Temporal and spatial population dynamics among patches connected by habitat selection

Douglas W. Morris

Studies of population regulation that do not explicitly include habitat may often misrepresent the nature of density dependence. Habitat's influence on population regulation can be assessed by cross-correlations of population density in different habitats (isodars). Different forms of habitat-dependent population regulation can be revealed by their isodars. Isodars can also be used to predict unique sets of interactions between estimates of fitness and population density in different habitats. I explore the role of habitat on population regulation and test the underlying theory with a long-term study of the population dynamics and reproductive success of white-footed mice living in nest boxes. The data revealed persistent but possibly declining seasonal populations connected by habitat selection. The theory predicts significant interactions between fitness, habitat and population density. Recruitment success (an estimate of a female's current reproductive value) depended upon seasonally lagged density but did not vary among habitats. Maternal survival (an estimate of residual reproductive value) confirmed the predictions because it depended not only upon seasonally lagged density, but also upon an interaction with habitat. There was no evidence of asynchrony in density dependence among habitats that could reduce the effectiveness of habitat selection in population regulation. The results are consistent with theories of habitat selection, they demonstrate the role of habitat selection in population dynamics and confirm the theories' ability to infer habitat's influence on population regulation.

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Biological populations are dynamic in space and in time. No species is everywhere abundant and no species can increase or decline indefinitely. Two polar alternatives suggest themselves. Either 1, density-dependent processes modify patterns of distribution and population growth or 2, stochastic events in time and space have similar influence. Both approaches have a long, colorful and contentious history. Yet we are left with the unpleasant reality that the dynamics of only a few natural populations are reasonably understood. One explanation may be that few studies have successfully linked appropriate temporal and spatial scales in studying the dynamics of natural populations.

But what are the appropriate temporal and spatial scales of population regulation? Many supposedly regulated populations are known to vary over time intervals corresponding to several generations of their members (Finerty 1980, Schaffer 1985, Royama 1992, Turchin and Taylor 1992). Many of these populations, and numerous others, also have predictable dynamics (often annual or seasonal) that correspond to either the lifetimes or breeding intervals of individuals. Populations may be "regulated" at large spatial scales where dispersing individuals "rescue" sub-populations from demographic and other stochastic "accidents" (Levins

1969, Brown and Kodric-Brown 1977, Hanski 1982, 1990,1991), or by out-of-phase dynamics (Reeve 1988). At smaller spatial scales, density-dependent dispersal of individuals among habitats of varying quality can act as a strong regulatory factor on local population dynamics (Lidicker 1962, 1975, 1985a, b, Anderson 1970, MacArthur 1972, Van Horne 1983, Morris 1988, Pulliam 1988, Pulliam and Danielson 1991). Population dynamics can be stabilized (Hassell et al. 1987, Mountford 1988) or destabilized (Hassell 1987, Stewart-Oaten and Murdoch 1990) by reproduction in spatially segregated patches.

An ecologist could legitimately choose any of these scales and their interactions as a paradigm for studying population regulation. It would be foolish, however, to choose a population for study simply because its dynamics are known to vary over different spatial and temporal scales. Productive studies should key on dynamic populations that vary in both space and in time and in which there is strong evidence that at least some of the dynamics are density-dependent.

This paper's objectives are 1, to evaluate the role of density in determining both temporal and spatial population dynamics 2, to assess the existence and importance of interactions between temporal population dynamics and density-dependent habitat selection in population regulation and 3, to test whether spatial patterns of population density can be used to infer how the relationships between fitness and density change among habitats. I achieve objective 1 by illustrating the importance of habitat to studies of population regulation and by the analysis of long-term data on the spatial/temporal population dynamics of white-footed mice. Objective 2 is achieved by analyzing the relative importance of density, habitat, time and their interactions on juvenile recruitment and maternal survival. I show how theories of habitat selection can be used to predict spatial/temporal density dependence in fitness and demonstrate their application to white-footed mice (objective 3). The interactions involving recruitment and survival are used to test the theory.

The density of this population varies among years, between seasons and among habitats. Habitat selection appears to be density-dependent (Morris 1989a, 1991) and there is strong evidence that habitat selection has played a role in the evolution of white-footed mouse life history (Morris 1992a). Populations of white-footed mice in fragmented agricultural landscapes (such as the one reported here) are composed of metapopulations that exchange individuals (Fahrig and Merriam 1985, Merriam et al. 1989, Merriam and Lanoue 1990, Merriam 1991). Most importantly, the population occupies nest boxes and it is thereby possible to assess how recruitment has varied in space, in time and in response to changes in population density.

The importance of density-dependent habitat selection to population regulation

One of the central objectives in empirical studies of population regulation is to determine the functional relationship between estimates of reproduction and survival with population density. Theories of density-dependent habitat selection alert us to the possibility that this functional relationship varies with habitat. If so, then simply documenting the average effect of density among habitats may frequently lead to biased interpretations of population regulation.

Imagine a landscape composed of two equally represented habitats within which reproductive success declines with increased density and between which individuals select habitat according to an ideal free distribution (Fretwell and Lucas 1970; Fig. 1). Assume, for simplicity, that individuals can select any point in the landscape without cost. Population densities in the two habitats will be adjusted such that average reproductive success of individuals is the same in each. A study that ignores habitat will yield biased estimates of density, and thereby biased estimates of the effects of density dependence, whenever the proportions of the two habitats represented in the data fail to correspond to their representation in the landscape (Fig. 1). Even studies that stratify the estimates of density among habitats will yield different results between landscapes containing different proportions (or even different kinds) of habitats. All would reveal density-dependent
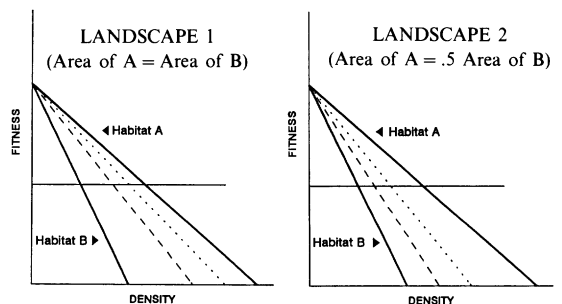
Fig. 1. Left: An ideal free distribution between two habitats is achieved when the densities in each habitat are adjusted such that average reproductive success is equivalent in each (horizontal line). The average density in the landscape, and the average decline in fitness, is a weighted average of the areas of the two habitats in the landscape (dashed line, both habitats assumed to be equally common in this example). The dotted line represents the average decline in fitness revealed by a study that has twice as many sampling points located in habitat A than it does in habitat B. Right: The functional relationships with density within habitats are identical to those on the left, but habitat A is assumed to be composed of one half the area as on the left. The average decline in fitness is reduced. The dotted line is the average revealed by the same sampling program used in the figure on the left. Stratified designs would also yield different average relationships between fitness and density (compare the slopes of the dashed lines).

