State-dependent optimization of litter size

Douglas W. Morris

Four inter-related theories demonstrate that the quality or state of the parent influences its optimum litter size. A review of each model highlights their similar predictions, sets the stage for an expanded theory and demonstrates that three are really special cases of state-dependent optimization. The state-dependent theory helps to explain three paradoxes in life history. 1. Why the most commonly observed litter size is often smaller than the one that yields the maximum number of recruits. 2. Why litter size may increase or decrease in "high-quality" habitat. 3. Why there may be no reproductive cost associated with increased litter size. Tests of state-dependent optimization are likely to be complicated because the essential state variables are often left undefined, and because many state variables may interact with one another to determine a parent's quality. Composite state-variables, such as female body size, may overcome some of the limitations that otherwise arise from interacting variables. In white-footed mice, significant body-size effects interact with the environment and with a variety of life-history characters. The resulting networks of interactions, complicated as they are, may be caused by a relatively small number of underlying processes. Density-dependent habitat selection appears, at least for white-footed mice, to represent a fundamental process accounting for much of the environmental state-dependent variation in litter size.

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Many life history traits arise through the optimization of tradeoffs between different components of life history. Mean litter size, for example, may represent the optimal tradeoff between the number of young produced and subsequent juvenile as well as parental survival (Williams 1966, Charnov and Krebs 1974). Genotypes that code for litters smaller or larger than the optimum will yield relatively few descendants and will become less frequent than those that code for the optimum litter size. Thus we might expect, through evolutionary time, to observe that litter size approaches the optimum value (Lack 1947, 1948), at least in those species where the tradeoffs are so severe that individuals pay huge consequences for litters greater than or less than the optimum, and in relatively stable environments where the optimum is more or less constant (Sikes 1998). Clutch size is indeed fixed in some species, but is highly variable in many others (e.g., Morris 1985, Roff 1992).

A fixed strategy would be less than ideal in species exposed to a wide range of environmental circumstances that influence tradeoffs (Morris 1987, Sikes 1998). A more effective way to deal with tradeoffs in variable environments, where the optimum litter size varies through time and space, would be for the genotype to maintain a wide reaction norm (Bradshaw 1965, Gupta and Lewontin 1982, Via and Lande 1985). Depending on the environment, and the state of the individual (McNamara and Houston 1992, 1996), a variety of litter sizes could be produced.

State-dependent life histories have major consequences for the ways that we view and interpret reproductive costs. If reproductive investment (e.g., litter size, offspring size and quality, post-natal care) depends on the parent's state, reproductive costs associated with future survival and fecundity may be similar for all reproducing individuals (Morris 1987, 1992a, Mappes et al. 1995, Tannerfeldt and Anderbjörn 1998). Evolu-

tion of the life history would no longer depend primarily on selection associated with the costs of different levels of reproductive investment but may hinge, instead, on costs of reproduction versus no reproduction (Morris 1986, 1992a), or on selection for increasing individual quality. An example is the apparent selection on clutch (litter) size that actually represents selection on the ability of parents to secure high-quality territories or to live in high-quality habitats (e.g., Rockwell et al. 1987, Cooke et al. 1990, Dhondt et al. 1992, Mappes et al. 1995, Riddington and Gosler 1995). There may appear to be no selection at all if the health or nutritional state of the parent is non-heritable (Price et al. 1988, Price and Liou 1989; appearances can be deceptive because there may be selection for individuals to optimally allocate available resources to reproduction).

The application of state-dependent theory presents several problems because a parent's state is an all-encompassing variable. High-quality parents may be defined by their health, condition, nutritional state, social status, etc., or by the habitats in which they live (e.g., the abundance and nutritional value of resources, resource renewal rates, predatory risks, abundance of pests and pathogens, etc., and their spatial/temporal variances). Whereas it is relatively easy to imagine how an individual's health, condition, or nutritional state might influence litter size, it is quite another matter to imagine the causal links associated with these and other differences in individual quality. My main objective, therefore, is to explore how the complexities of state-dependent theory, and its influence on litter size, can be simplified for empirical analysis.

