

FITNESS AND PATCH SELECTION BY WHITE-FOOTED MICE

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Abstract.—The fitness of white-footed mice living in nest boxes was monitored in patches of forest, edge, and fence-row habitat to test theories of habitat selection. Reproductive success was significantly greater in the forest than in the other two habitats, a result that supports theories based on exclusive access to resources. The frequency distributions of litter production and recruitment success within habitats were not significantly different from random expectation. All litters produced in a particular habitat had equal chances of success, regardless of which box they were born in. Small-scale patches within habitats appear not to differ in the fitness achieved by individual colonists. The pattern of habitat use was inconsistent with the selection of individual breeding sites that maximize reproductive success. Site selection appears to be modified by processes acting at larger spatial scales. This interpretation is in agreement with census data that demonstrate the role of spatial scale as a predictor of density in these and other small mammals.

Ecologists have developed a variety of models that demonstrate profound implications of habitat selection to the spatial distribution, population dynamics, community structure, and evolution of biological species (see, e.g., Fretwell and Lucas 1970; Southwood 1977, 1988; Rosenzweig 1979, 1981, 1985, 1989; Pimm and Rosenzweig 1981; Holt 1985, 1987; Rosenzweig and Abramsky 1986; Morris 1987*a*, 1988, 1989*a*). These evolutionary models either explicitly or implicitly assume that habitat selection should maximize individual reproductive success. That is, individuals should distribute themselves across habitats in a way that maximizes their marginal fitness return (Fretwell and Lucas 1970; Rosenzweig 1974, 1981; Charnov 1976). Density-dependent versions further assume that average fitness declines with increases in population density, leading to an evolutionarily stable strategy of habitat selection (Pulliam and Caraco 1984).

The form of the habitat-selection strategy depends on the spatial distribution of reproductive success. When there is little variation in the quality of breeding sites within a habitat or little variation in fitness among individuals, the marginal return to an individual by habitat selection is close to the average of all individuals within the habitat. A strategy of selecting habitats on the basis of average reproductive success maximizes individual fitness (the ideal free distribution, Fretwell and Lucas [1970]; Pulliam and Danielson 1991). If some individuals are capable of achieving higher fitness than others by exclusive access to resources, however, subordinate individuals may be forced to select habitats of below-average quality

(the ideal despotic distribution, Fretwell and Lucas [1970]). The strategy changes if there is variation among sites within a habitat and if some individuals are able to exclude others from preferred sites. Individuals that select habitats to attain the best unoccupied breeding site will have higher expectations of fitness than individuals that select habitats on the basis of average breeding-site quality (Pulliam and Danielson 1991).

If so-called source habitats (those with many favorable breeding sites) produce a large surplus of emigrants, sink habitats (those with few favorable breeding sites) may contain a major component of the overall population (Pulliam 1988). Under these conditions population density may be a poor indicator of habitat "quality" (van Horne 1983; Pulliam 1988), even though individuals are selecting the highest-quality sites available. Similarly, occupation of sink habitats suggests that individuals may often occupy areas where populations can be sustained only by continued surplus immigration from source habitats (Pulliam 1988; Pulliam and Danielson 1991).

Pulliam and Danielson (1991) assumed an exponential distribution of breeding-site quality and simulated the preemptive model to evaluate the effects of habitat on population dynamics. They found that the loss of high-quality habitat for species that sample relatively few sites may cause extinction, whereas the same loss of habitat will reduce but not eliminate species that sample more sites. The relationships between population size and habitat quality can become complex but are easily simulated as long as the frequency distribution of breeding-site quality, the relative abundances and distribution of sites of differing quality, and the intensity of site sampling by individual colonists are known.

My purpose is to assess whether the preemptive model or some other is the best descriptor of habitat selection by free-living mammals. My research protocol has been to accumulate long-term data on the breeding quality of individual sites (nest boxes) occupied by female white-footed mice (*Peromyscus leucopus*) living in different habitats. Each nest box has been in the same location since 1983. This design allows me to empirically define the distribution of breeding-site quality and to test which of the different habitat-selection models corresponds to site selection by individuals.

