63	38
	% dispersal	32.9	19.9	7.9
Autumn/winter	Stay	122	181	377
	Leave	27	50	23
	% dispersal	18.1	21.6	5.8

The number (but not the density) of mice in a habitat was inversely related to per capita dispersal rates

Each isodar was highly significant (Fig. 4). The isodar for forest versus edge appeared linear (linear AIC = −149.27, quadratic AIC = −147.3). But our suspicion about differences in fitness functions between fencerows and the other two habitats was reflected in significant quadratic models that provided better fits for the isodars than did linear regressions (forest vs fence, linear AIC = −114.3, quadratic AIC = −118.5; edge vs fence, linear AIC = −141.5, quadratic AIC = −146.0). Cubic regressions produced poorer fits than quadratic models in each case (Table 3). None of the isodar intercepts was significantly different from zero, but density was greater in forest by a constant proportion

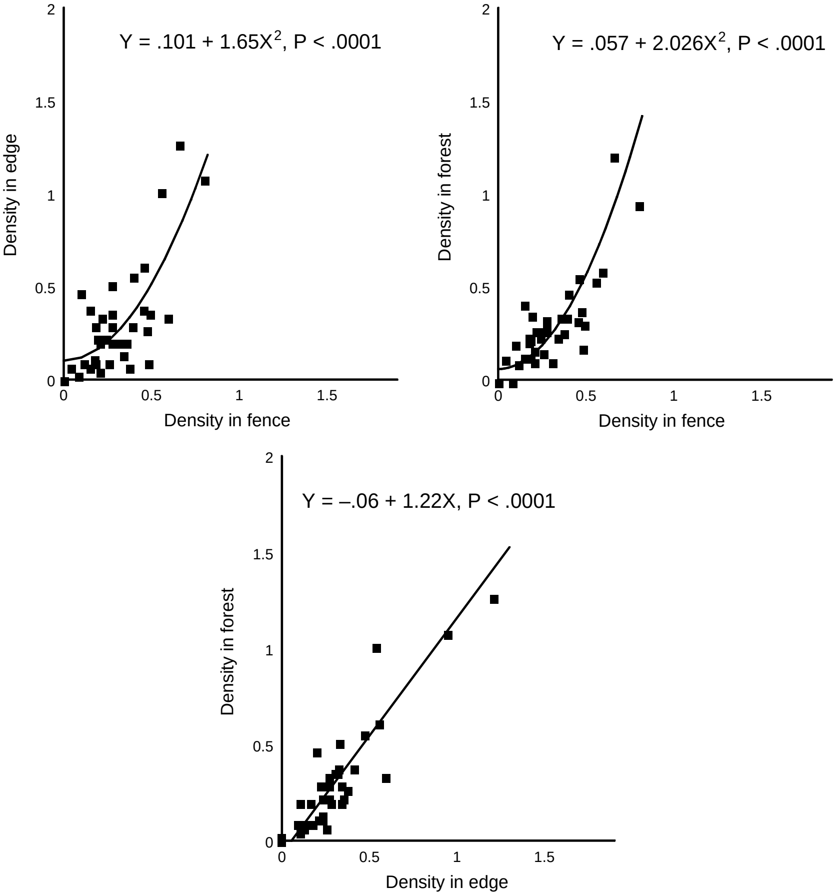


Fig. 4. Cross-correlations (isodars) of white-footed mouse density (mean number of different adult mice nest-box^{-1} × season^{-1}) in three different habitats in southern Ontario, Canada. The expected density in edge habitat was greater than that in the fencerow (= fence), and the expected density in the forest exceeded that in both of the other habitats (all isodars based on geometric-mean regression).

than in the edge (the densities in the two habitats diverge with increasing population size). The curved fencerow isodars both had positive quadratic terms (the diverging difference in density increases with density in the fencerow, Table 3); the linear component was non-significant in both cases ($P > 0.5$). We eliminated the linear term, then re-analyzed the two fencerow isodars using only the squared density in fencerows as the independent variable. The AIC was increased in both cases (forest vs fence AIC = −120.2, edge vs fence AIC = −148; Table 3). Though the fencerow isodars were curved upwards, the ranks of density corresponded with the ranks of per capita dispersal (forest > edge > fencerow). The number of mice living in each habitat, however, depends on its area and thereby on the number of nest boxes located within it. The rank order of number

Table 3. Results of linear, quadratic, and cubic solutions to the habitat isodars (fenceN^2 solutions represent isodars with the squared density in fencerows as the independent variable). None of the intercepts was statistically significant. All slopes for linear models were > 1.0. Linear terms for the two quadratic isodars were non-significant, but squared terms were significant ($0.01 < P < 0.02$). Bold type corresponds to the isodar yielding the best fit with the data on mouse densities.

