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Environmental networks, compensating life histories and habitat selection by white-footed mice

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Summary

Analysis of 6 years' data on a population of free-living white-footed mice documents both phenotypic and environmental control of litter size. Litter size was positively correlated with maternal body size. Maternal size depended upon both seasonal and annual variation. Paradoxically, the proportion of small versus large litters varied among habitats independently of the effects of body size. The result is an influence of habitat on life history that yields patterns of reproduction and survival opposite to the predictions of demographic theory. The habitat producing the largest litters had a relatively high ratio of adult/juvenile survival. Litter size was small in the habitat where the adult/juvenile survival ratio was smallest. All of these anomalous patterns can be explained through density-dependent habitat selection by female white-footed mice. Life-history studies that ignore habitat and habitat selection may find spurious correlations among traits that result in serious misinterpretations about life history and its evolution.

Keywords: evolution; habitat selection; life history; litter size; Ontario; *Peromyscus*; seasonality

Introduction

Female reproductive success in a population of white-footed mice (*Peromyscus leucopus*) in southern Ontario varies among habitats (Morris, 1989). Adult females living in different habitats have similar expectations of life and opportunities for reproduction but juvenile survival is at least twice as high in forest as it is in either forest edge or overgrown fencerows. Further, the success rate of litters at recruiting at least one offspring to the adult population is four times greater in spring than it is in autumn (Morris, 1989).

These marked differences in juvenile survival necessarily mean that at least this feature of white-footed mouse life history varies seasonally and across habitats. Life-history theory suggests that such differences in age-specific survival should also be correlated with differences in female reproductive effort (e.g. Schaffer, 1974a; Stearns, 1976). Environments where juvenile survival is high, relative to that of adults, select for increased reproductive effort. Yet it is unclear whether temporal variation and habitat heterogeneity should have independent or interactive effects on life history. It is also unclear how important such effects might be to current interpretations of life-history evolution. I attempt to clarify both issues by evaluating the separate and joint environmental effects of habitat, seasonal, and annual variation in litter size.

Litter size is a function of maternal body size in *Peromyscus* (Drickamer and Vestal, 1973; Fleming and Rauscher, 1978; Myers and Master, 1983). I include maternal body size as a covariate in the environmental analyses.

Patterns revealed by the analyses were reversed and unexpected:

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1. Maternal body size varied among years and between seasons, but not among habitats. Litter size varied among habitats, but not among years or between seasons.
2. Litter size was larger in fencerows, where the ratio of adult/juvenile survival was high, rather than in the forest, where the ratio was lower.

Field methods

Small wooden nest boxes (Morris, 1986) were placed within second growth deciduous forest, in forest margins, and along overgrown fencerows on a 40 ha field site in an agricultural landscape between lakes Erie and St. Clair in southwestern Ontario (42°10′ N, 83°30′ W). Boxes were placed at suitable sites within 10 m of permanent stations located at 30 m intervals. White-footed mice using the boxes were monitored during the spring and autumn from 1981 to 1987. Females were assigned the status of mother only if they were the sole lactating occupant of the box. Details of the nest box sampling, classification of litters and recruits, and general descriptions of the deciduous woods and fencerows can be found in Morris (1989).

Boxes were examined during daylight hours only. The exit hole was blocked during each examination and all mice over 1 week old were removed from the box, aged, sexed, measured (body length and tail length), and individually marked with metal ear tags. Mice were returned to the same box from which they were removed. The age of immature and juvenile mice was estimated from developmental stage (Layne, 1968).

A supplemental feeding experiment was initiated in an adjacent large woodlot of similar history and plant species composition. Its purpose was to assess the possible influence of resource abundance on any habitat patterns in life history. Fifty nest boxes were mounted on trees near the intersections of a 5 × 10 grid (30 m spacing) in autumn 1986. The grid was divided into two equal 4 × 5 control and treatment plots separated by a 2 × 5 nest-box buffer. Thirty feeding stations at 30 m intervals offset from the nest-box grid by 15 m were established in July 1987. An open-ended, hollow, sheet-metal feeder in the shape of an inverted T was attached to a tree at each station. The vertical column (5 cm diameter, 56 cm tall) of each feeder was filled with an equal mixture (by volume) of whole oats and sunflower seeds and 'capped' with an empty metal can. White-footed mice foraged in the connecting 54 cm long (5 cm diameter) horizontal tube.