METHODS

Field Research

Small wooden nest boxes were situated within second-growth deciduous forest, along the edge of a small woodlot and a larger one, and along overgrown fence rows emanating from the woodlots on a 40-ha farm between Lake Erie and Lake Saint Clair in southwestern Ontario (42°10'N, 83°30'W). Boxes were placed at permanent sites within 10 m of stations located at 30-m intervals. The life histories of white-footed mice were monitored at roughly monthly intervals three times each spring and twice each autumn from 1983 to 1988 (each of the 79 permanent boxes was examined 18 times during the spring and 12 times during autumn). Fifteen of the boxes were in forest habitat (the small woodlot), 28 in forest edge, and 36 in fence rows. Details of the nest-box sampling, classification of litters

and recruits, and general descriptions of the deciduous woods and fence rows can be found in Morris (1989a).

During each examination all mice more than 1 wk old were removed from the boxes, aged, sexed, measured, and individually marked with metal ear tags. The age of immature and juvenile mice was estimated by developmental stage (Layne 1968), and all adults and most young mice were weighed. All animals were classified as reproductive (testes descended for males, perforate vagina, lactation, and/or pregnancy for females) or not.

The woodlot nest-box array was overlain by a live-trap grid with station intervals at 15 m. Every station was live-trapped twice each spring and autumn using six trap rotations in which single Longworth live traps were set at all stations on every third trapline. Traps were placed within 1 m of each station. Each trap contained mattress stuffing as bedding and was baited with a peanut-butter-and-flour mixture, oatmeal, and a slice of potato. Traps were set in the evening and collected at first light the following day. All soiled traps were thoroughly washed with detergent, rinsed in clear water, and dried before being reset. Captured rodents were individually marked with metal ear tags. Age, sex, reproductive condition, and body measurements were recorded, and the animals released.

Analysis of Breeding-Site Quality

I calculated three different estimates of breeding-site quality: (1) number of litters observed per site (multiple litters were observed in the boxes on only four occasions); (2) number of litters that were successful at recruiting at least one offspring to the adult nest-box population; and (3) number of successful recruits produced per litter. These values were calculated separately for each habitat and season and then summed among years. There was no preferential movement of animals from one habitat to another (Morris 1989a).

My tests of the theory are based on plots of the actual frequency distributions of the three estimates of breeding-site quality. If breeding sites within a habitat are of variable quality and if animals sample more than a single empty site, the ideal preemptive model predicts that some boxes (high-quality sites) should consistently attract more lactating females than others. These high-quality sites are selected because they produce more recruits per litter than sites of lower quality. This effect will be revealed in my analysis by a frequency distribution with a large number of boxes with few litters and relatively few boxes with many litters. But what frequency distribution should we expect by chance alone?

During any sampling interval a given nest box could either contain a lactating female with young or not (the number of lactating females occupying boxes in a habitat was always less than the number of boxes available). I was thus able to calculate the expected distribution of litter observations per box by binomial probabilities where P was the probability that a box within a given habitat would contain at least one litter that season. Expected frequencies were generated separately for each habitat and season to circumvent habitat and seasonal differences in the probabilities of encountering litters. Each habitat thus had both an expected and observed frequency distribution for each seasonal comparison. I summed the stratified data across habitats, grouped categories so that expected values were

greater than 5.0, and compared observed and expected frequency distributions by goodness-of-fit tests (*G*-test with Williams's correction; Sokal and Rohlf 1981). I conducted similar tests on the binomial probabilities that a given litter was successful and on the probabilities that a marked litter mate was recruited as an adult.

Differences between observed and expected distributions could be obscured if habitats vary in the direction of departures of observed from expected results. I therefore analyzed each habitat separately in a replicated goodness-of-fit design and evaluated for heterogeneity among habitats by interaction *G*-tests (Sokal and Rohlf 1981). Sample sizes for these latter tests were necessarily small for some comparisons and by themselves could inflate my estimates of type I statistical errors. Observed and expected values were very similar for every comparison, and all heterogeneity tests were nonsignificant (see below). This means that my results of breeding-site selection were unlikely to be influenced by differences in habitat, and my summaries of the pooled data thus provide a reasonable assessment of site selection by white-footed mice.