Comparison	Model	F	df	P	R^2_{adj}	AIC
Forest vs edge	Linear	145.6	1,35	<0.0001	0.81	**−149.27**
	Quadratic	70.8	2,34	<0.0001	0.79	−147.30
	Cubic	47.4	3,33	<0.0001	0.79	−146.33
Forest vs fencerow	Linear	35.1	1,35	<0.0001	0.49	−114.28
	Quadratic	23.3	2,34	<0.0001	0.55	−118.52
	Cubic	15.3	3,33	<0.0001	0.54	−116.86
	FenceN^2	47.2	1,35	<0.0001	0.56	**−120.15**
Edge vs fencerow	Linear	62.1	1,35	<0.0001	0.63	−141.50
	Quadratic	39.2	2,34	<0.0001	0.68	−146.01
	Cubic	26.3	3,33	<0.0001	0.68	−144.94
	FenceN^2	80.7	1,35	<0.0001	0.69	**−148.01**

of mice was opposite that of per capita dispersal (fencerow > edge > forest; Table 2).

Irrespective of the significant isodars, substantial variation in population density was unaccounted for by habitat selection (Fig. 4, 5). The data suggest that a variety of stochastic influences overlay the ability of habitat selection to regulate populations in heterogeneous environments (Morris 2001). Populations varied dramatically through time with both seasonal and multi-annual fluctuations plus a general trend of gradually declining population density (Fig. 5, Morris 1996a). Nevertheless, the periods of population growth and decline confirmed our assumption that they usually coincided with spring and autumn seasons.

Discussion

Dispersal by white-footed mice obeys the general predictions of reciprocating dispersal. Emigration was biased away from the high-fitness forest habitat, dispersers flowed from forest to edge habitat during periods of population growth, and dispersers emigrated from edge to forest habitat during population decline. Dispersal among habitats occupied by white-footed mice reciprocates and appears intricately dependent on habitat selection. The pattern of dispersal depends on population dynamics, but the strategy depends on density-dependent habitat selection. Nevertheless, the overall pattern of dispersal in white-footed mice was balanced; the net loss of animals from a habitat was approximately equal to its net gain. What processes account for both reciprocating and balanced dispersal in white-footed mice?

One possibility is that the effect of dominant individuals varies both seasonally and between habitats. Seasonal and habitat-dependent dominance can produce both reciprocating dispersal between seasons, as well as a net balance of emigrants between habitats (Morris et al. 2004). Balanced dispersal could thus emerge if the well-documented seasonal asymmetry in female territoriality in white-footed mice (Burt 1940, Nicholson 1941, Stickel 1968, Metzgar, 1971, Rowley and Christian 1976, Wolff 1986) also varies between habitats.

Another possibility is that the general trend of declining abundance by this population of white-footed mice biases episodes of dispersal toward periods of declining population size. Such a bias would act to increase the flow of individuals leaving low density and low fitness habitats, and would tend to equilibrate the net flux of migrants. Though such an effect is possible, a large proportion of migrants moved in each direction during each season.

Our rather crude estimates of the timing of dispersal, and the equally crude designations of periods of population increase and decline, could also influence the results, though not enough to alter the conclusion of reciprocating dispersal by white-footed mice. DWM and his assistants sampled mice during their two primary breeding seasons, in April, May and June as well as August, September and October. Recruitment in late-autumn after the October nest-box check would have allowed adult population densities to continue increasing into November. If so, reciprocating dispersal predicts preferential migration toward the edge and fencerow