I begin by first reviewing four different approaches to state-dependent life history. Three are special cases of the general theory. I illustrate the complexity of state-dependent control on litter size by drawing the interactions among state variables that affect litter size in white-footed mice. Though much of the variation in litter size is related to maternal body size, two other variables, habitat and population density, play predominant roles in white-footed mouse life history. Habitat and density are linked through theories of habitat selection that allow us to understand habitat's effect on litter size and juvenile survival. I conclude with a short section detailing productive avenues for future research on state-dependent life history.

Four theories of state-dependent litter size

Optimal investment and individual optimization

The amount of time and resources that a parent can allocate to reproduction is likely to depend on its state. High-quality parents should be able to invest more in reproduction than parents of lower quality, or than parents living in lower-quality habitats. How do differ-

ences in reproductive investment translate into the number of offspring produced?

The answer depends on two crucial assumptions (Smith and Fretwell 1974, Morris 1985, 1987, Lloyd 1987, Lalonde 1991). 1. Increased investment in individual offspring reduces the number of young that can be produced in any given reproductive event, as well as during an individual's lifetime (Daan et al. 1996). 2. Increased investment in individual offspring will tend to increase their subsequent survival or reproduction. The optimum balance between these two assumptions will determine litter size (the optimal investment hypothesis, Morris 1985, 1987).