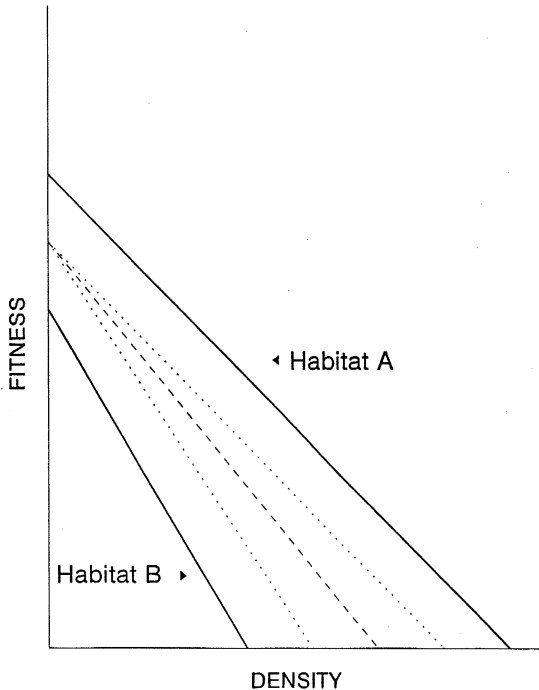Fig. 2. Similar average population densities can be produced in different landscapes whose habitats vary in their relationships between reproductive success and population density. Solid lines represent habitats A and B in a landscape in which the relationships between fitness and density diverge from one another but only habitat A is occupied at low density. Dotted lines represent an alternative landscape with diverging fitness-density functions in which both habitats are occupied at all densities. The single dashed line represents the average effect in both landscapes. A study that ignored habitat would conclude that processes of density-dependent population regulation are similar when, in fact, they are different.

regulation because average reproductive success declines with density in each case. But the functional relationship would be different in each instance, even if the relationship within habitats was identical.

It may frequently be the case, however, that the functional relationships "within" habitats vary among landscapes. This leads to the discomforting prospect that a study ignoring habitat may conclude that the relationship between reproductive success and population density in different landscapes is identical, when in fact the average effect is produced by completely different relationships (Fig. 2).

How, then, does one include habitat's influence on population regulation? The approach I use here is to record paired temporal estimates of population density and reproductive success in different habitats. I search for habitat differences in reproductive success using density as a covariate. Significant fitness × habitat × density interactions reflecting different fitness-density functions would reveal each habitat's different role in temporal population regulation. Moreover, habitat selection theories allow us to predict, a priori, what the form of the interaction should be and how fitness should vary among habitats.

Isodar theory: A priori predictions for spatial density dependence

Imagine as before a landscape composed of two habitats. Assume that each has the same relationship between fitness and density except that fitness at any given density is greater in habitat A than it is in habitat B (Fig. 3, top left). Assume further that individuals select between the two habitats in an ideal-free manner. Average reproductive success will be the same in each habitat (Fretwell and Lucas 1970). When theories of density-dependent habitat selection adequately describe spatial distribution we can infer differences in regulation between habitats using isodars, lines that plot the joint densities in the habitats assuming ideal habitat selection (Morris 1987, 1988, 1989b, 1990, 1992a). The isodar (Fig. 3, top right) is constructed by plotting the densities in the habitat with the higher fitness-density curve (habitat A) against the corresponding ideal den-
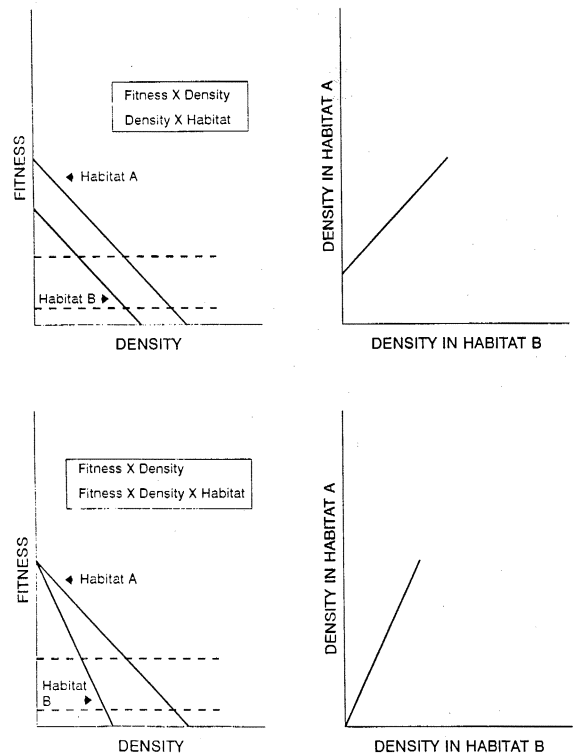
Fig. 3. Models of ideal-free habitat selection and their resulting isodars that can be used to predict unique sets of interactions among fitness, density and habitat. Intersections of the fitness-density curves with the dashed lines represent examples of predicted densities assuming ideal-free selection. The interaction graph for parallel population regulation (top) yields two-way interactions only (if comparisons are restricted to densities where both habitats are occupied, fitness should decline with increased density, and density should be consistently greater in habitat A than it is in habitat B). The graph for divergent regulation (bottom) yields a three-way interaction where the relationship between fitness and density depends upon habitat.

sity in the other (habitat B, the ideal-free isodar is given by the intersections of the fitness curves with horizontal lines of equal fitness). The isodar is the solution to the evolutionarily stable strategy of ideal habitat selection that, in this case, has a slope of 1.0 (parallel population regulation, Morris 1988). Note, over the range of densities where both habitats are occupied, that fitness varies with density, that density depends upon habitat, but that there is no three-way interaction between fitness, density and habitat.