These analyses make two key assumptions. First, the rank quality of boxes (sites) within a habitat and season are constant among years. All boxes were located in habitats dominated by deciduous trees and shrubs whose age structure suggests minor habitat changes during the 6-yr duration of this study. It thus seems reasonable to assume that annual differences in site quality were less than differences among sites.

Second, within any given habitat and season, the probabilities of nest-box selection, litter success, and recruitment are constant among years. The number of litters observed varied among years (Morris 1989*a*) and may influence the expected distribution of nest-site colonization. If boxes are colonized at random, violation of the equal-probability assumption should have no effect on the expected distribution (the outcome of n sampling experiments of size m each with different binomial probabilities is equal to the outcome of one $n \times m$ experiment using the arithmetic mean of those probabilities). If, however, females preferentially select some sites over others, only the best sites will be colonized during years of low mouse density. Those same sites should still be occupied during years of high density and would invariably lead to distributions with more boxes with many litters than expected by the binomial distribution. It would thus appear necessary to consider alternate techniques to generate expected frequencies of nest-box occupancy only after finding significant differences between observed and binomial distributions.

I previously analyzed for habitat, seasonal, and annual effects in both litter success and recruitment (Morris 1989*a*). Recruitment was closely linked to litter success and, once habitat and seasonal effects were accounted for, there was no significant residual variation in litter success among years (Morris 1989*a*). This verifies my assumption that litter success and recruitment can be considered homogeneous among years.

I compared observed and expected distributions of the capture frequencies of mice in the forest habitat to assess the possible modifying effect of nest boxes on habitat selection. During any sampling interval a given live trap could either

capture an animal or not. I tested for selective use of stations by contrasting observed frequencies of habitat use with binomial expectations.

RESULTS

Litter Observations per Site

Different litters were observed in the boxes a total of 357 times from 1983 through 1988 (175 observations in the spring, 182 observations in the autumn). "Colonization probabilities" per box ranged from a low of .103 in the edge during spring to a high of .211 in the same habitat during autumn. I used these individual habitat colonization rates to generate the binomial probabilities of 0, 1, 2, . . . , n litter observations per box where $n = 18$ in spring and 12 in autumn. These values were multiplied by the number of boxes in each habitat to generate the expected number of boxes per observation class and then summed across habitats to yield the final expected distribution of nest-site colonization for each season. The seasonal frequency distributions of litter occupation were not significantly different from random expectations (spring, fig. 1, $G_{\text{Williams}} = 1.99$, $P > .5$; $G_{\text{H}} = 13.41$, $P > .05$; autumn, fig. 2, $G_{\text{Williams}} = 7.42$, $P > .1$; $G_{\text{H}} = 1.21$, $P > .9$).

Litter Success

Many litters were too young for individual offspring to be marked; these were excluded from the analyses of litter success. I had sufficient data, nevertheless, to assess litter success on 122 litters during the spring and 145 litters during the autumn. Overall, only 52 of the 267 valid litters were known to be successful at recruiting at least one offspring to the adult population. Litter success was greater in the forest (17 of 47 litters) than in the other two habitats (22 of 123 fence-row litters and 13 of 97 edge litters) and also greater during the spring than during the autumn (37 of 122 litters were successful in spring compared with 15 of 145 during the autumn; for detailed analyses of these differences, see Morris 1989a). Litter success varied between a low of 5% in the edge during the autumn to a high of 50% in the forest during the spring.

The frequency distributions of successful litters per site revealed relatively few boxes with high numbers of successful litters (figs. 3 and 4). I calculated expected distributions from the binomial probabilities of litter success stratified by habitat. There were no significant differences between the observed and expected distributions in the spring ($G_{\text{Williams}} = 1.24$, $P > .1$; $G_{\text{H}} = 0.53$, $P > .9$). Whereas it would be improper to analyze the autumn data explicitly (with only two categories and a hypothesis intrinsic to the data there are no degrees of freedom for the goodness-of-fit test), I can, nevertheless, display both the observed and expected results. The two distributions are nearly identical (fig. 4).