The optimum litter size is easiest to predict if we make two additional assumptions (Fig. 1). 3. All offspring receive an equal proportion of the parent's investment (the principle of proportional investment,
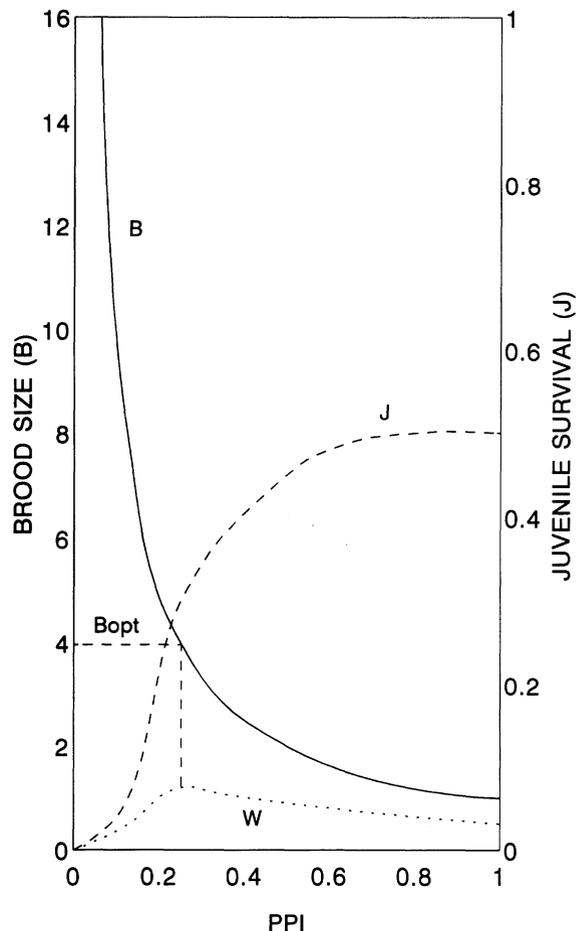
Fig. 1. The optimal investment hypothesis. Solid line – the principle of proportional investment. Each offspring receives an equal amount of the total available for reproduction. Reproductive effort varies with the parent's state. Dashed line – curve of diminishing returns of offspring survival (J) with proportional investment per offspring (PPI). Dotted line – the resulting fitness curve (W, product of offspring survival times brood size, B) that illustrates a single state-dependent optimum litter size (B_{opt}, after Morris 1987).
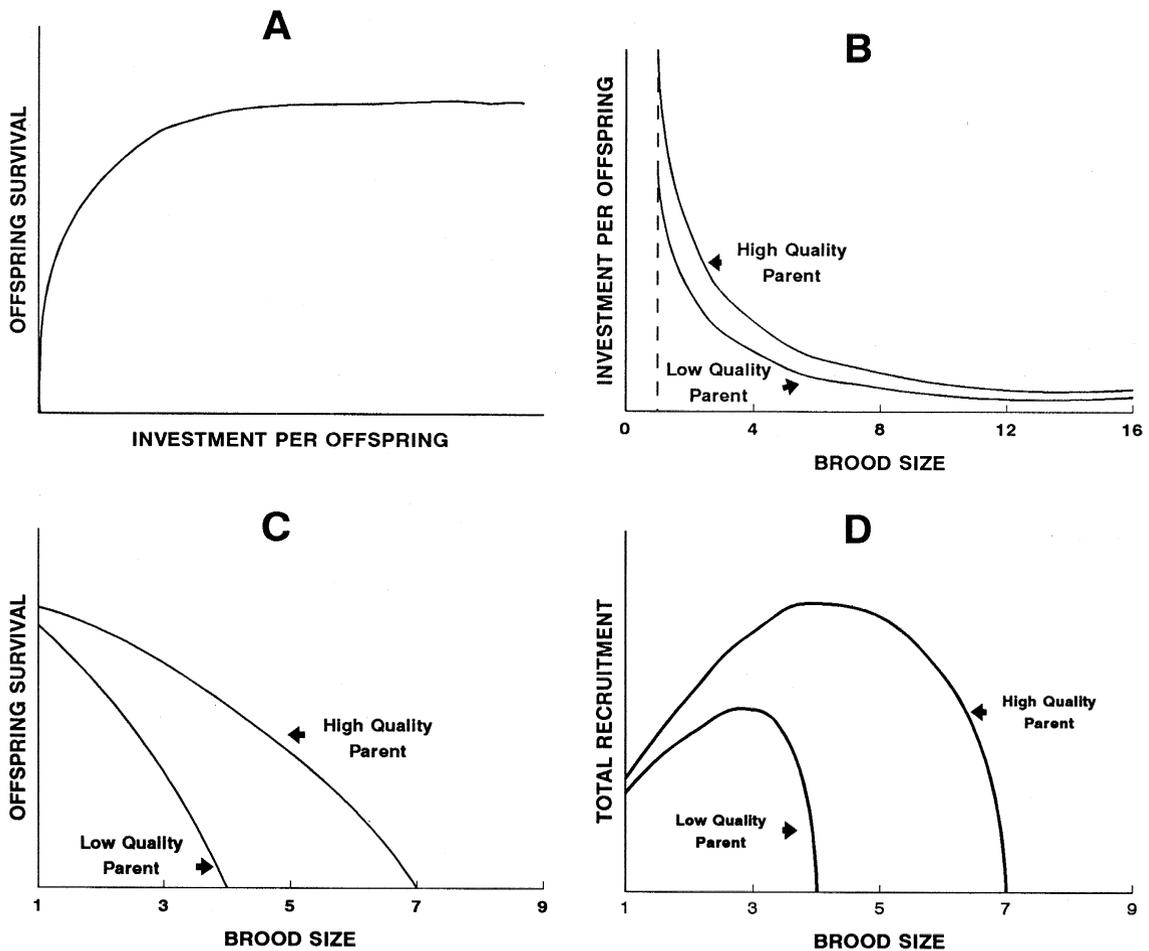
Fig. 2. State-dependence as an explanation of Mountford's hypothesis. A. Offspring survival increases at a declining rate with increasing parental investment. B. Investment per offspring from high and low quality parents as a function of brood size (the vertical dashed line corresponds to a brood size of one). C. Offspring survival for low and high-quality parents assuming the survival curve in A. D. The total recruitment from each kind of parent (the product of the curves in C times brood size, after Morris 1996a).

each of n offspring receives n^{-1} of the total investment, Morris 1987). 4. Offspring survival increases at a decelerating rate with increased parental investment.

The decelerating survival curve has huge effect on litter size by those parents that occasionally err in their reproductive allocations (Morris 1987, 1996a, Aparicio 1993, Sikes 1998). Parents that produce a litter less than their state-dependent optimum should do so with a slight increase in juvenile survival (more investment per offspring with small dividends in survival). But parents that produce a litter larger than their optimum are likely to suffer greatly reduced recruitment (Fig. 2).