Now assume that the fitness curves diverge from one another (Fig. 3, bottom left). With ideal-free habitat selection the resulting isodar has a slope greater than one (Fig. 3, bottom right, diverging population regulation, Morris 1988). Similarly, if the curves converge (convergent population regulation), the isodar slope will be less than unity (Morris 1988). Note, with non-parallel ideal-free population regulation, that the relationship between fitness and density depends upon habitat (Fig. 3, bottom) and that this is differentiated from the previous example of parallel ideal-free population regulation by the slope of the isodar (greater than or less than one).

Many species may select habitat such that the average reproductive success is greater in one habitat than it is in the other [e.g., ideal despotic (Fretwell and Lucas 1970) or ideal pre-emptive (Pulliam 1988) distributions]. Isodar solutions for these forms of ideal habitat selection can be generated by plotting the intersections of the fitness-density curves with parallel lines of positive slope (average reproductive success consistently greater in one habitat than it is in the other, Fig. 4). For both forms of habitat selection, fitness depends upon habitat. With divergent regulation, the habitat with the greatest density should also have higher average fitness. Only non-parallel fitness-density functions yield a complete set of interaction terms (Fig. 4, bottom). Curvilinear or nonlinear functions can be detected by patterns in residual variation about the isodar regression.

Thus, one can collect replicated density estimates between pairs of habitats connected by habitat selection and use the isodar to 1, test for habitat-dependent population regulation and 2, to predict a priori the pattern of interaction between fitness, density and habitat assumed by the theory. I use both approaches to assess spatial population regulation in a population of white-footed mice (*Peromyscus leucopus*) occupying forest, edge and fencerow habitats in southern Ontario, Canada. White-footed mice are known to be territorial during the breeding season (Burt 1940, Nicholson 1941, Stickel 1968, Metzgar 1971, Rowley and Christian 1976, Wolff 1986), implying that fitness should be greater in one habitat than in another (interaction terms should correspond to those diagrammed in Fig. 4). This prediction is consistent with previous tests that inferred a despotic distribution to explain white-footed mouse habitat selection (Morris 1988, 1989a, 1991, Halama and Dueser 1994).
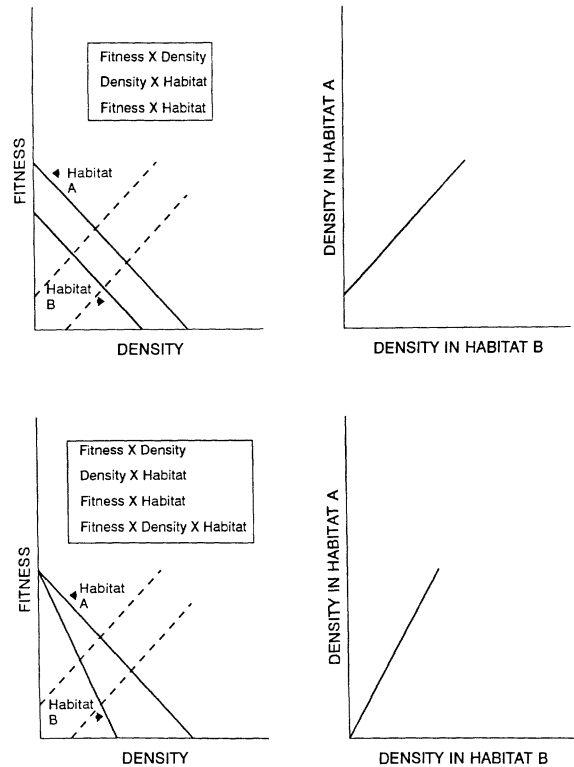

Fig. 4. Interaction graphs for ideal despotic and ideal pre-emptive habitat selection where average fitness is greater in one habitat than it is in the other. Intersections of the fitness-density curves with the dashed lines represent examples of predicted densities assuming ideal habitat selection. The graph for parallel regulation (top) yields all possible two-way interactions between fitness, density and habitat. The graph for divergent regulation (bottom) yields these plus a three-way interaction where the relationship between fitness and density depends upon habitat. Note that fitness differences between habitats act to increase the density in habitat B relative to that for ideal-free habitat selection. The isodar for parallel regulation has a lower intercept for the same pair of habitats than that in Fig. 3, the isodar for divergent regulation has reduced slope. Regardless, one would normally require information on behavior to differentiate between the predictions of ideal free versus other ideal forms of density-dependent habitat selection.

The isodar approach has at least one potential shortcoming. Delayed density-dependent effects may vary among habitats thereby modifying the rules of habitat selection. If the density-dependent response is delayed in some but not all habitats, or if density dependence is otherwise asynchronous among habitats, density may no longer be a reliable indicator of habitat quality (see also Van Horne 1983, 1986, Maurer 1986, Wiens 1989, Hobbs and Hanley 1990, Kareiva 1990). Yet the same asynchronies that destroy the effectiveness of habitat selection may often act to increase population persistence (e.g., Hassell and Sabelis 1987). Many natural populations are known to exhibit delayed density-dependent dynamics (Finerty 1980, Schaffer 1985,

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Royama 1992, and many others) often in response to the dynamics of their predators or prey whose habitat selection may lead to asynchronous spatial effects. Movements between habitats take time, even if in response to density, and habitat selection may thereby itself act as an additional time-lag influencing population dynamics. My analysis of temporal-spatial variation allows me to assess delayed density-dependence in each habitat.

Methods and study area

My analyses of spatial-temporal density dependence are based on 12 years' data on the population dynamics, demography and life history of white-footed mice. These common nocturnal rodents occupy wooden nest boxes in forest, forest edge and fencerow habitats embedded in an agricultural landscape in southern Ontario, Canada. Nest boxes have been monitored at approximately monthly intervals during the reproductive season [twice each autumn (September, October, not in 1982), and three times during each spring (April-June, except spring 1983, April and May checks only)]. Nest boxes were attached to trees whenever possible and were located at suitable sites within 10 m of permanent 'stations' at 30-m intervals. Boxes were arrayed in a grid pattern in the forest and along linear transects elsewhere (Morris 1989a).