If females preferentially select the best sites, boxes with many litters should have higher litter success on average than boxes with fewer litters. I tested this prediction by contrasting the observed distribution of successful litters per box (for boxes with different numbers of litters) against binomial expectation. Preferential selection of high-success sites should result in an observed distribution

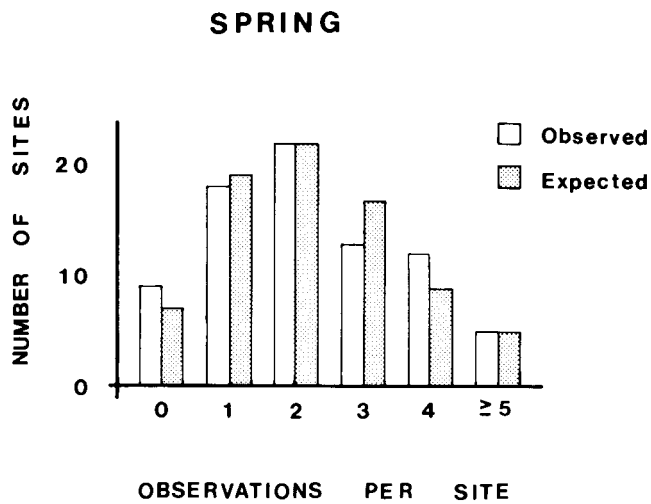


FIG. 1.—Observed and expected frequency distributions of white-footed mouse litters during the spring.

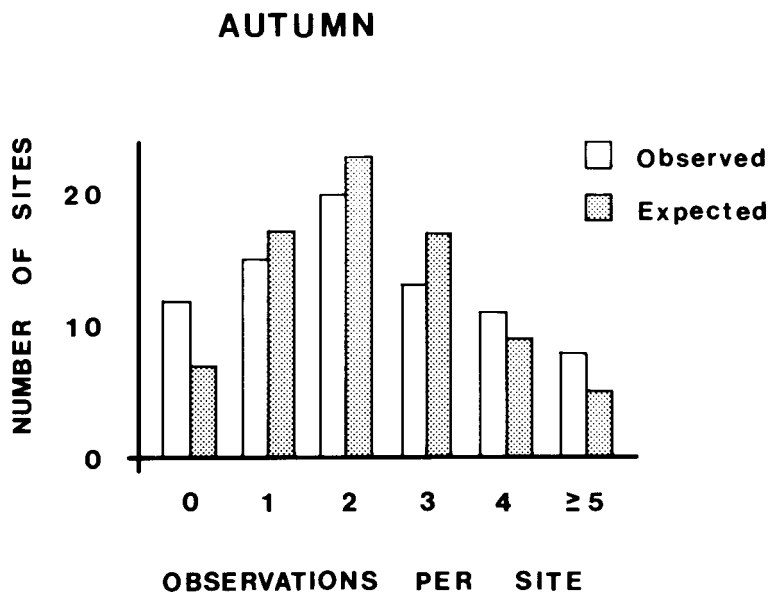


FIG. 2.—Observed and expected frequency distributions of white-footed mouse litters during the autumn.

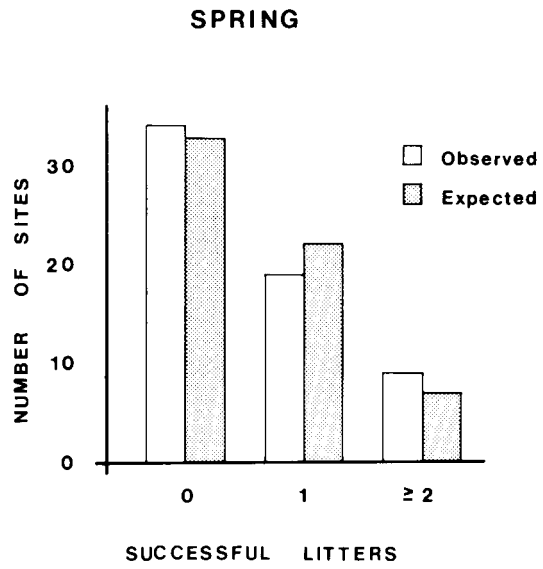


FIG. 3.—Observed and expected frequency distributions of the number of breeding sites with successful litters (spring data).