In white-footed mice that I have studied the modal litter size of four is less than the size that yields the greatest number of descendants (five; Morris 1986, 1992a, 1996a). Litters of size six and greater produce fewer recruits than all other litter-size classes (Morris 1986). Female mice with an expected mean litter size of five are also likely to produce even larger litters that have low recruitment. Females with a smaller expected mean litter size will have fewer offspring recruited from those litters than from litters of five offspring, but they will also produce fewer of the very large unproductive litters. The asymmetry between small rewards from underinvesting and large penalties for overinvesting will tend to reduce the optimum litter size for each female regardless of her state. If the distribution of litter sizes is either symmetrical (as in white-footed mice) or positively skewed, the most frequently observed litter size will tend to be less than the one that produces the greatest number of recruits (Mountford 1968, Morris 1996a).

Research on great tits is also consistent with optimal investment theory because it documents 1, reduced growth rates of nestlings in enlarged broods, 2, reduced recruitment of those offspring, and 3, increased growth rates of offspring from reduced broods (Smith et al. 1989). The theory is supported as well·by Barber and

Evans' (1995) observation of an increase in relative recruitment from experimentally reduced broods in yellow-headed blackbirds (the prediction of reduced recruitment in enlarged broods failed, but there was no estimate of survival through the crucial post-fledging period).

Pettifor et al. (1988), building on research by Perrins and Moss (1975) on great tits, tested a parallel theory that they called the individual optimization hypothesis. Refined from Lack's (1947) original ideas, the hypothesis assumes that parents vary in their ability to produce and rear young. The hypothesis also assumes that the clutch size that maximizes the number of descendants from that brood is tailored to individual abilities, and thereby predicts that the optimum clutch size should vary among parents.

Note that the mechanisms responsible for the optimal investment hypothesis will also yield individual optimization. The two hypotheses are essentially the same except for two differences. 1. Individual optimization, as originally described, does not allow for investment errors by parents (this assumption is important because natural variability will produce a frequency distribution of brood sizes around each phenotype's optimum [Mountford 1968, Aparicio 1993, Morris 1996a] that may have dramatic influences on the number of young produced, on the average success of parents producing broods of different sizes, and thereby on our ability to confirm or reject the hypothesis). 2. The hypothesis becomes ambiguous when parents and their offspring from different litters compete over reproductive investment. Parents may curtail investment in a litter that would increase the littermates' survival in order to invest in another (Morris 1986, 1992a). Optimization of the inclusive fitness of the parent may modify the investment and subsequent recruitment from litters that would otherwise appear "sub-optimal". Individual optimization may therefore best be viewed as a specific case of the optimal investment hypothesis that is, itself, a restrictive case of the more encompassing state-dependent theory.

Consistent with individual optimization, parent great tits did not produce more recruits from artificially increased or reduced broods than they did from natural broods. The competing reproductive cost hypothesis was rejected because parents rearing enlarged broods did not suffer increased mortality or decreased fecundity.

The sum of evidence for individual optimization is equivocal. Pettifor's (1993) studies on blue tits support the hypothesis, but Barber and Evans (1995) rejected it for yellow-headed blackbirds, and Dhondt et al. (1990) argued that gene flow between habitats may make it impossible for both great and blue tits to produce the optimum clutch size. The modal clutch size produced (9 or 10 young in great tits, 11 or 12 young in blue tits) was similar in different habitats, while the most produc-

tive one varied (8 to 12 offspring in great tits, 9 to 14 offspring in blue tits). Dhondt et al.'s results appear to illustrate significant non-adaptive variance in clutch size but do not exclude the possibility of residual state-dependent variation. A single optimum can exist among habitats if habitats with low juvenile survival compensate parents with higher resource availability (Fig. 3). The optimal investment per offspring would vary among habitats, as would fitness, but not the optimum brood size.