All three habitats are composed of secondary forest. Red and white oaks (*Quercus rubra, Q. alba*), hickories (*Carya* spp.), elms (*Ulmus americana, U. rubra*) and ash (*Fraxinus americana*) dominate the forest canopy. Hawthorns (*Crataegus* spp.), prickly ash (*Zanthoxylum americanum*), red-osier dogwood (*Cornus stolonifera*), brambles (*Rubus* spp.) and saplings help to create a variably dense understory. Ground vegetation varies from vernal flowers (e.g., trout lily (*Erythronium americanum*), Canada violet (*Viola canadensis*), mayapple (*Podophyllum peltatum*)) in the forest and centre of the fencerows, to a mixture of herbs and grasses along the disturbed boundaries of the edge and fencerows (e.g., goldenrod (*Solidago* spp.), teasel (*Dipsacus sylvestris*), yellow sweet clover (*Melilotus officinalis*)).

Supplemental live-trap censuses (single Longworth live traps placed at 15-m intervals in a grid pattern) were conducted in the forest each spring and autumn from 1983 through spring 1989. Censuses consisted of two trap rotations of three nights each where every third trap-line was sequentially trapped each of the three nights.

All mice captured in live traps were individually marked with ear tags, measured (body length), weighed, sexed, classified by reproductive status (females; lactating, pregnant, vagina perforate or imperforate, males; testes descended or abdominal) and released. All juvenile, sub-adult and adult mice found in nest boxes were processed similarly and returned to the nest box. Immature mice less than three days of age were counted and sexed, if possible, but otherwise left undisturbed.

Litters were assumed to occupy a single nest box. Juvenile mice of similar development estimated to be 20 d of age or less (Layne 1968) and accompanied by a lactating female, or immature mice (eyes closed) at similar stages of development, were assumed to be siblings. Females were assigned the status of mother only if they were the sole lactating female found in a box containing a valid litter.

Densities for live-trap data were estimated by the minimum number of adult mice known to be alive during each season. Densities for nest-box data were calculated as the mean number of adults occupying boxes in a given habitat over all censuses during each season (this estimate standardized the data by habitat and for variable numbers of nest-box checks in the spring versus autumn seasons). Further details on sampling can be found in Morris (1989a).

My analyses of spatial and temporal density dependence on reproductive success are based on two binary estimates of a female's evolutionary fitness; litter success and maternal survival. Litters from which at least one offspring was later 'recaptured' in a nest box as an adult were classified as successful. All others were unsuccessful. Most litters produced by this population of *P. leucopus* are not successful and most litters that are successful are represented by a single surviving offspring (Morris 1989a). Litter success should thus be a reliable estimate of a female's reproductive success from a given reproductive episode (e.g., current reproductive value).

Mothers recaptured in boxes in a subsequent season were classified as 'survivors', those that were not recaptured in a second season represented the 'not known to survive' category. Seasonal survival should be a reasonable indicator of a female's potential for iterated reproduction (e.g., residual reproductive value) because most reproduction in this population occurs in the April-June and September-October reproductive seasons (Morris 1989a; see Rintamaa et al. 1976, Goundie and Vessey 1986, Wolff 1986, and Wolff et al. 1988 for independent confirmation of this seasonal pattern in other populations of *Peromyscus*).

Statistical analysis

Probabilities of litter success were estimated by stepwise logistic regression (SPSSPC+, Norušis 1990) according to the following model:

$$\theta_i = \exp(\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \dots$$
$$+ \beta_i X_i / [1 + \exp(\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \dots + \beta_i X_i] \quad (1)$$

where θ_i represents the probability of a successful litter, β_i's are regression coefficients, and X_i's are independent variables suspected of having significant effects on litter success. Independent variables included year of study, litter size, season, habitat, mean adult density, mean adult density during the previous reproductive season, mean adult density one year previous and all season × habitat × density interactions. Categorical variables were coded such that logistic regression coefficients represent the difference of a given category from the average of all categories (Norušis 1990). The significance of the logistic model was assessed by log-likelihood-ratio tests, the significance of the individual coefficients was assessed by the WALD statistic (square of the ratio of the logistic regression coefficient to its standard error, Norušis 1990). The probability of maternal survival was evaluated similarly. All other statistical analyses were performed in MINITAB (PC Version 8).

The logistic regressions I present here are not intended to reveal the best possible models for either litter success or maternal survival. Rather, the regressions are used primarily as inferential tools to assess spatial and temporal effects on the two estimates of reproductive success. I am especially eager to know how the relative roles of density, season, habitat and their interactions on reproductive success correspond to the isodar predictions. Logistic regression models are sensitive to mis-specification. My use of eq. (1) assumes that inclusion of other independent variables will not modify the spatial and temporal patterns reported below.

Results

Reliability of nest-box density estimates

Nest-box estimates of density in the forest plot compared favorably with the independent live-trap estimates (Fig. 5, $r = 0.95$ for log-transformed data, $r = 0.92$ for untransformed data). The density of adults found in nest boxes appears to be an accurate and unbiased estimator of the density of adult animals in the population.

Patterns of density in space and time

The population dynamics of white-footed mice in each habitat were dominated by seasonal fluctuations reflecting the discontinuous breeding seasons of this species (Fig. 6). Mean annual population densities in each habitat declined steadily (Fig. 6, $n = 10$). Temporal changes in population density were more tightly linked between the forest and edge habitats than between these two habitats and the distal fencerows (Fig. 7). The density in the forest tended to be greater than in either

of the other two habitats (forest median = 0.58 adult mice per nest box, edge = 0.52, fence = 0.47) but the differences were only marginally significant (Friedman's two-way non-parametric analysis of variance, $S = 5.7$; $df = 2$, $P = 0.058$).

I searched for crude differences in population regulation among habitats by plotting the log of the net reproductive rate ($\ln N_{t+1} - \ln N_t$) versus the log of population density ($\ln N_t$) (e.g., Royama 1992) in an analysis of covariance. The regression was highly significant (Table 1, Fig. 8) and negative (slope = -1.14), reflecting population persistence with no apparent differences in regulation among habitats.

