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State-dependent life histories, Mountford's hypothesis, and the evolution of brood size

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Summary

1. Mountford's cliff-edge hypothesis states that asymmetrically low survivorship in large broods can account for the common observation that mean brood size is less than the most productive size. A graphical model demonstrates how state-dependent life histories can explain Mountford's hypothesis. The model is based on the optimal allocation of parental resources to reproduction. It assumes that the optimum brood size depends upon the state of each phenotype in the population.

2. Variability among individuals will cause some to produce either smaller or larger broods than their optimum. Juvenile survival is expected to decline with increases in brood size beyond the parental optimum. Juvenile survival from large broods produced by low-quality parents will be exceptionally low, thereby generating Mountford's cliff-edge effect.

3. I tested the model with field data on the success of litters produced by small and large females of the white-footed mouse. The data, in this initial test of state-dependent life history theory, were consistent with the state-dependent explanation. Small females that produced large litters had significantly lower recruitment from those litters than did larger females that produced litters of the same size.

4. Interactions among litter size, juvenile survival, maternal body size and the timing of reproduction document that detailed natural history will be an essential feature in future tests of state-dependent theories.

Key-words: body size, brood size, habitat, individual optimization, life history, litter size, *Peromyscus*.

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Introduction

Mountford (1968) demonstrated an important role for phenotypic variability in the evolution of an optimum brood size. The expected number of descendants produced per brood, by any given genotype, is determined by the interaction between the frequency distribution of brood size and the proportion of offspring recruited to the population. The evolutionarily optimum brood size will be less than the most productive whenever juvenile survival is asymmetrically low in large broods, and when the phenotypic distribution of brood sizes is either symmetrical or positively skewed. Females producing broods larger than the most productive size will often leave fewer descendants than if they had produced a brood smaller than the one that, on average, yields the most recruits.

Genotypes for brood sizes less than the most productive will have a lower probability of catastrophic

failure from large broods and will thereby attain higher fitness than will genotypes whose mean brood size is equal to that which yields the maximum number of surviving offspring. Boyce & Perrins (1987) referred to this model as the 'cliff-edge effect' because the reproductive success of individuals producing large broods 'falls off the cliff' relative to that of individuals producing smaller broods. No specific mechanism has been proposed to account for asymmetrically low survival in large broods.

Mountford's hypothesis is similar to another set of theories suggesting that phenotypic variability in brood size is itself related to an optimization process (e.g. Smith & Fretwell 1974; Morris 1985, 1987; Pettifor, Perrins & McCleery 1988; Lalonde 1991). A recent version demonstrates that the optimum brood size can be determined by considering the 'state' of the parent (McNamara & Houston 1992). 'High-quality' parents of a given genotype will be able to successfully produce

a larger brood than will 'low-quality' parents of the same genotype.

I describe a mechanism by which the allocation of parental investment to broods of different sizes can account for the asymmetric survival assumed by the cliff-edge hypothesis. This means that the cliff-edge hypothesis and its attendant effects are likely to be special cases of a more general theory of state-dependent life histories.

I test the investment mechanism with a population of white-footed mice (*Peromyscus leucopus* [Rafinesque]) living in southern Ontario, Canada. The frequency of the most productive litter size ($n = 5$) in this population is less than expected on the basis of the number of recruits produced (the same pattern has been reported for muskrats (Boutin, Moses & Caley 1988), but the phenomenon was originally recognized and is best known in birds, e.g. Perrins 1965; Klomp 1970; DeSteven 1980; Nur 1984; Boyce & Perrins 1987; Møller 1991). Part of the explanation for the white-footed mouse pattern is that juvenile survival in large litters 'falls off the cliff' (Morris 1992a). Offspring from the largest litter-size class (6–8 littermates) have, on average, substantially lower recruitment than do offspring from all smaller litter-size classes. Data on recruitment from females of different sizes are consistent with a state-dependent explanation for the cliff-edge effect in this species.