Feeders were checked at frequent intervals, re-filled as needed, and removed in June 1988. Nest boxes in the control, treatment, and buffer plots were checked once each month over the duration of the experiment. Data from this experiment were analysed separately from those used to assess spatio-temporal variation in life history.

Environmental networks

The number of environmental effects that can be assessed in any single study is limited by logistic and sampling constraints. The number of observations required to test for interactions increase exponentially with the dimensionality of the statistical design. If n is the minimum average sample size required to obtain a reliable estimate of a given variable (life-history trait in my analyses), then the minimum total sample (N) required to assess interactions among different factors is given by

$$N = \sum_{i=1}^{k} \sum_{j=1}^{l} (n) \tag{1}$$

where k is the number of factors of the same order in the analysis and l is the number of levels of each factor. It is, therefore, impractical to expect successful field designs with more than about three factors. Three-way designs can generate complex interactions, yet we will often wish to assess interactions among even larger sets of factors (a total of five are used in this paper). How can these complicated designs be effectively analysed and interpreted?

The interactions among any set of variables can be easily visualized as a simple network (Fig. 1). Each factor is represented by a single point arranged as the vertices of a polygon. The two-way interaction between any pair of factors is represented by the straight line connecting those factors. In a saturated network there is a single straight line between each point and all other points. Any polygon represents an *m*-way interaction where *m* is the number ($m > 2$) of straight-line segments joining the connected factors. Main effects (e.g. unequal representation among the levels of a single factor) are graphed as 'loops' at each vertex of the polygon (Fig. 1).

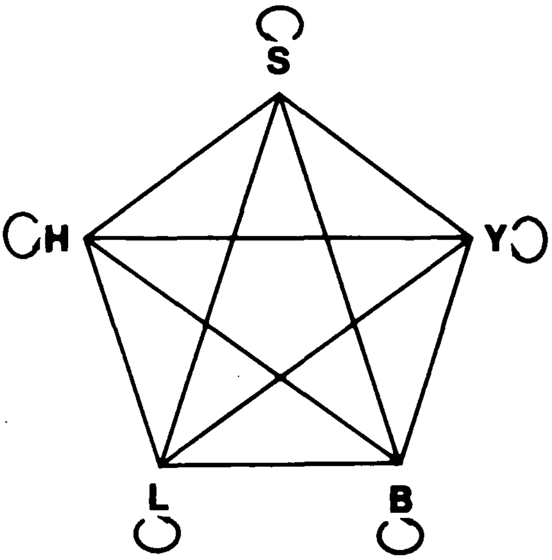

Figure 1. A saturated network displaying all possible interactions among habitat (H), season (S), year (Y), maternal body size (B) and litter size (L) of white-footed mice. Curved arrows represent main effects (different numbers of litters).

We can use this simple graphical procedure to display interactions among any set of variables and to visualize all of their potential or expected interactions. The interaction between year, season, and body size of white-footed mouse mothers, for example, is given by the triangle SYB in Fig. 1. The relative complexity of the interactions and the relationships among different factors can be evaluated by comparing the theoretical network with that actually observed (below). This form of 'network analysis' produces a sort of roadmap to guide one through the maze of interactions in factorial designs. It details interactions among subsets of factors, and clearly reveals all of these interactions in a single figure that can be used for further scrutiny and interpretation.

Note that the ability to interpret a *k*-way analysis applies only to the *k* factors included in the design. Network diagrams are susceptible to specification error and cannot be used to evaluate the possible role of external factors. If time and resources permit, it may thus be profitable to collect data at a higher order than the intended analysis. This strategy allows an evaluation of the potential importance of additional factors that may interact with those of the original design.