The seasonal population dynamics illustrated in Fig. 6 suggest more or less consistent declines in adult population density over the non-reproductive winter season. I tested for this effect by regressing ($\ln N_{spring} - \ln N_{autumn}$) versus $\ln N_{autumn}$. The regression was significant ($F_{(1, 27)} = 11.35$, $P = 0.002$) and revealed consistent population decline (slope = -1.02, autumn density greater than spring density in 27 of 29 observations) even though large numbers of autumn-born juveniles were available for recruitment. None of the above analyses suggests asynchronous density dependence among habitats.
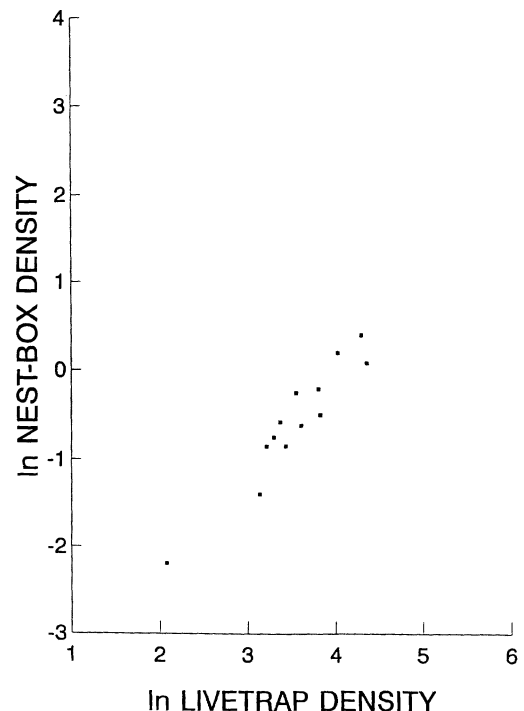

Fig. 5. Nest-box estimates of adult population density in the forest compared favorably with independent estimates of the minimum number known alive from live-trapping studies in the same habitat.
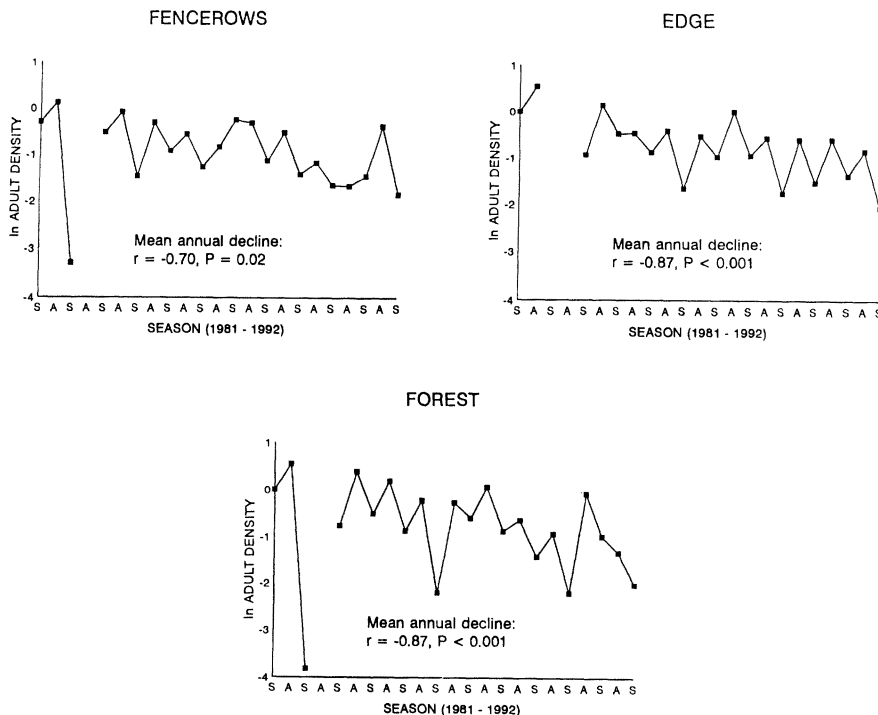
Fig. 6. Densities of adult white-footed mice occupying nest boxes fluctuated seasonally. Mean annual densities declined steadily over the duration of the study period (1981–1991). No adults were found in nest boxes in the edge habitat in the spring of 1982. Boxes were not sampled in the autumn of that year.

Density-dependent habitat selection

All regressions of population density in one habitat against population density in another habitat at the same time (isodars) were highly statistically significant (Fig. 7). The scatter of points was greater for fencerow contrasts than it was for the cross-correlation of densities between forest and edge habitats. I interpret this as an indicator of spatial effects on the ability of habitat selection to adjust local population density (Morris 1994). The mean distance that individuals must move between habitats is necessarily greater between the linear fencerows and either forest or edge than it is between those two adjacent habitats.

Isodar contrasts between forest and edge, as well as between edge and fencerow yielded slopes not significantly different from 1.0 (95% confidence intervals of the geometric mean regression (GMR) slopes = 0.97–1.38 and 0.99–1.73 respectively). The isodar slope for forest and fencerow, however, was significantly greater than 1.0 (95% confidence interval GMR slope = 1.4–2.06).

Note that the isodar for the forest vs edge passes through the origin with a slope of approximately 1.0. This suggests that the respective fitness-density curves for these two habitats are not only parallel to one another, they are congruent. Fitness should be similar in both habitats. The isodar for the forest versus fencerow comparison has a slope greater than one,

implying that fitness should be significantly greater in the forest than in the fencerow. We thus predict a significant fitness × habitat × density interaction driven by high fitness in the forest habitat (compare the forest vs fencerow isodar in Fig. 7 with the predictions in Fig. 4). The final isodar, that contrasting forest edge and fencerow is intermediate between the other two. This suggests that my estimates of fitness in the edge should also be intermediate between those of the forest versus fencerow.