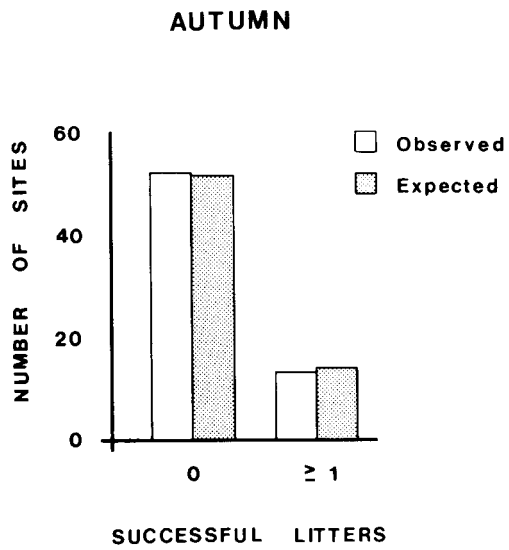


FIG. 4.—Observed and expected frequency distributions of the number of breeding sites with successful litters (autumn data).

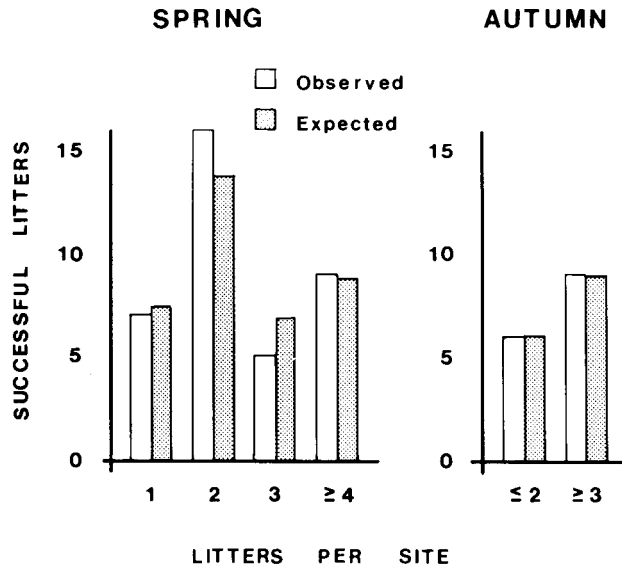


FIG. 5.—Observed and expected frequency distributions of the number of successful litters produced at sites with different numbers of litters.

with higher success rates in those boxes with many litters. There were no significant differences between the observed and expected distributions in the spring ($G_{\text{Williams}} = 0.92, P > .5; G_H = 2.27, P > .5$), and the autumn distributions were almost congruent (fig. 5). Nest boxes with many litters had no higher rate of success at recruiting at least one offspring to the adult population than boxes with fewer litters. A given litter thus had an equal chance of success regardless of whether it was produced in a box chosen by a few or by many females.

Recruits per Litter

The 52 successful litters contributed 70 known recruits to the adult population. Recruitment rates were highest in the forest during the spring (17 recruits from 22 litters) and lowest in the edge during the autumn (4 recruits from 60 litters). I calculated the expected distribution of recruits for boxes with different numbers of litters by multiplying the recruitment rate per litter for each habitat and season by the total number of litters observed in the boxes. As before, these were summed across habitats to generate the expected seasonal distribution. These frequency distributions were not statistically different from those actually observed (spring, $G_{\text{Williams}} = 2.71, P > .1; G_H = 4.67, P > .1$; autumn, $G_{\text{Williams}} = 4.65, P > .05$ [I was unable to calculate G_H for autumn contrasts because boxes with three litters yielded zero recruits in the fence-row and forest habitats]; fig. 6). Each litter produced in a given habitat had an equal expectation of recruits regardless of whether it was produced in a box selected by few or by many females.