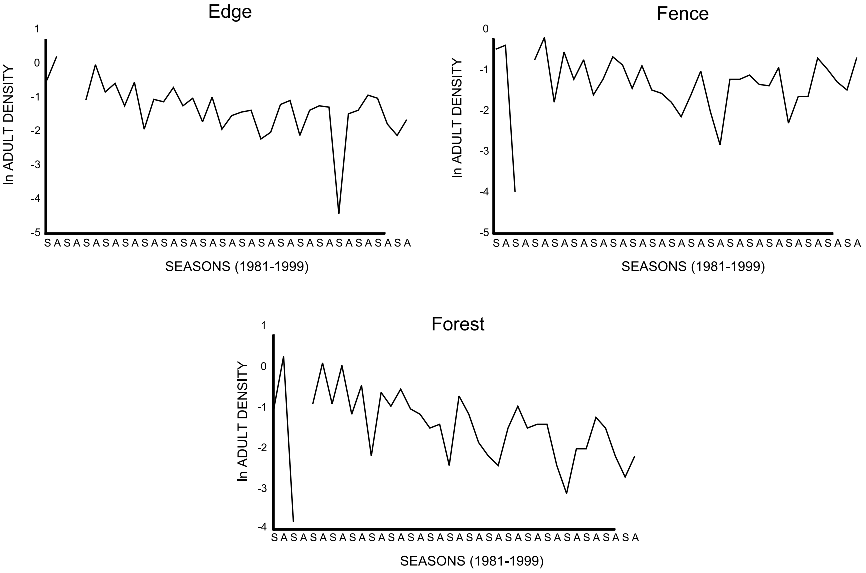


Fig. 5. Population densities of adult white-footed mice (mean number nest-box^{-1}) varied between seasons and among years in three different habitats in southern Ontario, Canada. Mean density tended to decline over the 19-year period (note logarithmic scale). There was no census during autumn 1983, and no adults were captured in the edge habitat during spring 1982. "Fence" is short-hand for fencerow habitat.

habitats during part of the period that we classified as the season of population decline. Similarly, populations in early spring may have continued to decline after animals began to reproduce, and dispersal would be biased toward forest habitat during the period classified as population increase. While each effect would make it more difficult to detect seasonally-biased dispersal, neither is likely to explain the overall pattern of balanced dispersal. Many animals would be available for emigration out of the forest when population density is high in autumn, but few immigrants would remain when population density is low in the spring.

Yet another possibility is that the seasonally-lagged density dependence exhibited by white-footed mice (Morris 1996a) confounds decisions on habitat choice. Regardless of direction, the time-dependent pattern of dispersal depends critically on the timing of habitat selection relative to patterns of population growth (Morris et al. 2004). Long time-lags between population growth and habitat selection would, during population increase, tend to ameliorate reciprocating dispersal as population growth rates would decline in donor habitats more quickly than in receiver habitats.

Seasonal and other lags may also influence the behavioral decision to disperse if fitness depends on previous densities. Animals may be confused by otherwise reliable behavioral cues of density-dependent habitat quality. The problem of time lags may often be compounded by developmental, reproductive, condition-dependent (Ims and Hjermann 2001), or other proximate (Stamps 2001) lags. Young individuals must develop to an appropriate life-history stage before they can disperse, while their parents may be similarly constrained by the period of parental care. Habitat and density assessment also takes time and adds an additional lag to habitat selection. Behavioral time lags are unlikely to account for balanced dispersal, however, because it is reasonable to expect that lags associated with habitat selection are of much shorter duration than those associated with population growth. Indeed, our ability to draw isodars for a variety of rodent species, across a wide spectrum of ecosystems (Morris 1988, 1994, 1996b,c, 1999, Rosenzweig 1991, Knight and Morris 1996, Morris et al. 2000), suggests that rodent habitat selection occurs much more quickly than intrinsic population dynamics.

The geographical orientation and scale of the three habitats also predisposes rodents toward balanced dispersal. Animals living in edge habitat probably include forest habitat in their home ranges. Animals living in forest boxes forage in the edge and beyond. Some animals that moved from a forest box to edge, or vice versa, may not have truly dispersed but simply shifted the center of their foraging and social activities. This "landscape" perspective is reinforced by the reduced dispersal to and away from fencerows that emanate from different sides of the woods. Edge and fencerow boxes located far away from the forest would be less disposed to receiving immigrants from the forest boxes than would closer boxes. But emigrants from those same boxes would also have a lower probability of reaching the forest. The salient point is that even though dispersal was reduced in the distal fencerows, the small number of emigrants was balanced by the number of immigrants.