Spatial and temporal density dependence in fitness

I was concerned that the significant negative trends in mean annual population density might jeopardize my ability to detect temporal density dependence in litter success and maternal survival. I performed two logistic regressions to eliminate this possibility. First, I used the actual density estimates as independent variables in one set of analyses. Second, I detrended the densities in each habitat by replacing the actual density estimates with the residuals from the least squares regression of mean annual population density against time [these estimates were generated separately for each habitat to account for any differences in either mean density or in population decline; all analyses exclude data for 1982 because I had no estimate of autumn population densities that year (the boxes were checked in spring only)].
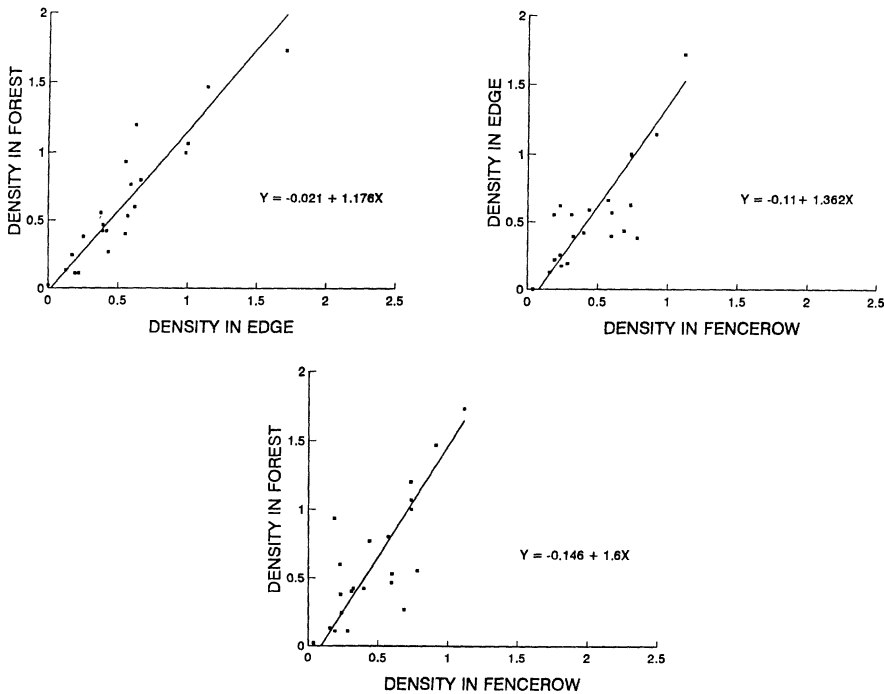
Fig. 7. Cross-correlations of adult density (isodars) between forest, edge and fencerow habitats. Equations were generated by geometric mean regression.

The detrended analyses, while suitable for temporal comparisons, are not appropriate tests of fitness × habitat × density interactions because they effectively exclude between-habitat differences in density.

Litter success

Both sets of analyses gave comparable results for litter success (Table 2). Each analysis was highly significant and each revealed a significant interaction among litter success, season and seasonally lagged population density. Contrary to predictions, habitat effects, as well as interactions of habitat with other variables, were not part of the final stepwise solution to the logistic model. The detrended analysis revealed seasonal effects that were not statistically significant in the original analysis.

I repeated the analyses using only season, habitat, density the previous reproductive season, and their interactions. This allowed me to increase sample sizes. The solutions and signs of the logistic regression co-efficients were identical to those of the original analyses.

Table 1. Analysis of covariance of log net reproductive rate versus log density for fencerow, edge and forest habitats.

Source	df	ss	P
ln N_t	1	54.01	<0.001
Habitat	2	0.37	0.63
Error	55	21.37	
Total	58	75.75	

I interpret the results as follows (Tables 3 and 4). Most litters were unsuccessful at recruiting offspring into the adult nest-box population. Spring litters were
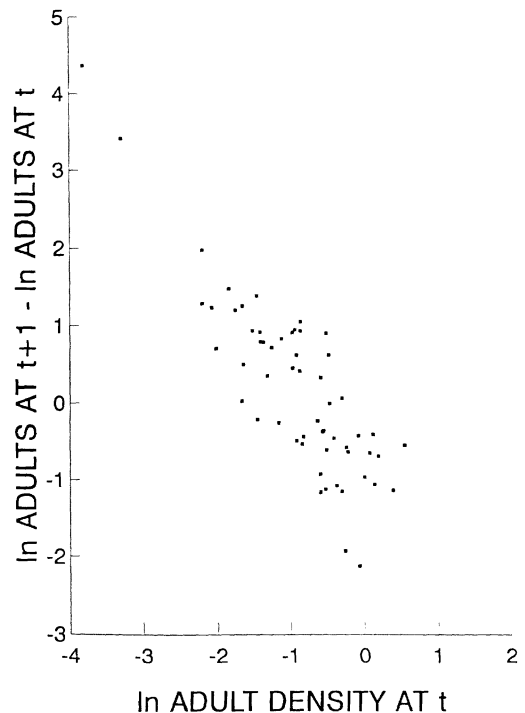

Fig. 8. Population growth rate of white-footed mice is a negative function of adult population density.

Table 2. Significant logistic regression models of spatial and temporal density dependence in litter success of white-footed mice in southern Ontario. Analyses are based on 155 spring litters and 143 autumn litters.

Analysis[a]	Dependent variable	Source[b]	df	LR χ^2 [c]	P
Normal	Litter success	Season × Density-season	1	27.53	< 0.0001
Detrended	Litter success	Season	1	12.12	0.0005
		Season × Density-season	1	5.80	0.016

[a] Normal analysis based on the original estimates of adult population density, detrended analysis based on the residual densities from the habitat-specific regressions of mean adult density over time.
[b] Density-season = adult density in the previous reproductive season.
[c] -2 Log-Likelihood-Ratio χ^2.

more successful than autumn litters (Table 3, detrended analysis). Seasonal differences in spring litter success were modified by delayed density dependence from the previous autumn season.

I explored the details of the season × seasonally lagged density interaction by hierarchical loglinear analysis (Norušis 1990). I created two density categories above and below the median score for the appropriate seasonal adult density and performed separate analyses for spring and autumn litters. The autumn analysis (187 litters) revealed highly significant main effects for litter success (more litters unsuccessful than successful) and seasonally lagged density (more litters were produced in autumns following high spring density than when spring density was low) but no significant interaction (Table 4). The spring analysis (155 litters), on the other hand, revealed the expected significant interaction between litter success and seasonally lagged density (Table 4, see also Table 3). The interaction was caused by higher spring success in years following high autumn densities than in years following low autumn densities (Table 4). The season × seasonally lagged density-dependent interaction in litter success in spring was thus different from the pattern in autumn where litter success was insensitive to variation in spring densities.

Maternal survival
Temporal and spatial density dependence for maternal survival was noticeably more complex than that for litter success (Tables 5 and 6). In analyses using the actual density estimates, maternal survival was heterogeneous across years, but this effect did not interact

Table 4. Numbers of successful and unsuccessful spring and autumn litters produced by female white-footed mice in southern Ontario.