STATE-DEPENDENT LIFE HISTORIES AND THE DISTRIBUTION OF BROOD SIZE

Classic age- and stage-dependent effects on life history can be viewed as special cases of a wider class of state-dependent models (McNamara & Houston 1992). Resources allocated to reproduction will depend upon a parent's current and expected future state. The quality of a parent's state should thus be strongly correlated with its ability to invest in reproduction. The optimum brood size produced by a given level of reproductive investment will depend, in turn, upon the relationship between parental investment and offspring survival (Fig. 1a) (Smith & Fretwell 1974; Morris 1985, 1987; Lalonde 1991). The model I present here assumes that there is a lower threshold of investment below which no offspring survive, and an upper asymptote beyond which additional investment fails to improve offspring survival (this assumption is similar to that of both Morris (1987) and Lalonde (1991)).

If parents partition their reproductive investment equally among offspring, each of n offspring can expect to receive $1/n$ of the parents' total investment. Average investment per offspring will decline as a negative exponential function of increasing brood size (Fig. 1b, the principle of proportional investment, Morris 1987). Assume from the above that parents in a high-quality state can allocate more resources to reproduction than can parents in a low-quality state. For a given brood size, high-quality parents will invest

more in individual progeny than will their low-quality competitors. High-quality parents devoting more resources to reproduction and the rearing of offspring are likely, for any given brood size, to be rewarded with a higher average survival of their offspring than low-quality parents investing less (Fig. 1c). In both cases juvenile survival 'falls off the cliff' in the largest litters.

The products of the survival curves times brood size yield the expected recruitment of descendants from parents that devote different allocations of investment to individual offspring (Fig. 1d). The maximum height of the curve corresponds to the optimum investment per offspring that maximizes the single-brood recruitment of offspring (Lalonde 1991). High-quality parents have a higher optimum brood size than do low-quality parents.

STATE DEPENDENCE AS A MECHANISM FOR THE CLIFF-EDGE HYPOTHESIS

The offspring survival curves of parents in both high- and low-quality states demonstrate the asymmetric survival in large broods demanded by the cliff-edge hypothesis (Fig. 1c). Pettifor *et al.* (1988) have proposed another version, the individual optimization hypothesis. According to this hypothesis, each parent should optimally allocate its investment to produce the appropriate brood size that maximizes offspring recruitment. The consequence of this deterministic version of optimal investment is that total offspring recruitment should increase consistently with increased brood size because only those females that can 'afford' large broods produce them.

Individual optimization may be rare because natural variability, from both genetic and environmental origins, will, for any given population, produce a frequency distribution of brood sizes around each phenotype's (or class of phenotypes) optimum value (see also Aparicio 1993). This is an addendum to Mountford's (1968) original model for the evolution of litter size that assumed fixed survival for litters of different sizes. Optimal investment suggests that juvenile survival is a function not only of litter size, but also of random genetic effects, maternal effects, environmental effects, and their interactions. Depending upon their state, some females will produce small broods with relatively mild fitness consequences. Others will produce large broods with devastating consequences for the recruitment of progeny.

The result is a reduction in the optimum brood size for virtually every phenotype, and with heritable variation, each genotype, in the population. Large broods with low survival produced by small-brood-size phenotypes will amplify the already existing asymmetry of survival in larger brood sizes. The mean brood size will be less than the most productive (Morris 1992a) because juvenile survival 'falls off the cliff'.