In the example analysed here, I am interested in the environmental interactions that relate habitat, seasonality, annual variation, and maternal body size to the litter size produced by white-footed mice. My field design enabled me to collect data simultaneously on litter size produced by females of known body size in different habitats replicated across seasons and among years. My overall sample size is fixed and insufficient to analyse all five variables at once. My sample is large enough, however, to analyse subsets of factors. The resulting network diagram will serve as an empirical icon for the pattern of interaction and its interpretation.

Analytical protocol

In this paper I test interactions among the three environmental and two life-history variables of Fig. 1 by hierarchical log-linear analyses (SPSS/PC+; Norusis, 1988). Hierarchical analyses generate the most parsimonious statistical model capable of 'explaining' the effects of the different factors on life history (Bishop *et al.*, 1975). The likelihood-ratio chi-square, like sums of squares in analysis of variance, was partitioned into additive effects (Norusis, 1988). Partial chi-squares were calculated to evaluate the effects of individual factors and their interactions while 'controlling' for the effects of other factors and interactions. In this way, a specific interaction term or main effect could be evaluated for its relative contribution to patterns in white-footed mouse life history. Statistical significance corresponded to type I error rates of 5% or less.

I partitioned litter size into large (>4, 164 litters) and small (1– 4134 litters) classes for analysis. Body size of mothers was estimated by body length and similarly partitioned into two classes of roughly equal frequency (small (<93 mm, 143 animals) and large (≥ 93 mm, 155 animals)). I included only those litters whose estimated age was 21 days or less and which were found in the presence of a lactating female.

The raw data of the analyses are the number of small and large litters produced by large and small females in different habitats, seasons, and years. The analyses function as factorial median tests for the dependent variables of number of offspring and maternal body size. They avoid complications of parametric analysis while simultaneously reducing sampling intensity to a minimum (only two levels per factor in Equation 1). A third dependent variable, the number of litters produced, is implied by the analysis and given by the number of observations within each cell of the factorial design. Any significant main effect implies unequal numbers of litters among the different classes of that variable (e.g. among the three different habitats, loop H in Fig. 1).

I analysed all possible three-way combinations of the five variables, then graphed the significant interactions on a network diagram. The pattern of the network describes the empirical interactions and facilitates an interpretation of environmentally induced variation in white-footed mouse life history.

Ratios of adult to juvenile survival are crucial to tests of life history theory. I summarize previous analyses on this same population that have evaluated age-specific differences in white-footed mouse survival among habitats and between seasons.

Results

All factors in the network are interdependent with at least one other, implying that even higher-order interactions are possible (Fig. 2, Table 1). Yet the set of observed interactions was much smaller than expected in a saturated network (compare Fig. 2 with Fig. 1). This suggests that

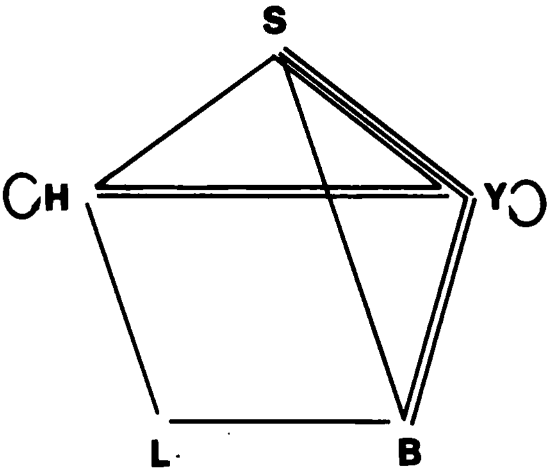

Figure 2. The empirical network of interactions and main effects among habitat (H), season (S), year (Y), maternal body size (B) and litter size (L) of white-footed mice. Significant two-way interactions (H × Y, S × Y, B × Y) are graphed separately for clarity and to simplify comparisons with Table 1. Note that the number of possible interactions is far fewer than theoretically possible (Fig. 1).

interactions among certain sets of factors are relatively insensitive to interactions among other sets. An understanding of these separate sets of interactions should help to detect environmental control of life history.