Episodes of reciprocating dispersal may also lead to an overall balanced pattern if density-dependence among habitats varies through time. Whether dispersal is biased toward any particular habitat would depend on population density, and how it varies among habitats at different times. The curved fencerow isodars (Fig. 4), for example, suggest that reciprocating dispersal can itself vary with density. The reason for this prediction is that directional dispersal occurs only when density-dependent fitness differs among habitats (Morris et al. 2004). Differences in density between fencerows and the other two habitats occurred only at low and (especially at) high population sizes (Fig. 4). Thus, dispersal at high population sizes would reflect the higher density of animals in forest and edge habitats. But at low and intermediate population sizes, the densities in fencerows tended to equal those in the forest and edge (Fig. 4). Since relatively few animals moved between the fencerows and the other habitats (Fig. 3), it is hardly surprising that there was no consistent seasonal pattern in fencerow dispersal.

We caution readers that none of the possible explanations for a net balance in dispersal disagrees with the overall pattern of seasonally reciprocating dispersal, and of predictions from habitat-selection theory. But it may be a mistake, nevertheless, to search for a ready-made ecological solution to a strategy of movement that is of paramount evolutionary significance (Gaines and McClenaghan 1980, Morris 1991b). Would it not be possible for a population, and particularly so for that of a habitat generalist such as *P. leucopus*, to possess multiple forms of dispersal? Some individuals might be forced to migrate out of habitat that produces a "surplus" of individuals (source–sink dynamics). Animals using cues related to habitat quality could evolve a conditional strategy with a fixed dispersal rate linked to those cues (balanced dispersal). While such a conditional strategy should be inferior to one based on density-dependent habitat selection, the relative fitnesses of the two strategies might be similar if the difference in habitat quality is constant through time. A strategy based only on density-dependent habitat selection may be inferior to simpler conditional strategies if the costs (and time) of assessing and responding to complex density-dependent cues are high. Both types of strategies may coexist if periods of consistent differences in habitat quality are interrupted by stochastic pulses that alter density and fitness. While a theoretical analysis of competing strategies is beyond the scope of this contribution, there appears to be adequate variation within and among habitats to maintain multiple dispersal strategies.

The potential existence of multiple strategies also highlights the importance of including density-dependent habitat selection in the analysis of dispersal. Had we simply analyzed the percent of animals moving from one habitat to another, we would have concluded, incorrectly, that white-footed mice in our study area are regulated by source–sink dynamics (a greater proportion of mice living in forest boxes dispersed than did those in edge and fencerow habitats). Had we included only the sum of all rodents dispersing, we would have concluded (again incorrectly) that dispersal by white-footed mice confirms the balanced dispersal model (the number of immigrants was balanced by the number of emigrants; the rate of dispersal was inversely related to carrying capacity). We were able to confirm that dispersal by white-footed mice reciprocates between habitats only by explicitly modelling the effects of habitat selection, and by including its unique predictions in our analysis.

Whether multiple strategies exist or not, it is apparent that dispersal by white-footed mice is determined, at least in part, by density-dependent habitat selection. The associated reciprocating dispersal adds another dimension to our understanding of metapopulations. Populations undergoing periodic (e.g. seasonal) changes in abundance are likely to experience associated cycles of dispersal. A study during a period of population increase would identify a different habitat as a donor than would a study during population decline. This result, plus the recent discovery of source–sink inversions (Boughton 1999), suggests that ecologists must possess a reasonable time-series of population densities and dispersal to properly identify sink and source (receiver and donor) habitats. Similar care must be practised before invoking balanced dispersal as an explanation for local movements among habitats.

We are encouraged by the close fit of movement by habitat-selecting white-footed mice with a priori predictions of reciprocating dispersal. We believe that these data, and several converging studies that verify density-dependent habitat selection in many different systems (Rosenzweig and Abramsky, 1985, Morris 1987, 1989, 1997, Rosenzweig 1991, Swain and Sinclair 1994, Rodríguez 1995, Swain and Kramer 1995, Knight and Morris 1996, Abramsky et al. 1997, Morris and Davidson 2000, Fernandez-Juricic 2001) point strongly to habitat selection as the appropriate null model for spatial ecology (Morris and Brown 1992, Morris 1995, 2003a,b). Indeed, all three theories of dispersal are based on underlying strategies of habitat selection. Irrespective of their abilities to explain dispersal, each theory adds to an increasing line of evidence emphasizing the crucial and diversified roles that habitat, and habitat selection, play in ecology and evolution.

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