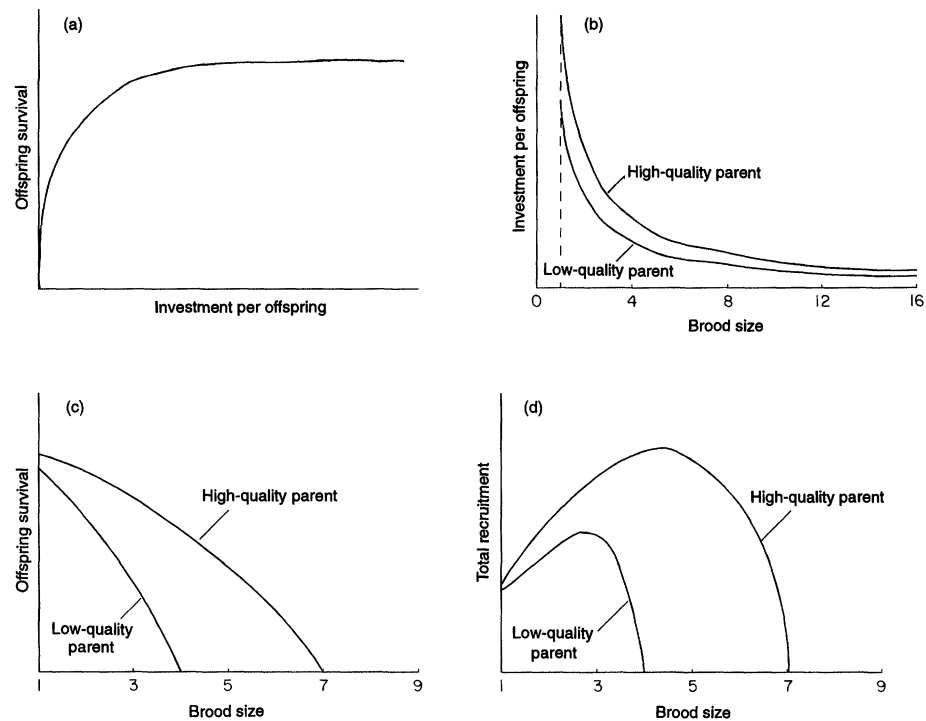


Fig. 1. Optimal investment as a mechanism explaining the cliff-edge hypothesis. (a) The curve of diminishing returns of offspring survival with increased parental investment. (b) The principle of proportional investment. Each doubling of brood size reduces the average investment per offspring by one-half. The vertical dashed line corresponds to a brood size of one. For any given brood size, high-quality parents can invest more resources per offspring than can low-quality parents. (c) Offspring survival as a function of brood size (assuming the investment curve in (a)) for high-quality and low-quality parents. The investment of the low-quality parent in this example is two-thirds the value of the high-quality parent (as in (b)). Offspring of high-quality parents can expect a higher average survival at all brood sizes. In each case, offspring survival 'falls off the cliff' in large litters (these conclusions depend upon the assumption of a decelerating investment curve (a)). (d) The expected total recruitment from broods of different sizes produced by high- and low-quality parents (the product of the survival curves in (c) times brood size). The fitness of all brood sizes is greater for the high-quality parent that also has a larger optimum brood size. The distribution of brood sizes in the population should reflect the distribution of parental quality (the optimal investment hypothesis). Sub-optimum broods produced by high-quality parents inflate the average survival of small broods. Super-optimum brood sizes produced by lower-quality parents devalue the average survival of large broods and reinforce the cliff-edge effect in (c). All curves have been drawn as continuous functions to simplify the illustrations.

Tests of state-dependent life history are likely to be complicated by difficulties in assessing appropriate state variables. State-dependent life history theory assumes that life history traits depend upon the individual's state (or as above, its quality). To avoid circularity, one must choose an appropriate estimate of an individual's state to study the functional relationship with life history. The problem is that any one state variable depends upon many others and their potential interactions.

In the test I outline below, I estimate a female white-footed mouse's state by her body size, and evaluate its ability to account for the cliff-edge effect on litter size. An additional state variable, the time of year when a female reproduces, interacts with body size and the distribution of litter sizes to produce the observed recruitment from litters of different sizes.

STATE-DEPENDENT LIFE HISTORY OF WHITE-FOOTED MICE

Peromyscus body size increases at a decelerating rate with increased age (Myers & Master 1983). Litter size

increases with parity (Drickamer & Vestal 1973; Fleming & Rauscher 1978) and with the age-related differences in female body size (Myers & Master 1983; Morris 1992a, b). A cliff-edge effect could arise if both litter size and recruitment success are related to female body size. The optimum litter size for small females may be less than that for large females (see also Fleming & Rauscher 1978). Juvenile mortality in a large litter produced by a small female should then be greater than that of a litter of the same size produced by a large female. Such a mechanism would inflate juvenile mortality in larger litters and thereby produce the asymmetric survival in large broods required by the cliff-edge hypothesis.

This paper tests the state-dependent theory's assumption that offspring survival is asymmetrically low in large broods (juvenile recruitment 'falls off the cliff') and three of its predictions (Fig. 1). (i) Large litters produced by small females should have lower recruitment success than litters of equal size produced by large females. (ii) Differences in recruitment between small and large females should be greatest in the large litter-size classes. (iii) Recruitment rates

should decline with increased litter size and the recruitment rates of large females should be greater than those of small females for each litter-size class.