One should not assume that parents in high-quality states, or that live in high-quality territories, necessarily produce larger litters than parents in low-quality states or those that occupy low-quality territories or habitats. Consider the case where juvenile survival is higher in one habitat than it is in another. Offspring of parents living in a "high-quality" habitat may experience, for example, lower risks of predation and parasitism. If
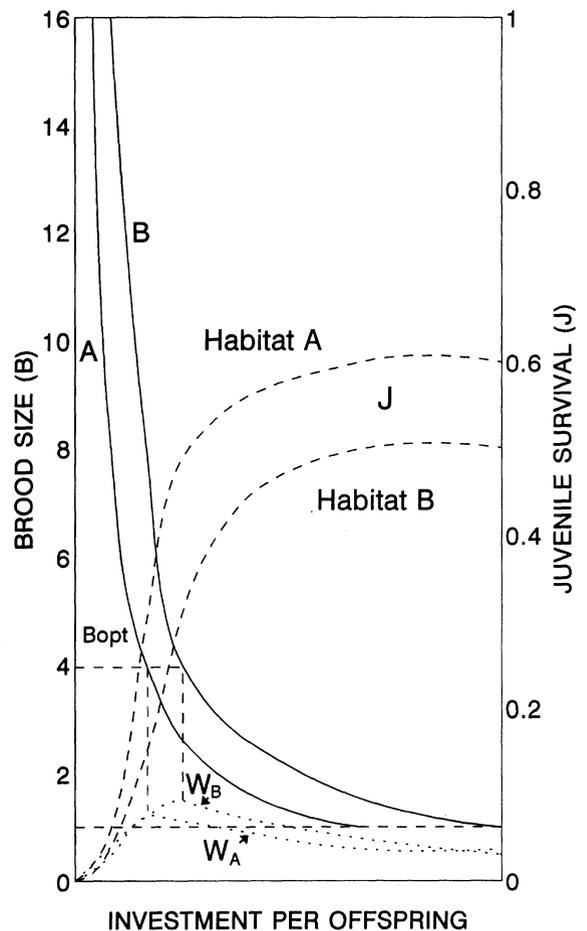
Fig. 3. An example of compensating differences in habitat that yield the same optimum litter size (B_{opt}) even though fitness differs. Habitat B has lower juvenile survival (J) than does habitat A, but higher resource levels that can be allocated to offspring (greater investment per offspring – solid lines). The horizontal dashed line corresponds to broods of one offspring. Dotted lines illustrate the fitness (W_i) expected in each habitat.

parents are otherwise of similar quality (as might be expected from density-dependent habitat selection with an ideal free distribution [Fretwell and Lucas 1970]), the optimum litter size may actually be smallest in the best habitat because the increase in juvenile survival more than compensates for any increase in litter size that would occur with less investment per offspring (Morris 1987). Consistent with this aspect of the theory, litter sizes produced by white-footed mice are smaller in forest habitat with high juvenile survival than they are in fencerow habitat where weasel predation reduces juvenile recruitment (Morris 1989, 1992b; it should be noted that habitat selection in this population does not obey an ideal free distribution and parents in different habitats may thereby vary in quality [Morris 1991, 1994]).

The ability to predict the habitat that should yield the largest litter size becomes complicated when habitat interacts with other measures of parental quality. Consider the case where parents that occupy high-quality habitat also have more total resource to invest (tied, again, to density-dependent habitat selection as may occur with ideal despotic [Fretwell and Lucas 1970] or ideal pre-emptive distributions [Pulliam 1988]). Individual offspring in any size litter can expect to receive, on average, more investment in the high-quality habitat than can offspring in low-quality habitat. The difference in investment in individual offspring increases their survival and would tend to counterbalance the original habitat effect (Morris 1987).

There are many other possibilities where the optimum strategy may itself interact with the parent's state. A parent in a low nutritional state may, for any given level of investment, produce offspring of lower quality (e.g., lower-quality milk or resources, transfer of parasites and pathogens) than parents in a higher state. Alternatively, a parent in a given state may produce offspring of lower quality in some environments than in others. The optimum litter size would depend not only on the parent's state, but also on the environment within which it lived. There are other possibilities. Parents in different states may provision young at different rates and thereby modify development time. Any tradeoff between development and increased litter size would be modified by the parents' state. Similar possibilities exist when the payoffs of reproduction vary among seasons, and especially so if seasonal effects interact with the parents' state.