Litter success in autumn	Density in preceding spring	
	Low	High
Successful	12	13
Unsuccessful	48	114

Log-linear analysis: More litters were successful than were unsuccessful and more litters were produced following high spring densities than following low spring densities.
Litter success: Partial LR $\chi^2 = 112.13$, df = 1, P < 0.0001
Seasonally lagged density: Partial LR $\chi^2 = 24.55$, df = 1, P < 0.0001
Interaction: LR $\chi^2 = 3.18$, df = 1, P = 0.07

Litter success in spring	Density in preceding autumn	
	Low	High
Successful	25	32
Unsuccessful	61	37

Log-linear analysis: The success of litters depended upon seasonally lagged population density.
Interaction: LR $\chi^2 = 4.93$, df = 1, P = 0.026

with any other variable. Maternal survival depended upon seasonally lagged density. Habitat differences in survival were modified by seasonally lagged density dependence.

The detrended analysis appeared to provide a clearer interpretation of temporal variance in maternal survival (Table 6). Maternal survival was less than average in fencerows (habitat effect significant, but this effect was linked to density, see the normal analysis above), greater than average in the forest, no

Table 3. Significant coefficients from the stepwise logistic regressions assessing litter success among years, litter size-classes, seasons, habitats, seasonally lagged density estimates and their interactions.

Variable	B	WALD	df	P
		Normal analysis		
Constant	−1.4	71.12	1	< 0.0001
Spring × Lagged density	1.17	24.91	1	< 0.0001
		Detrended analysis		
Constant	−1.35	65.43	1	< 0.0001
Spring	0.52	11.48	1	0.0007
Spring × Lagged density	1.01	5.66	1	0.017

Table 5. Significant logistic regression models of spatial and temporal density dependence in maternal survival of white-footed mice in southern Ontario. Analyses are based on 192 spring litters and 175 autumn litters.

Analysis[a]	Dependent variable	Source[b]	df	LR χ^2 [c]	P
Normal	Maternal survival	Year	7	14.69	0.04
		Density-season	1	5.34	0.02
		Habitat × Density-season	2	24.55	< 0.0001
Detrended	Maternal survival	Habitat	2	20.37	< 0.0001
		Density-season	1	21.48	< 0.0001

[a] Normal analysis based on the original estimates of adult population density, detrended analysis based on the residual densities from the habitat-specific regressions of mean adult density over time.
[b] Density-season = adult density in the previous reproductive season.
[c] −2 Log-Likelihood-Ratio χ^2.

Table 6. Significant coefficients from the stepwise logistic regression assessing maternal survival among years, litter size-classes, seasons, habitats, and their interactions (residuals from the long-term decline in mean density, detrended analysis).

Variable	B	WALD	df	P
Constant	−1.15	52.01	1	< 0.0001
Forest habitat	0.50	5.24	1	0.02
Fencerow habitat	−0.82	19.08	1	< 0.0001
Seasonally lagged density	1.83	19.38	1	< 0.0001

Table 7. Numbers of white-footed mouse mothers surviving from one breeding season to the next in southern Ontario.

Maternal survival	Density in the previous season	
	Low	High
Survived	35	69
Not known to survive	158	151

Log-linear analysis: Maternal survival depended upon seasonally lagged density.
Interaction: LR $\chi^2 = 9.71$, df = 1, P = 0.002

different from average in the edge and varied positively with seasonally lagged densities (Table 6). Interestingly, seasonally lagged density was a better positive indicator of maternal survival than was season, though it is clear that season and density are interrelated (Fig. 6 and Table 6). Detrending also eliminated the effects of annual variation on female survival that was shown to be significant in the normal analysis.

As with litter success, I examined the details of maternal survival at low and high seasonally lagged densities by hierarchical loglinear analysis. These analyses provided a modest increase in sample size because they evaluated only a subset of the variables included in the logistic regressions. The analysis (413 litters) demonstrated the dependence of maternal survival on density during the previous reproductive season. Maternal survival was greater when seasonally lagged density was high than when it was low (Table 7, see also Table 6).

I also evaluated maternal survival at both low and high seasonally lagged densities in each of the three habitats (habitat × density-season interaction). The hierarchical loglinear analysis in the fencerow habitat

(215 litters) revealed highly significant main effects (most mothers did not survive until the next reproductive season, more females reproduced at high than at low density, Table 8), but no significant interaction between survival and density.

The analysis in the edge habitat (128 litters) was different. Maternal survival depended upon the seasonally lagged density but, as demonstrated previously, maternal survival was greater following seasons of high, as compared to low, density (Table 8). The results of this analysis were confirmed in the forest habitat (70 litters) where there was again a significant interaction between maternal survival and seasonally lagged density, and where maternal survival was also greater following seasons of high versus low density (Table 8). Consistent with the survival × habitat × density interaction and the predictions from the isodar analyses, seasonally lagged maternal survival was lower at high density in the fencerow (0.12) than in the edge (0.35), and much lower than in the forest habitat (0.47, Table 8).

Discussion

The analyses I present here clearly demonstrate a persistent population of white-footed mice that has, nevertheless, declined consistently over the 12 years included in this study. The decline may be associated with gradual changes in vegetation structure as the forest matures. White-footed mice in southern Ontario are known to prefer complex vegetation profiles most often associated with intermediate, rather than mature, stages

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Table 8. Numbers of white-footed mouse mothers surviving from one breeding season to the next in three different habitats in southern Ontario.

Maternal survival in fencerows	Density in the previous season	
	Low	High
Survived	12	14
Not known to survive	67	122

Log-linear analysis: Most mothers did not survive until the next reproductive season and more females reproduced when densities in the previous season were high than when they were low.
Maternal survival: Partial LR $\chi^2 = 139.48$, df = 1, $P < 0.0001$
Seasonally lagged density: Partial LR $\chi^2 = 15.29$, df = 1, $P < 0.0001$
Interaction: LR $\chi^2 = 1.10$, df = 1, P = 0.29

Maternal survival in forest edge	Density in the previous season	
	Low	High
Survived	16	29
Not known to survive	46	37

Log-linear analysis: The probability of a mother surviving from one breeding season to the next was greater when density the preceding season was high than when it was low.
Interaction: LR $\chi^2 = 4.66$, df = 1, P = 0.031

Maternal survival in forest	Density in the previous season	
	Low	High
Survived	4	29
Not known to survive	13	24

Log-linear analysis: The probability of a mother surviving from one breeding season to the next was greater when density the preceding season was high than when it was low.
Interaction: LR $\chi^2 = 5.26$, df = 1, P = 0.022

of forest succession (M'Closkey 1975, 1976, M'Closkey and Lajoie 1975, Morris 1979).