First, I concentrate on the significant interactions of the two life history variables. I then detail how the number of litters observed varied among habitats, seasons, and years. I follow with an

Table 1. Significant interactions and main effects from all possible three-way interaction designs evaluating the interdependence of habitat, season, year, maternal body size, and litter size of white-footed mice.

Source	LR χ^2	df	p
H × S × Y*	33.18	10	0.0003
B × S × Y	11.09	5	0.0496
H × Y	27.33	10	0.0023
S × Y	11.75	5	0.0384
B × Y	12.24	5	0.0317
L × H	13.78	2	0.001
L × B	21.32	1	<0.0001
Y	61.17	5	<0.0001
H	53.61	2	<0.0001

B = maternal body size; H = habitat; L = litter size; S = season; Y = year; LR = likelihood-ratio.
* Estimated from the saturated model.

analysis of the food supplementation experiment, the effects of parity, and patterns of age-specific survival.

Maternal body size

Maternal body size depended upon both seasonal and annual variation (body size–season–year interaction, and body size–year interaction; B × S × Y and B × Y respectively), but was independent of habitat (Table 1). Large mothers produced larger litters than small mothers and vice versa (litter size–body size interaction, L × B, Tables 1 and 2).

Table 2. Size distribution of 298 litters produced by small and large mothers.

	Maternal body size (mm)	
Litter size	<93	>93
1–4	84	50
>4	59	105

Litter size

Litter size, as pointed out above, depends upon maternal body size. The environmental interactions for litter size can therefore be expected to mirror those for maternal body size. The observed pattern is opposite to this expectation. Litter size, unlike maternal body size, did not depend upon seasonal or annual variation. Litter size depended, instead, upon habitat (litter size–habitat interaction, L × H, Table 1). The body sizes of mothers in the different habitats were similar, but mothers living in the fencerows produced larger litters than expected (Table 3). Mothers occupying forest edge tended to produce a disproportionate number of small litters.

Table 3. Size distribution of 298 litters observed in fencerow, edge, and forest habitats.

	Habitat		
Litter size	Fencerow	Edge	Forest
1–4	52	60	22
>4	96	42	26

Does litter size change when mothers move from one habitat to another? There are insufficient data to tell. Few adult females actually move between habitats. Of the 54 different females that I know produced more than one litter, only eight produced litters in more than one habitat. Even if I had a large sample of females that reproduced in more than one habitat, the analysis would be seriously confounded by the dependence of litter size on maternal age and parity.

Number of litters

The number of litters observed varied among years (year main effect, Y), an outcome reflecting variation in population density through time. Variation in litter production among years depended upon spring and autumn reproductive performance (season–year interaction, S × Y). The number of litters observed also varied among habitats (habitat main effect, H). This is expected because there were more nest boxes in the fencerows (36) than in the other two habitats (28 in edge (increased to 32 in autumn 1984), 15 in forest). The dependence of litter production on habitat was conditional upon which season and year were contrasted (habitat–season–year interaction, H × S × Y; habitat–year interaction, H × Y). These interactions are expected if the pattern of habitat occupancy changes as a function of the temporal dynamics of population density (i.e. density-dependent habitat selection).

The food supplementation experiment

Perhaps litter size responds to habitat-dependent differences in the resources available for reproduction? If increased resource supply alone leads to larger litters, the proportion of large litters should have been greater in the food supplemented grid of nest boxes than in the control. Contrary to this expectation there were no significant differences in the proportions of large and small litters between the treatment and control grids ($n = 43$, $\chi^2 = 0.66$, $p = 0.42$, Table 4). The proportion of large litters was also not significantly different among the control, treatment, and original forest grid ($n = 57$, $\chi^2 = 0.71$, $p = 0.70$).

Table 4. Size distribution of 43 litters observed in control and supplemental food grids in autumn 1987 and spring 1988.