The tests assume that body size is an unbiased estimate of a female's state as it relates to her reproductive investment. This assumption is unlikely to be true, even for a composite state variable such as body size. This paper does not attempt to estimate the covariance between body size and other state variables. The intent is to demonstrate whether or not state-dependent theory is a plausible explanation for Mountford's cliff-edge effect in this population of white-footed mice. The tests should not be construed as taking the place of the definitive manipulation experiments necessary to assess fully, state-dependent life history theory. Body size in mammals is, nevertheless, allometrically related to a wide variety of other life history and state variables (e.g. Eisenberg 1981; Myers & Master 1983; Peters 1983; Stearns 1983; Calder 1984; Boyce 1988; Harvey & Read 1988) and is the obvious candidate for an initial test of state-dependent theory. Other state variables are doubtless important, but represent a nearly infinite set. I suggest that, for white-footed mice, other candidates be evaluated after the effects of body size have been accounted for, and only when warranted by our knowledge of natural history.

Methods

Life histories of female white-footed mice occupying small wooden nest-boxes located at 30-m intervals have been monitored since 1981 in forest, forest edge, and fence-row habitats in south-western Ontario (42°10'N, 83°30'W). Animals living in the boxes were observed at approximately monthly intervals three times each spring, and twice each autumn (except autumn 1982, and spring 1983 when boxes were checked twice). The vast majority of litters are born during the spring and autumn reproductive seasons (Morris 1989, 1992a; see also Rintamaa, Mazur & Vessey 1976; Goundie & Vessey 1986; Wolff 1986; Wolff, Lundy & Baccus 1988).

Boxes were checked in the field during daylight only. At each check, all animals 3 days of age and older were removed from the boxes, measured (body length [= body size], mass), sexed, and assessed for reproductive condition (males, testes descended or scrotal; females, lactating or pregnant, vagina perforate or imperforate). Body length was used as the estimate of body size to avoid complications of increased mass with pregnancy, and decreased mass with lactation, among wild-caught females. All animals older than 7 days were given a unique ear tag for identification. Tagged animals only were used in my estimates of recruitment. Immature (eyes closed) and juvenile mice were aged on the basis of development (Layne 1968). Each nest box was cleaned and given a new supply of cotton nesting, and all animals were

released in the same box from which they were removed.

The recruitment of individually marked young from females with litters of known size was estimated from 1981 and 1983–92 (data for 1982 were excluded because the boxes were not checked in autumn of that year). Only those data from boxes with individually identified mothers and offspring that were not fully co-ordinated were included. Offspring were judged to have been successfully recruited if they later occupied nest boxes as adults. Further details of the field protocols can be found in Morris (1986, 1989, 1991, 1992a).

Most litters produced by this population of white-footed mice are unsuccessful at producing any descendants (Morris 1986, 1989). In the analyses of 304 litters presented here, 115 descendants were produced from 76 successful litters (i.e. litters that produced at least one recruit). No descendants were recorded from the remaining 228 litters. These estimates of recruitment are no doubt less than the total (see also Goundie & Vessey 1986; Wolff 1986, 1992; Wolff *et al.* 1988). Note that my test compares small and large females. The test does not require a measure of total recruitment, or the inclusion of potential parity and litter-size effects on dispersal (e.g. Wolff *et al.* 1988). It requires only that the estimate is precise and unbiased between the two classes of females.

The test also requires precise estimates of maternal body size. Field estimates of maternal body size are subject to observer bias and could vary among research personnel who have helped me collect data (including measurements of female body size) since 1986. The data collected by each observer correspond to one or more years of the long-term study. Potential bias in body-size measurements among observers was assessed via log-linear analysis (Norušis 1992). The test was based on two maternal body-size classes, one less than, and one equal to or greater than the population median (93 mm, see Morris 1992a for additional details). I tested for heterogeneity in the proportions of small and large females across years, confirmed that heterogeneous data corresponded to individual field observers, deleted the heterogeneous set, and repeated the analysis. The final set of unbiased data was used in all subsequent analyses.

The utility of maternal body size as a significant state variable influencing litter size was confirmed by regressing mean litter size against mean maternal body size across adjacent body-size classes. The existence of the cliff-edge effect was reassessed by contrasting the observed and expected recruitment from litters of different sizes. Expected values were generated by multiplying the overall recruitment rate per offspring by the number of offspring in each litter-size class. This procedure assumed that the survival of littermates was statistically independent within litter-size classes. The assumption is valid for this population of mice (Morris 1992a).