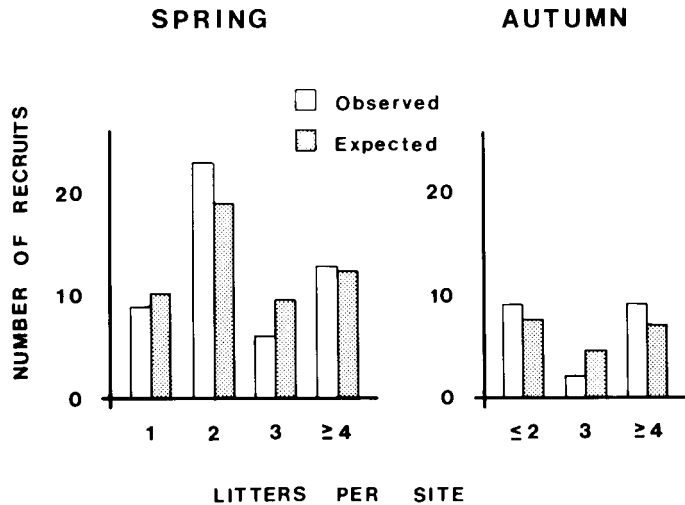


FIG. 6.—Observed and expected frequency distributions of the number of recruits produced at sites with different numbers of litters.

Capture Frequency

I calculated binomial expectations of capture frequency separately for each season and year combination from 1983 through 1988 and contrasted these with the actual distributions of captures. Only one of the 12 contrasts was statistically significant (table 1). This result is well within the bounds of the proportion of tests expected to be significant by chance alone (95% binomial confidence interval = 0.2–0.37). Within the forest habitat, white-footed mice did not appear to prefer any one trapping station to any other.

Habitat Selection by White-footed Mice

I recently confirmed the central assumption of density-dependent habitat selection for white-footed mice with the observation that mean litter size declines with increased adult density (Morris 1989a). Female white-footed mice are territorial during the breeding season (Burt 1940; Nicholson 1941; Stickel 1968; Metzgar 1971; Rowley and Christian 1976), and their pattern of habitat selection should be in agreement with exclusive access to resources. My studies of reproductive success clearly showed a fitness advantage for female white-footed mice occupying forest relative to those occupying edge and fence-row habitats (Morris 1989a). The average breeding quality of the forest was greater than that of the other two habitats, a result consistent with both despotic and preemptive habitat-selection models.

The work that I report here shows that, for this population of white-footed mice, there is no significant difference in site quality within habitats. Breeding-site quality within a habitat can thus be considered constant, and the preemptive model, based on the equivalent quality of breeding sites within a habitat, should

TABLE 1
 STATISTICAL SUMMARY OF TWELVE CONTRASTS
 COMPARING THE ACTUAL FREQUENCY DISTRIBUTION
 OF CAPTURES WITH BINOMIAL EXPECTATION

Year and Season	G_{Williams}
1983:	
Spring	4.85
Autumn	3.48
1984:	
Spring	.51
Autumn	.66
1985:	
Spring	.20
Autumn	.06
1986:	
Spring	.17
Autumn	6.71*
1987:	
Spring	1.56
Autumn	.03
1988:	
Spring	.18
Autumn	3.86

* $P < .05$.

account for the pattern of habitat occupancy by white-footed mice. Constant fitness within habitats reduces habitat selection to a simple decision. An individual female should occupy a vacant box in the forest whenever she encounters one. I tested this prediction with a modified version of Pulliam and Danielson's (1991) simulation of preemptive habitat selection.

Pulliam and Danielson modeled sampling intensity as the number of empty sites encountered. They further assumed that this sampling intensity was constant. It is more realistic to assume that the number of vacant sites encountered during habitat sampling should decline as sites are preempted with increased population density. Such a process is difficult to model unless we know the number of sites in each habitat. My grid of 15 forest boxes in the small woodlot was surrounded by 16 boxes along the forest edge. Assuming random sampling, one can calculate the expected number of empty forest nest boxes encountered (E) as

$$E = mF(G + F)/N(G + F) \quad (1)$$

$$= mF/N,$$

where m is the number of boxes sampled, F is the number of unoccupied boxes in the forest, G is the same for the forest edge, and N is the total number of boxes (31). An optimum habitat selector should occupy a forest box whenever $E \geq 1$ and should be nonselective otherwise.