	Plot	
Litter size	Control	Supplemental food
1–4	17	9
>4	9	8

The influence of parity

Litter size in white-footed mice is known to depend upon parity (Drickamer and Vestal, 1973) though much of this relationship can be attributed to increased body size and age (Myers and Master, 1983). Nevertheless, differences in survival and colonization among habitats could result in habitat-dependent differences in parity and age distributions. I assessed this possibility by examining the proportion of young versus old females breeding in the three habitats. I contrasted the proportion of females breeding in their first year versus those that were known to have survived the previous winter.

I was able to classify the relative ages of mothers from 193 of the 298 litters. The vast majority (144) of these animals were over-wintered females breeding during spring. One spring-breeding female was known to have survived two winters. No females that reproduced in the spring had been born the same year, whereas in autumn, there were equal numbers (24) of lactating females that had been born the same year compared with those known to have survived the previous winter. I therefore restricted my analyses of differences in age distributions to autumn comparisons. The proportions of lactating females in the two age-classes were similar among habitats ($n = 48$, $\chi^2 = 0.69$, $p = 0.71$, Table 5). Parity appears to be an unlikely candidate to explain habitat-dependent differences in litter size.

Table 5. Age classification of 48 lactating females observed in fencerow, edge, and forest habitats during autumn.

	Habitat		
Age class	Fencerow	Edge	Forest
Born the same year	12	9	3
Over-wintered	10	9	5

Juvenile recruitment

I have previously analysed patterns of juvenile survival in this population of white-footed mice (Morris, 1989, 1991). Those analyses demonstrate, unambiguously, that juvenile recruitment is far greater in spring than in autumn. They also clearly show that recruitment is much higher among mice born in the forest compared with those in either edge or fencerow habitats (Table 6).

Table 6. Estimates of production and subsequent recruitment of juvenile white-footed mice in three habitats during spring and autumn reproductive seasons (summary of 6 years' data).

	Habitat		
No. of animals	Fencerow	Edge	Forest
Spring			
Marked	344	249	129
Recruited	22	31	28
Proportion	0.06	0.12	0.22
Autumn			
Marked	342	273	129
Recruited	9	5	9
Proportion	0.03	0.02	0.07

Adult survival

The proportion of mothers known to be alive during the month following parturition was greater than that for juvenile recruitment, and also greater during spring than during autumn (Table 7; Morris, unpublished observations).

I was concerned that these estimates of maternal survival might not reflect opportunities for subsequent reproduction (a female lactating in late September that is recaptured in October, for example, may not have been capable of producing two autumn litters). I recalculated maternal 'survival' to correct for this possible bias by including only those females that were subsequently recaptured in a nest box in the next reproductive season, or while pregnant, or while nursing the next litter. The outcome of analysis of these data was the same as that above (mothers of 83 spring-born litters 'failed to reproduce', compared with 106 mothers of autumn-born litters ($G_{\text{Williams}} = 6.22$; df = 1, $0.01 < p < 0.025$)). There was no detectable bias in the original analysis.

Table 7. The survival of white-footed mouse mothers in three habitats during spring and autumn reproductive seasons (summary of 5 years' data, data from 1981 excluded because survivorship estimates during that year were based on a higher frequency of nest box observations).

	Habitat		
No. of litters	Fencerow	Edge	Forest
Spring			
Observed	66	36	25
Mothers that survived	25	18	12
Proportion	0.38	0.50	0.48
Autumn			
Observed	64	52	18
Mothers that survived	21	13	6
Proportion	0.33	0.25	0.33

Discussion

Adult body size and litter size, like other life-history traits, evolve in the context of environmentally induced variation that favours some phenotypes over others. A thorough understanding of the evolution of these traits must, therefore, include carefully documented patterns of their spatial and temporal variability. But what patterns do we expect to find?

Adult body size depends upon age and growth rate, which should respond to changes in *per capita* resource availability. Resource availability, in turn, is a function of primary productivity which varies with climatic changes between seasons and among years. Assuming that changes in resource levels occur more rapidly than changes in population density, we can predict, for white-footed mice, that both maternal body size and litter size should vary between seasons and years.