The state-dependent theory's predictions were tested by plotting the respective recruitment rates of small and large females as functions of litter size. Differences in recruitment rates among small and large females producing litters of different sizes were assessed by goodness-of-fit tests.

The time of year and habitat in which a female reproduces are known to affect litter success in white-footed mice (Morris 1986, 1989). Litter success is at least three times greater for litters born in the spring than it is for litters born in the autumn, and about twice as great for litters born in the forest than it is for litters born in either the edge or fence-row habitats. The time and place where females reproduce may also act as significant state variables influencing the evolution of litter size. I partitioned litters into four size classes (≤ 3 , 4, 5, ≥ 6) and used log-linear analyses to evaluate whether season or habitat of birth alter the relative success of litters of different sizes. This test is crucial because differential success of large vs. small litters in different seasons and habitats could conceivably account for my observation that the most productive litter size occurs less frequently than expected. Season and habitat may, however, interact with maternal body size and thereby explain why the pattern of juvenile survival is different for small vs. large mothers. I again used log-linear analyses to simultaneously evaluate the separate and combined effects of maternal body size, time of year and habitat on the production of litters of different sizes. No expected cell frequencies were less than one in any of the log-linear analyses.

Results

Measurements of maternal body size were heterogeneous across years (338 litters, likelihood ratio $\chi^2 = 37.4$, d.f. = 10, $P < 0.0001$). This effect was eliminated following the removal of data for both 1989 and 1990 (304 litters, likelihood ratio $\chi^2 = 11.7$, d.f. = 8, $P = 0.19$). One observer collected data in both years and appeared to have consistently underestimated maternal body size (30 females were less than the median body size, only 4 were greater). The 1989 and 1990 data were excluded from all further analyses.

Mean litter size was highly correlated with mean maternal body size (304 litters, $r = 0.89$, $P < 0.001$, Fig. 2). The high correlation suggests that much of the state-dependence in white-footed mouse litter size should be related to maternal body size.

Juvenile survival varied among litter-size classes (goodness-of-fit test, Sokal & Rohlf 1981, $G = 10.72$, d.f. = 2, $P < 0.005$, Fig. 3). Litters of size five produced more recruits than expected (standardized residual = 2.11). Mean litter size (4.48, SE = 0.08) was less than the most productive litter size (5). Juvenile survival 'fell off the cliff' in the largest litter-size class (standardized residual = -2.39), consistent with Mountford's hypothesis (see also Morris 1992a).

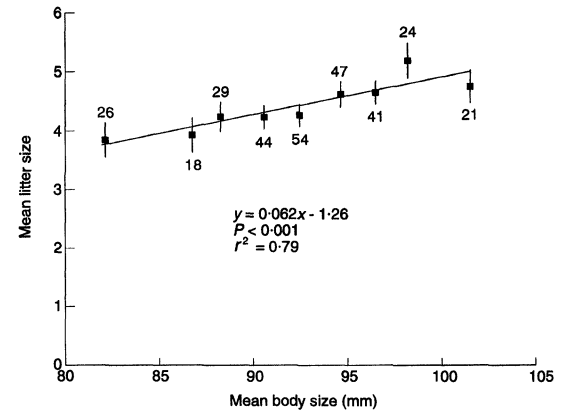


Fig. 2. Mean litter size depends upon mean maternal body size (vertical lines correspond to standard errors, numbers refer to sample sizes of females in adjacent body-size classes).

In agreement with the state-dependent theory, juvenile recruitment from large litters produced by small females (i.e. < 93 mm) was substantially less than that of larger females producing litters of the same size (prediction 1, Figs 4–6). Also consistent with the theory, large females that produced litters of size five had significantly higher recruitment than small females that produced five offspring (prediction 2, Fig. 6). The third prediction was rejected. Recruitment rates declined with increased litter size for small females only (Fig. 5).