I counted the number of forest and adjacent edge boxes that were occupied by lactating females during each season of every year and compared a plot of the data with that expected for $m = 1, 2, 3, 4,$ and 8 . This analysis implicitly assumes

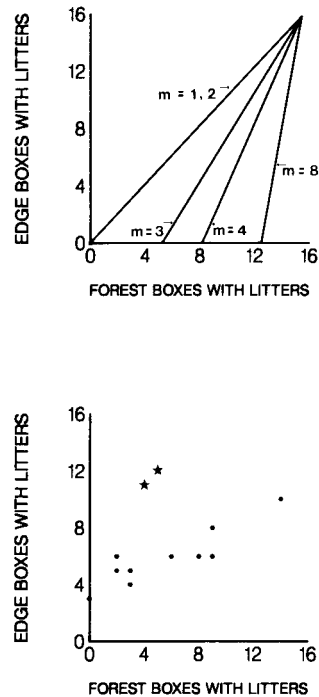


FIG. 7.—*Above*, predicted relationships of nest-box occupancy by lactating females in forest edge and forest habitats. The plots are those for a preemptive habitat selector that randomly samples different numbers of nest boxes (m) in the two uniform habitats. *Below*, the empirical pattern of nest-box occupancy by lactating females in forest-edge and forest habitats. Stars represent statistical outliers.

that pregnant or lactating females have equal chances of occupying nest boxes in the two habitats, that nest-box sampling is random, and that there are no complicating influences such as those that could be caused by neighboring habitats and populations or by seasonal and annual variation. The empirical plot did not appear to represent any of the theoretical expectations (fig. 7).

There was a trend for litter occupancy of edge boxes to increase with that in the forest, but the analysis was nonsignificant ($r = 0.48$, $P > .1$). Removal of outliers (autumn 1986 and autumn 1987) resulted in a highly significant relationship between the number of nest boxes occupied by lactating females in the edge versus that in the forest ($r = 0.89$, $P < .001$, geometric mean regression, edge = $3.37 + 0.45$ forest). This suggests strong density dependence but there is no consistent ecological explanation for the outliers.

DISCUSSION

The prediction "occupy vacant forest boxes before occupying one in another habitat" requires that females sample nest boxes in both habitats. There are at least two reasons why such intense sampling is unrealistic for females who begin

their sampling in fence rows. One, the linear orientation of the fence-row habitat may bias habitat sampling (females traveling along the fence-row could move either toward forest or away from it). Two, sampling and dispersal movements take time that cannot be spent establishing, foraging in, or reproducing in a home range. This time represents a cost of habitat selection that devalues any tendency to search for a new home range (Morris 1987c). Most fence-row females are likely, therefore, to preferentially sample the fence row rather than the more distal forest habitat. The combination of movement costs and biased habitat sampling is sufficient to account for continued occupancy of the fence row even though average reproductive success is greater in the forest.

Neither of the fence-row mechanisms are likely for animals that live in the forest edge. Edge boxes are, by definition, adjacent to the forest and female home ranges on the order of 0.1–0.5 ha (Stickel 1968; Lackey et al. 1985), and the even-greater exploratory and dispersal distances of juveniles (Lackey et al. 1985) demonstrate the ability of *Peromyscus leucopus* to sample sites in both habitats. A preemptive habitat selector should select a vacant site in the forest before accepting one along the forest edge. This is apparently not the case for *P. leucopus* (fig. 7).

The empirical data suggest, nevertheless, that there may be a tendency to preferentially select sites in the forest at high density. This intermediate preference is toward the habitat where fitness is greatest, but the same preference is not expressed at low density. The habitat-occupancy pattern is incapable of equalizing the expected fitness of individuals living in different habitats.

The potential of individual females to select habitats in a way that equalizes average fitness may be constrained by the life history of *P. leucopus*. Most litters produced are unsuccessful at recruiting even one offspring to the adult nest-box population (Morris 1986, 1989a). The life history of white-footed mice is thus dominated by a bet-hedging strategy whereby postpartum estrus guarantees that a female is able to enter the litter-success lottery as often as possible (Morris 1986). This "need" for multiple reproductive episodes must weigh heavily on any decisions of habitat movement that have the potential to delay or interfere with reproduction.