Climatic conditions that affect productivity are unlikely to vary among similar-aged habitats at the small spatial scale of my study sites (the same may not be true in a comparison of mature and successional sites with different production/biomass ratios). We should expect no consistent spatial patterns in either maternal body size or in the size of the litter will be produced.

Demographic theories, on the other hand, predict that reproductive effort should evolve to reflect age-specific mortality (Schaffer, 1974a; Stearns, 1976; Horn and Rubenstein, 1984). An environment in which the ratio of juvenile to adult mortality is high should lead to selection for reduced reproductive effort: the opposite to increased effort. We should expect that a female white-footed mouse of a given body size should maximize her reproductive success by producing a smaller litter in the fencerow where juvenile mortality is high.

What predictions can be made about seasonal patterns? Juvenile survival declined sharply in autumn relative to spring. Maternal survival also declined, but not to the same degree. Thus the ratio of juvenile to adult survival is 2.5 times greater in spring than in autumn (spring ratio = 0.25, autumn ratio = 0.10). All other things being equal, the demographic theory predicts a reduced reproductive effort in autumn.

The habitat-dependent pattern of white-footed mouse life history appears flatly inconsistent with these four predictions. Litter size varied among habitats rather than between seasons or among years. Furthermore, the expected litter size for a female of a given body size was much smaller in the forest habitat where juvenile survival was greatest, than it was in the fencerow where juvenile survival was low (expectations of adult survival were similar among habitats (above, Morris, 1989)).

Yet the evolution of litter size depends not only on reproductive effort, but also on differences in recruitment from litters of different sizes (Lack, 1948; Morris, 1986, unpublished observations; Boutin *et al.*, 1988). In this population of white-footed mice, litters of size five produce more recruits than any other litter-size class. Most litters are unsuccessful at recruiting offspring, female lifetimes are short, and evolution has favoured a bet-hedging strategy of frequent iterated reproductions (Morris, 1986). Given these limitations on white-footed mouse life history, a lack of seasonal differences in litter size may not be all that surprising. But the differences in litter size among habitats, and the unexpected pattern of those differences, are certain to intrigue many ecologists. Why has the theory failed to predict correctly the spatial pattern in litter size?

The influence of habitat

The number of recruits W produced per litter is given by

$$W = (L)(J) \tag{3}$$

where L equals litter size and J represents juvenile survival for litters of that size (e.g. Charnov and Krebs, 1974). In white-footed mice, J is higher for litters of size five than for any other litter-size class, and also varies among habitats. Thus, for any habitat i,

$$J_i = g_i(L) \tag{4}$$

and

$$W_i = (L)(g_i(L)) \tag{5}$$

Previous work has demonstrated, as well, that average litter size in white-footed mice declines with increasing population density (Morris, 1989). Therefore,

$$L_i = f_i(N_i) \tag{6}$$

where N equals population density. Substituting Equation 6 into Equation 5,

$$W_i = (f_i(N_i))(g_i(f_i(N_i))) \tag{7}$$

Thus the litter size that maximizes recruitment varies among habitats as a complex function of population density. How has evolution by natural selection moulded the life history of white-footed mice toward attaining this optimum?

The role of habitat selection

According to habitat selection theory, an individual should move from one habitat to another whenever its expectation of reproductive success is increased by doing so (Fretwell and Lucas, 1970; Rosenzweig, 1981). Assuming that reproductive success varies with density, the stable distribution of densities in different habitats will occur when no individual can increase its reproductive success by changing its habitat. In the context of an optimum litter size for white-footed mice, this means that the density in each habitat should be adjusted to maximize Equation 7.

I do not yet know all of the functional relationships of Equation 7 for this population of white-footed mice. I can, however, plot the empirical relationship between recruitment and litter size by habitat (Fig. 3). Considering recruitment from only a single generation, the optimum litter size in all habitats is clearly five offspring (Fig. 3). But litter size is a quantitative trait, and any genotype will produce a phenotypic distribution of litter sizes around some central value rather than a specific number of offspring (Mountford, 1968). If all genotypes produce similarly shaped phenotypic distributions of litter size, genotypes for litters of average size five will tend to produce more large litters than will genotypes for any smaller litter. Thus to determine the evolutionary optimum, we must consider the future success of offspring produced by litters of different sizes. This optimum will be smaller than that for a single generation whenever the average survival of offspring in large litter sizes is substantially lower than that of smaller litters (Mountford, 1968). Mountford's hypothesis seems to account for the observation that the most frequently encountered litter size in white-footed mice is less than the single-generation optimum of five (Morris, 1986, unpublished observations).