There was no interaction between season or habitat of birth on the success of litters in different size classes (304 litters, likelihood ratio $\chi^2 = 3.4$, d.f. = 3, $P = 0.33$, and likelihood ratio $\chi^2 = 3.9$, d.f. = 6, $P = 0.69$, respectively, four-way interaction likelihood ratio $\chi^2 = 4.4$, d.f. = 6, $P = 0.63$). The time of year and habitat in which a female reproduces cannot

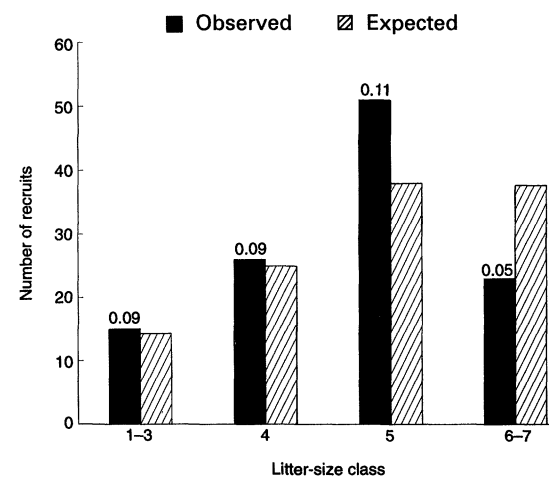


Fig. 3. Juvenile white-footed mouse survival was higher than expected for litters of size five and substantially lower than expected for litters of size six and seven. Proportions correspond to the observed recruitment rate per offspring produced. Expected values were calculated as the product of the number of offspring in a given litter-size category times the probability of successful recruitment from all offspring combined.

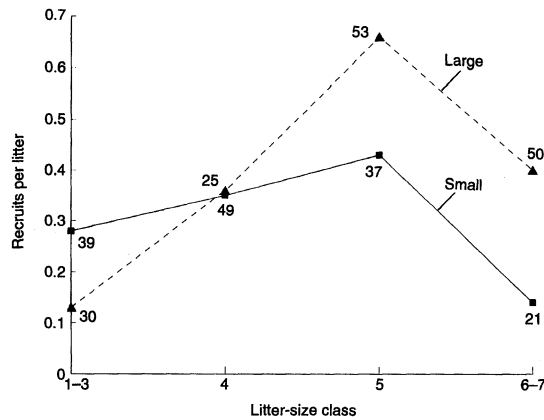


Fig. 4. Recruitment per litter by small and large white-footed mice. Compare with the theoretical predictions in Fig. 1(d).

explain, alone or together, why it is that litters of size five are less frequent than expected.

There was no effect of season or habitat on the litter size produced by small females (146 litters, likelihood ratio $\chi^2 = 1.5$, d.f. = 3, $P = 0.68$, and likelihood ratio $\chi^2 = 10.7$, d.f. = 6, $P = 0.1$, respectively). Large females, on the other hand, produced disproportionately high numbers of litters of size five in spring and disproportionately low numbers of litter sizes 1-3 during autumn (158 litters, likelihood ratio $\chi^2 = 7.8$, d.f. = 3, $P = 0.05$, Table 1). Again, there was no habitat effect on litter size (likelihood ratio $\chi^2 = 7.2$, d.f. = 6, $P = 0.3$). For large females, litters of size five yielded more recruits than expected because most were produced during spring. Small litters produced by large females had low recruitment because most were produced during the autumn reproductive season.

Discussion

In this population of white-footed mice the size of litter that a female produces is related to her own body size. Large females are more likely to produce a large litter than are small females, and vice versa. Yet some

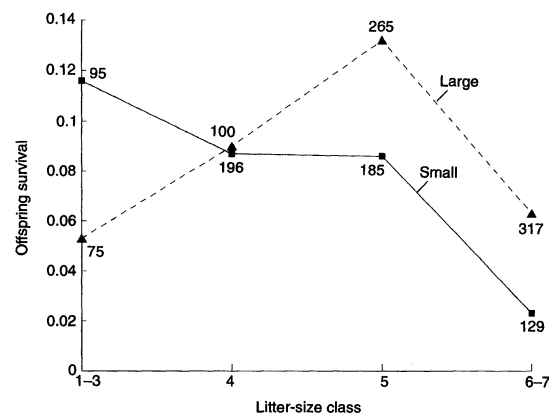


Fig. 5. Recruitment per offspring by small and large white-footed mice. Compare with the theoretical predictions in Fig. 1(c).