Current patterns of habitat occupancy by this population of white-footed mice may thus represent a set of effects incorporating the lack of differences in fitness among breeding sites within habitats, the lottery of litter success, novel habitat distributions, biased habitat sampling by the mice, and the dispersal costs associated with the establishment of home ranges. These effects have important implications to our understanding of habitat selection. They suggest, for example, that density-dependent habitat selection should be most pervasive at the scale of individual breeding sites within habitats (litter size declined with density, all sites yielded similar expectations of reproductive success). They also suggest that the role of habitat selection in determining abundance may decline with increases in habitat scale. Migration between habitats should decrease with increasing patch size. As patch size increases, population density would become more of a reflection of the average reproductive rewards of the habitat, and of the regulation of abundance within it, than a consequence of interhabitat movements and preferen-

tial settlement. Yet it is crucial to note that this form of habitat use ultimately owes its origin to density-dependent processes at both large (within-habitat regulation) and small scales (habitat selection).

It is also important to note that studies of the habitat use of white-footed mice have consistently shown that density is related primarily to large-scale variation in habitat (Morris 1984, 1987*b*). The same is true of other small mammals for cases in which scaling studies of habitat have been used (Morris 1984, 1989*b*). It seems likely from these initial tests that large-scale patterns of abundance may characterize many vertebrate species. These scale effects and their implications need to be fully integrated into models of habitat selection (Morris 1987*c*), habitat analysis (Morris 1984, 1987*a*, 1989*b*), and management.

My interpretations of habitat selection by white-footed mice depend on the precision of my estimates of reproductive success. I have attempted to evaluate reproductive success through the consistent placement and monitoring of artificial nest boxes in alternative habitats. It could be argued that my observed differences in recruitment among habitats reflect only differences in the relative quality of nest boxes. In a habitat where most natural nest sites are of low quality, for example, nest boxes might be superior locations for rearing young compared with boxes located in a habitat with many natural nest sites of high quality. This effect should tend to inflate my estimates of reproductive success in habitats of low quality and to reduce my estimates in habitats of high quality. Thus, if the fence-row and forest-edge habitats are suboptimal for *P. leucopus*, any nest-box effect should reduce my ability to detect differences. Any differences that I detect must, therefore, be considered ecologically significant. Conversely, the only way that a nest-box effect is likely to be a serious problem is if there are more natural nest sites of high quality available in the fence-row and edge habitats than in the forest. This is unlikely, given the proclivity of *P. leucopus* for arboreal nests (Nicholson 1941; Lackey et al. 1985).

It could also be argued that nest boxes located in different habitats attract different kinds of female mice. It is difficult to imagine how such an effect could be caused by nest boxes unless their relative quality varies among habitats. In any case, the characteristics of females are similar in the three habitats. Lactating females occupying different habitats are of similar body size (Morris, in press). There is no difference among habitats in the proportion of lactating females born in the same year relative to those born in the preceding year (Morris, in press). Furthermore, results of the live-trap data that demonstrate an absence of trap-station preference are in agreement with the lack of preference of one breeding site over another.

There can be little doubt about the precision of my estimates of litter success. Data from 1981, as well as those from 1983–1987, consistently demonstrate that the majority of litters are unsuccessful at recruiting even one offspring to the nest-box population (Morris 1986, 1989*a*). Litter success is consistently and substantially greater during the spring than during the autumn (Morris 1989*a*), a result corroborated in an independent nest-box study of *P. leucopus* in Ohio (Goundie and Vessey 1986). Both studies document the dominating influence of the lottery of litter success on the life history of *P. leucopus*.

Future tests of habitat selection theory should continue to specify the empirical distribution of breeding-site quality. While it would be tempting to use these empirical distributions to simulate the effects of habitat on population dynamics, it is crucial to first evaluate the form of habitat selection, the cues used to assess habitat, and the constraints to habitat selection. The tests I present here on a species where it is possible to obtain reliable estimates of reproductive success show how unexpected and intriguing those cues and constraints may be. It is also apparent that habitat-selection strategies may mix the effects of site selection with those caused by larger-scale differences in the average quality of sites among habitats.

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