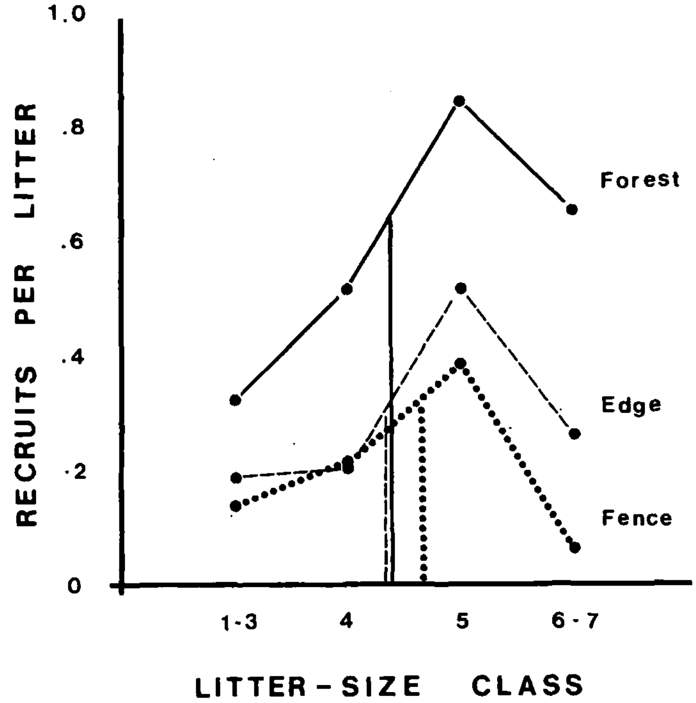

Figure 3. The observed number of recruits produced by different litter-size classes of white-footed mice living in fencerow, forest edge, and forest habitats (summary of 6 years' data, spring and autumn data combined). The optimum single-generation litter size (5) is the same in all three habitats, but juvenile survival and subsequent recruitment of each litter is greater in forest than in either fencerow or forest edge. Mean litter size for each habitat is indicated by a vertical line.

Perhaps Mountford's hypothesis can even account for variation in average litter size among habitats. Differences in litter size may simply reflect differences among habitats in the asymmetry of offspring survival from large litters. The evolutionarily optimum litter size might then be different in each habitat. If so, the relative survival of offspring produced in large litters should be greater in fencerows (large litter size) than in the forest (small litter size). The empirical data do not support this prediction (Fig. 3).

Rejection of Mountford's hypothesis as an explanation for among-habitat differences in litter size suggests that the reason for large litters in the fencerow must lie, instead, in the density-dependent terms of Equation 7. Other things being equal, Equation 7 implies that white-footed mice should be more abundant in the forest (greater average recruitment) than in either of the other two habitats. Since litter size in white-footed mice declines with increased density we predict that litters should be smaller in the forest than in the other habitats. This is a consistent explanation for the observation that fencerow litters are larger than those in the forest, but why are litters in the forest and edge of similar size?

The answer is that other things are not necessarily equal. Female white-footed mice are territorial during the breeding season (Burt, 1940; Nicholson, 1941; Stickel, 1968; Metzgar, 1971; Rowley and Christian, 1976), and aggressive interactions may place an upper limit on the population density in any single habitat. Furthermore, the ability to adjust densities among habitats will be related to dispersal distance and habitat configuration. Whereas it may be reasonable to assume that densities can be readily adjusted between adjacent forest and edge habitats, it is much less likely that there will be the same flux of individuals between these habitats and the more distant, linear fencerows. This view is supported by data. Of the 25 cases of known movement by adult mice away from boxes in the forest, 21 moved to boxes in the edge, compared with only four that moved to fencerow boxes (Morris, 1989). This combination of effects may result in an elevated density of individuals occupying edge relative to fencerow, and a corresponding reduction in average litter size comparable with that of individuals occupying adjacent forest.