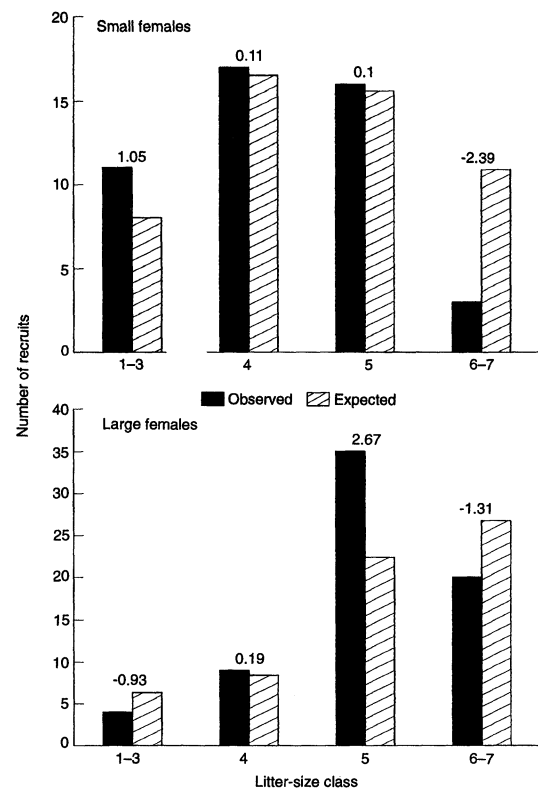


Fig. 6. Observed and expected numbers of recruits in different litter-size classes produced by small and large white-footed mice. Small females produce fewer recruits from large litters than expected, large females produce more recruits from litters of size five than expected. Numbers correspond to standardized residuals from expected values. Expected values were calculated as the product of the number of offspring in a given litter-size category times the probability of successful recruitment from all offspring combined.

small females producing large litters contribute substantially fewer recruits to the population than expected. Juvenile survival 'falls off the cliff' in large litters and helps to explain why mean litter size is less than the most productive.

Recruitment from large litters produced by large females was not different from expectation, but it was much lower than recruitment from litters of size five. The high rate of recruitment from litters of five offspring appeared to be linked to their biased production during spring when overall recruitment from all litters is high. Small litters that had low recruitment were more frequent during autumn when overall recruitment is low. No comparable bias was detected in small females.

Table 1. The litter size produced by large females depended upon the reproductive season

| Season | Litter size | | | |
|--------|-------------|----|----|-----|
| | 1-3 | 4 | 5 | 6-7 |
| Spring | 11 | 15 | 35 | 24 |
| Autumn | 19 | 10 | 18 | 26 |

Thus, the recruitment success of these female white-footed mice depends not only upon body size, but also upon interactions with other state-dependent aspects of their life history. Given the large number of state variables, it is remarkable that body size and its apparent interaction with seasonal reproduction of litters of different sizes provide such a close fit to the state-dependent explanation for Mountford's hypothesis.

The seasonal bias in litter size produced by large females is, nevertheless, difficult to explain. Large females that produce small litters in the autumn could represent old animals no longer capable of producing large litters, or rapidly growing spring-born females whose 'inexperience' limits litter size (Morris, in press a). Body size may also influence social interactions that modify reproduction and recruitment in territorial white-footed mice. Population densities fluctuate seasonally (Morris 1989, in press b) and density-dependent social interactions could also produce seasonally biased litter sizes. *Peromyscus* sociality is likely to interact with a related phenomenon, density-dependent habitat selection, that is known to influence litter size in this population of mice.

Regardless as to mechanism, patterns of juvenile survival vary among maternal states. The complexity of the patterns emphasizes how difficult it may be to predict the reproductive success associated with different state-dependent life history traits. It is crucial, therefore, to specify unambiguously the level of understanding that one wishes to achieve from any particular study. My research on white-footed mice demonstrates that small females producing litters larger than their body-size optimum have asymmetrically low recruitment. That result explains Mountford's cliff-edge effect in at least one population of white-footed mice. The current study is not appropriate to test all other aspects of the state-dependent theory. The implication is, nevertheless, that Mountford's hypothesis represents a special case of the more general state-dependent theory.

