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.

D. W. Morris, Centre for Northern Studies, Dept of Biology and Faculty of Forestry, Lakehead Univ., Thunder Bay, Ontario, Canada P7B 5E1.

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 lifetime 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
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 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 relationships between fitness and density.](image-url)

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.
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.

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).

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,
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+, Norusis 1990) according to the following model:

\[
\begin{align*}
\theta_i &= \exp(\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_i X_i) \\
&= \frac{1}{1 + \exp(-\beta_0 - \beta_1 X_1 - \beta_2 X_2 - \ldots - \beta_i X_i)}
\end{align*}
\]
where $\theta$ represents the probability of a successful litter, $\beta_i$'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 ($\ln N_{\text{spring}} - \ln N_{\text{autumn}}$) versus $\ln N_{\text{autumn}}$. 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.
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)].
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 coefficients were identical to those of the original analyses.

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

![Graphs showing density correlations](image)

Fig. 7. Cross-correlations of adult density (isodars) between forest, edge and fencerow habitats. Equations were generated by geometric mean regression.

![Graph showing population growth rate](image)

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

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

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>ss</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>In N₀</td>
<td>1</td>
<td>54.01</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Habitat</td>
<td>2</td>
<td>0.37</td>
<td>0.63</td>
</tr>
<tr>
<td>Error</td>
<td>55</td>
<td>21.37</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>58</td>
<td>75.75</td>
<td></td>
</tr>
</tbody>
</table>
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.

<table>
<thead>
<tr>
<th>Analysisa</th>
<th>Dependent variable</th>
<th>Sourceb</th>
<th>df</th>
<th>LR $\chi^2$c</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Normal</td>
<td>Litter success</td>
<td>Season $\times$ Density-season</td>
<td>1</td>
<td>27.53</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Detrended</td>
<td>Litter success</td>
<td>Season</td>
<td>1</td>
<td>12.12</td>
<td>0.0005</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Season $\times$ Density-season</td>
<td>1</td>
<td>5.80</td>
<td>0.016</td>
</tr>
</tbody>
</table>

*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 $\chi^2$.

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 $\times$ seasonally lagged density interaction by hierarchical loglinear analysis (Norusis 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 $\times$ 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 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.

<table>
<thead>
<tr>
<th>Variable</th>
<th>B</th>
<th>WALD</th>
<th>df</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>-1.4</td>
<td>71.12</td>
<td>1</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Spring $\times$ Lagged density</td>
<td>1.17</td>
<td>24.91</td>
<td>1</td>
<td>&lt; 0.0001</td>
</tr>
</tbody>
</table>

Normal analysis

<table>
<thead>
<tr>
<th>Variable</th>
<th>B</th>
<th>WALD</th>
<th>df</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>-1.35</td>
<td>65.43</td>
<td>1</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Spring</td>
<td>0.52</td>
<td>11.48</td>
<td>1</td>
<td>0.0007</td>
</tr>
<tr>
<td>Spring $\times$ Lagged density</td>
<td>1.01</td>
<td>5.66</td>
<td>1</td>
<td>0.017</td>
</tr>
</tbody>
</table>

Detrended analysis

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

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

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

<table>
<thead>
<tr>
<th>Litter success in autumn Density in preceding spring</th>
<th>Low</th>
<th>High</th>
</tr>
</thead>
<tbody>
<tr>
<td>Successful</td>
<td>12</td>
<td>13</td>
</tr>
<tr>
<td>Unsuccessful</td>
<td>48</td>
<td>114</td>
</tr>
</tbody>
</table>

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

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.
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.

<table>
<thead>
<tr>
<th>Analysis</th>
<th>Dependent variable</th>
<th>Sourceb</th>
<th>df</th>
<th>LR $\chi^2$c</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Normal</td>
<td>Maternal survival</td>
<td>Year</td>
<td>7</td>
<td>14.69</td>
<td>0.04</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Density-season</td>
<td>1</td>
<td>5.34</td>
<td>0.02</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Habitat × Density-season</td>
<td>2</td>
<td>24.55</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Detrended</td>
<td>Maternal survival</td>
<td>Habitat</td>
<td>2</td>
<td>20.37</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Density-season</td>
<td>1</td>
<td>21.48</td>
<td>&lt; 0.0001</td>
</tr>
</tbody>
</table>

*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 $\chi^2$.

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).

<table>
<thead>
<tr>
<th>Variable</th>
<th>B</th>
<th>WALD</th>
<th>df</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>-1.15</td>
<td>52.01</td>
<td>1</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Forest habitat</td>
<td>0.50</td>
<td>5.24</td>
<td>1</td>
<td>0.02</td>
</tr>
<tr>
<td>Fencerow habitat</td>
<td>-0.82</td>
<td>19.08</td>
<td>1</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Seasonally lagged density</td>
<td>1.83</td>
<td>19.38</td>
<td>1</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

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

<table>
<thead>
<tr>
<th>Maternal survival</th>
<th>Density in the previous season</th>
<th>Low</th>
<th>High</th>
</tr>
</thead>
<tbody>
<tr>
<td>Survived</td>
<td></td>
<td>35</td>
<td>69</td>
</tr>
<tr>
<td>Not known to survive</td>
<td></td>
<td>158</td>
<td>151</td>
</tr>
</tbody>
</table>

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

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

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.

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

<table>
<thead>
<tr>
<th>Maternal survival in fencerows</th>
<th>Density in the previous season</th>
<th>Low</th>
<th>High</th>
</tr>
</thead>
<tbody>
<tr>
<td>Survived</td>
<td></td>
<td>12</td>
<td>14</td>
</tr>
<tr>
<td>Not known to survive</td>
<td></td>
<td>67</td>
<td>122</td>
</tr>
</tbody>
</table>

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: $\chi^2 = 1.10$, df = 1, $P = 0.29$

<table>
<thead>
<tr>
<th>Maternal survival in forest edge</th>
<th>Density in the previous season</th>
<th>Low</th>
<th>High</th>
</tr>
</thead>
<tbody>
<tr>
<td>Survived</td>
<td></td>
<td>16</td>
<td>29</td>
</tr>
<tr>
<td>Not known to survive</td>
<td></td>
<td>46</td>
<td>37</td>
</tr>
</tbody>
</table>

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, $P = 0.031$

<table>
<thead>
<tr>
<th>Maternal survival in forest</th>
<th>Density in the previous season</th>
<th>Low</th>
<th>High</th>
</tr>
</thead>
<tbody>
<tr>
<td>Survived</td>
<td></td>
<td>4</td>
<td>29</td>
</tr>
<tr>
<td>Not known to survive</td>
<td></td>
<td>13</td>
<td>24</td>
</tr>
</tbody>
</table>

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, $P = 0.022$
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

\[ a - b_1 N_1 = a - b_2 N_2 \]

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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References


Row, New York.