What mechanism is responsible for the decline of litter size with increased population density? One explanation is that resources available for reproduction become depleted as the population grows. Variation in resource levels among habitats that cause differences in litter size should also affect growth and result in similar differences in maternal body size. Parallel reasoning would argue for reduced litter size in autumn when white-footed mouse densities are characteristically high (Morris, 1989) (this argument must be balanced against the high production of autumn seeds and nuts, choice foods of white-footed mice (Nicholson, 1941)). But, maternal body size was similar among habitats, and there were no seasonal differences in litter size.

Thus it seems likely that resource-independent density effects (e.g. increased territorial encounters) vary among habitats differing in structure and physical orientation. The intensity and kind of social interactions in edge and linearly arranged fencerow habitats may depart substantially from those in the forest. Any resource-independent effects that vary among habitats, whether behavioural, or mediated in some other way, could act to decouple the relationship between maternal body size and litter size.

It is surprising, nevertheless, that litter size failed to respond significantly to increased food availability in my field experiment. I can offer two possible explanations. First, the production of offspring depends upon a variety of nutritional and ecological requirements in addition to increased food supply. Some of these may vary with density. Second, even though litter size depended upon habitat in my long-term monitoring study, that relationship became apparent only with the accumulation of large samples over 6 years of data collection (data from 1981, 1983–1986 failed to reveal a significant effect of habitat on litter size though the trend was also in the direction of increased litter size in fencerow habitats (Morris, 1989)).

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Be that as it may, the habitat-dependent life history of white-footed mice departs substantially from that predicted by demographic theory. What are the evolutionary implications of these differences? The answer would seem to depend upon the rate of successful migration among habitats and the relative contribution of each habitat to overall population replacement. If fencerows function primarily as reproductive sinks (Lidicker, 1962; Pulliam, 1988), the expression of life history in that habitat will be dictated by evolutionary trends elsewhere. But if fencerow populations can sustain themselves, we might eventually expect demographic feedback toward reduced litter size. Both scenarios lead to habitat-dependent life histories.

At this early stage of understanding, we can only speculate on how common habitat-dependent variation in life history might be. It seems reasonable to assume that habitat-dependent life histories are possible in any habitat-selecting species that uses more than a single habitat. Indeed, demographic theory suggests that habitat differences in life history may occur whenever there are similar differences in age or stage-specific survival schedules. But some patterns in life history, such as those revealed in white-footed mice, are much more than a mere reflection of differences in survival and subsequent recruitment among habitats. The life history appears to be a by-product of the costs and benefits of density-dependent habitat selection. This means that the optimal study must not only document differences in life history among habitats, it must simultaneously evaluate processes and strategies of habitat selection.

An analysis of the data presented here, that ignored habitat, would miss its influence on life history and could suggest that evolution directly compensates for reduced juvenile survival by increased litter size. This spurious pattern could easily prejudice interpretations of life history. Any apparent compensation occurs not by direct evolution on life history, but by the evolutionary advantages of habitat selection. The interesting pattern is that the life history is structured on the basis of habitat. The interesting implication is that it can be modified by habitat selection.

This is not to suggest that demographic theory should be discarded as an explanation for general patterns of *P. leucopus*' life history. The consequences of habitat variation in juvenile survival, like temporally varying survival rates (Schaffer, 1974b), may have a significant impact on population-level responses in life history. It does suggest, however, that habitat heterogeneity needs to be incorporated into tests of life history theory.

By way of contrast, the results of comparative studies across species have suggested that, once the effects of body size have been accounted for, ecology has little influence on mammalian life history (Harvey and Clutton-Brock, 1985; Gittleman, 1986; Harvey and Read, 1988). The environmental control of litter size in white-footed mice stands as a stark counterpoint.

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