Regardless as to cause, the declining densities complicate an already complex problem of trying to disentangle the relative roles of spatial and temporal density dependence on the population dynamics and life history of this common and widely distributed species. Previous analyses of its life history have demonstrated that spring litter success is greater in forest than in either edge or fencerow (Morris 1989a, 1992a). The analyses I report here demonstrate that the habitat differences disappear when seasonal effects and their interaction with delayed density dependence are included in the analysis.

An interesting perversion of regulation in this white-footed mouse population is that the positive relationship between spring litter success and autumn density actually represents negative density-dependence. Persistent populations possess a negative relationship between net reproductive rate and current density (Fig. 8, Royama 1992). In white-footed mice, autumn densities generally exceed those in spring (Fig. 6), and the greater the autumn density, the greater the change in population size. High autumn densities are a harbinger of high winter mortality. Years with the highest spring litter success are associated with years having the lowest overwinter survival (negative density dependence).

Most importantly, the fitness tests confirm the a priori predictions of habitat selection theory. Patterns of population density in different habitats can, under the proper conditions, be used to infer underlying similarities and differences in reproductive success that represent the essence of population regulation. A crucial corollary is that regulation of the entire population depends upon not only the habitat and density-dependent patterns of fitness, but critically upon density-dependent habitat selection. One cannot, however, use patterns of habitat-dependent density to predict which life history or demographic components of fitness may or may not vary with habitat. The evolution of habitat selection depends on the final currency of fitness only, not on its components. It is thus important to obtain multiple measures of fitness if one wishes to have a reasonable chance to evaluate the theory, and especially if one wishes to simultaneously evaluate the interactions between habitat selection and life history.

The temporal pattern for maternal survival was similar to that for litter success. Females that produced spring litters following winters of high mortality not only had a higher probability of recruitment from any single litter than did females reproducing in other years, they also had potential to produce more litters during their lifetime. Unlike litter success, seasonally lagged maternal survival was greater in the forest habitat. One cannot exclude habitat from the explanation for local population regulation of white-footed mice.

The results presented here are consistent with earlier suggestions that habitat selection can be used to guide our understanding of population regulation and resulting community organization (e.g., Morris 1988). One of the greatest threats to the use of these theories would appear to be asynchrony in density-dependence among habitats. It is noteworthy that I detected no asynchrony among habitats that were otherwise quite dissimilar in physical orientation, in the nature of their boundaries and in their nearest habitat neighbors in the landscape.

The implications to regional studies of population density are dramatic. The isodar and fitness data demonstrate more or less equivalent dynamics in forest and edge habitat. Habitat selection would appear, therefore, to have little effect on population dynamics of white-footed mice occupying only forest and edge in a landscape composed of otherwise unacceptable habitats. Regional population dynamics would be caused entirely by local carrying capacity, within-habitat regulation and by metapopulation dynamics. Habitat selection may, however, play a major role in population regulation in another landscape that included fencerows as an alternative to patches of forest.

Lest one becomes too enamored by the role of density-dependent habitat selection in population regulation, there may be a simpler explanation for the patterns I report here. The temporal cross-correlations that I used to construct isodars are likely to generate significant positive slopes regardless as to which habitats are compared. Such an artefact could occur whenever differences in seasonal estimates of density are greater than the differences in estimates between habitats. Seasonal differences alone should not influence the relative densities in the different habitats and cannot account for differences in the slopes of the regressions among different pairs of habitats.

It could be argued, as well, that greater density-dependent maternal survival in the forest necessarily increases population density in that habitat. More or less independent population regulation could be proceeding in each habitat without any density-dependent habitat selection. Yet, one might wish to ask what mechanism, other than density-dependent habitat selection, could result in parallel declines in population density among habitats where reproductive success is consistently greater in one habitat than it is in the others. The criticism does not detract from the tests presented here demonstrating, for this population of white-footed mice, that predictions from regressions of density in different habitats are consistent with independent estimates of within-habitat reproductive success.

An argument in favor of independent regulation could apply when a linear isodar has a slope greater than 1.0 and when the intercept is zero (diverging fitness curves). If average reproductive success is the same in both habitats (IFD), the density in each habitat will grow at the same rate even if individuals do not move between them. This can not be the case for ideal distributions where fitness is greatest in the habitat with greatest density. To show this, assume ideal habitat selection. With linear fitness curves

$$W_1 = a - b_1 N_1$$

and

$$W_2 = a - b_2 N_2$$

where W_i represents fitness in habitat i, a is the maximum fitness at low density and is identical for both habitats, N is population density and b is the slope. Assuming an ideal free distribution,

$$W_1 = W_2,$$

thus

$$a - b_1 N_1 = a - b_2 N_2$$

and

$$N_1 = (b_2/b_1)N_2$$

as reflected by the linear isodar. But if

$$W_1 > W_2,$$

$$N_1 > (b_2/b_1)N_2$$

the density in habitat 1 always exceeds its predicted density and the pattern of densities can only fit the isodar if there is directional movement from habitat 1 to habitat 2. In the white-footed mice studied here, maternal survival was approximately four times greater in the forest than in the fencerow suggesting that densities were maintained at a constant difference by directional migration.

It thus appears, in this population of white-footed mice, that techniques based on theories of habitat selection can be used to infer habitat's role in population regulation and coincident density-dependent evolution, and to test the underlying theory. It also vindicates, to some extent, the use of the these same models to infer scales of habitat use (Morris 1987, 1992b) as well as habitat's influence on the structure of ecological communities (Morris 1988, 1989b, 1990, 1992a). But one can not simply replace temporal with habitat studies, even if the research is restricted to appropriate scales of habitat selection. Temporal contrasts are essential to test for asynchronous regulation among habitats that may invalidate the application of density-dependent habitat selection and to reveal the detail of density dependence. Much of the interesting detail may be missed, or worse misinterpreted, unless one also considers habitat.

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