Low recruitment might suggest that the population is dwindling toward extinction. If so, the selective advantage of litters less than the most productive size might be ephemeral and disappear with the population. Mean annual population size has declined over a 12-year period (Morris, in press b). White-footed mice in this part of North America are frequently most abundant in intermediate seral stages with complex structure (e.g. M'Closkey 1975; M'Closkey & Lajoie 1975). The population decline may thus be a typical response to long-term changes in habitat as the forest and fence-row trees mature. Whether the population stabilizes at a low density or not, it is nevertheless clear that Mountford's hypothesis applies, and that it can be explained by a state-dependent approach to life history.

The penalty associated with the production of brood sizes larger than the state-dependent optimum may be compensated in some species by a post-con-

ception increase in total investment via intensified or prolonged parental care. Individuals could thereby adjust their investment to the optimum required for broods of different sizes (individual optimization). Intensified investment has been demonstrated by experimental manipulations of brood sizes in blue tits and other avian species (Nur 1984; references in Lessels 1991), but this result is far from universal (Lessels 1991).

Variation in time to fledging could also reduce the consequences of over-investment in offspring. Yet, there are numerous studies that implicate the initiation of egg-laying and brood-rearing as key determinants of brood size and subsequent recruitment. Individuals that delay seasonal breeding frequently contribute fewer descendants than those that reproduce on time (e.g. Perrins 1965; Pettifor *et al.* 1988). This implies that temporal opportunities for the successful rearing of young may often be tightly constrained. Parents that miss the optimal timing of reproduction in either the initiation of breeding, or by prolonged investment, are likely to produce few descendants.

For many mammals, post-partum oestrus acts as a parallel constraint on individual optimization. Most litters produced by white-footed mice contribute no offspring to future generations. The chance that a given litter will contribute descendants to the population is small and leads to a bet-hedging strategy of frequent iterated reproduction via post-partum oestrus (Morris 1986). Post-partum oestrus compromises the mother's investment options because she must simultaneously optimize the nourishment devoted to both lactation and gestation to maximize her reproductive success.

Post-partum oestrus thus creates an inevitable conflict between the current litter and the mother over her investment in future offspring (Morris 1986). The mother's decision should be predicated only on the expected net rewards of further investment in the current litter compared to the expectation of expending that same investment in a future litter (Dawkins & Carlisle 1976; Coleman & Gross 1991). If the rewards of offspring survival with increasing maternal investment decrease with investment (a curve of diminishing returns, Fig. 1a), the return on investment by prolonged parental care in nearly independent offspring may not equal that of increased nourishment to recently born progeny. The end-result is an additional mechanism capable of reducing average offspring survival in very large litters, thereby accentuating the cliff-edge effect.

Variable recruitment through time (the bad year's hypothesis of Boyce & Perrins 1987) should also reduce optimum brood size. Females that give birth to large litters in bad years produce few descendants. Offspring produced by mothers that over-invest beyond their body-size optimum in a good year may survive as well as those born to females producing the

long-term optimum brood size. Juvenile survival again 'falls off the cliff', but only in bad years. Consistent with this interpretation, a re-analysis of Boyce & Perrins (1987) bad-years effect led Liou *et al.* (1993) to suggest an important role for variable maternal condition, as well as spatial and temporal variation, in producing a mean brood size less than the most productive. In those circumstances where natural selection has favoured a conservative brood size (as may occur with temporal variation in juvenile survival), the cliff-edge effect is unlikely to be detected except where individuals are exposed to environments, in space or in time, that greatly reduce juvenile survival. Again, we find an important role for state-dependent life history, and its associated errors, in the evolution of brood size.

Tests of state-dependent theory depend critically upon proper selection of appropriate state variables. The tests will be most effective whenever they evaluate theories that explicitly identify expected relationships associated with specific state variables. Yet one of the attractions of the state-dependent approach is that it may yield general theories of optimal life history that can be fine-tuned to the biology of a wide variety of organisms. The distinction between the two approaches is profound. In the first, the theorist chooses the state variable, but in the second, the empiricist faces the daunting challenge of variable selection. Interactions among state variables influencing the evolution of litter size in white-footed mice confirm the value of the state-dependent approach and demonstrate one of its greatest virtues. The selection of the state variable(s) must be based on a detailed understanding of natural history.

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