Unit pricing

Theories of optimal reproductive investment assume, at least implicitly, that investment is linked to parental quality. One of the questions the theories attempt to answer is, what brood or litter size optimizes that effort? But what is the optimum litter size if parents' reproductive effort is adjusted after conception relative to the number of offspring? What is the optimum litter size if the efficiency of investment varies with litter size (Sikes 1998, Sikes and Ylönen 1998)?

Efficiency could vary if reproduction entails fixed and variable expenditures. Fixed expenditures could include behavioral (e.g., mating, nest construction, increased foraging) and physiological differences between reproductive and non-reproductive individuals. The expenditure per offspring would be highest in small litters. Variable expenditures would include energy and time channelled to offspring development and growth. Energy expended on thermoregulation, for example, often varies with litter/clutch size (Royama 1966, Mertens 1969). During the period while offspring are in the nest, each offspring in a small or very large litter will require more energy from its parent(s) than an offspring from a litter near the thermoregulatory optimum size. Parents producing the optimum size will be more efficient than parents producing smaller litters because litter size increases more rapidly than does the additional energy requirement of the enlarged litter (Royama 1966). Physiological and behavioral allometries may also cause parents to use proportionately more energy, or to forage with proportionately greater risks, with increasing litter size, and especially so for litters beyond the thermoregulatory optimum. In each instance, an optimum litter size smaller than the maximum will occur if selection minimizes the cost per offspring (the "unit pricing" hypothesis; Sikes 1998, Sikes and Ylönen 1998).

Unit pricing assumes that one can estimate costs per offspring in terms of a reliable fitness currency. Energetic costs (e.g., those associated with gestation and post-natal care) are likely reliable estimates for laboratory animals or for those foraging in relatively benign environments. An energetic currency may be a less accurate estimate of total fitness "costs" in environments where time allocated to foraging and parental care results, for example, in proportionately greater risks of predation. An energetic currency may be appropriate, nevertheless, if energetic demands increase foraging time and its associated risk, but the relationship may be far from linear. In general we can expect the accuracy of the energetic currency to vary with habitat and its landscape context, with population density, with temporal variation and with their interactions.

One may be able to estimate the accuracy of an energetic currency by comparative studies examining model species at different times, in different places, and in different environmental contexts. Initial studies should concentrate, if possible, on semelparous species (with some form of extended parental care) or those species that produce a single litter during a given reproductive season. Unit pricing, or at least its analysis, may be ambiguous when reproductive investment is allocated among competing litters.

A general theory

Optimal investment, individual optimization and unit pricing are rather specific examples of the influence of the state of the parent on life history, and particularly on litter size. A more general approach would also examine the role that parental state has on the state of offspring and how that modifies the number and state of descendants produced in the future. The approach can be made tractable by evaluating interactions among functions that determine parental and juvenile survival and the respective states of parents and offspring in the future (Houston and McNamara 1992, McNamara and Houston 1992, 1996). Different strategies, such as the litter size that a female produces as a function of her state, can be contrasted by dynamic programming (e.g., McNamara and Houston 1986, Mangel and Clark 1988), the optimal strategy being the one that yields the long-term maximum growth rate (number of descendants). Alternatively, one could determine the optimal strategy by defining a state-(stage) based population projection matrix and calculate population growth rates for different parameter values in the matrix (Caswell 1989). Both approaches subsume earlier age-dependent models of life history because age is a component of the organism's state.

The general state-dependent theory is valuable for exploring the evolution of optimal life-history strategies, including litter size (McNamara and Houston 1992) because it provides a general overview of life history simultaneous with the ability to examine the detailed life history of individual species, or even of their separate populations. The theory has high pragmatic value in those instances where we know the key functional relationships determining an organism's state, and where we wish to evaluate the effects of environmental change on life-history strategies. But the theory implicitly assumes that we already have answers to many equally difficult questions. What, for example, are the key state variables that influence a particular component of life history? What are their functional relationships? How do the different state variables interact with one another? How are the interactions affected by temporal and spatial variation? What are the relative roles of density and frequency-dependent interactions? These questions can be answered only by detailed studies of potentially complex interactions in model species.

The state-dependent litter size of white-footed mice

The white-footed mouse (*Peromyscus leucopus*) is a common, widely distributed species that occupies a variety of habitats throughout much of North America. Extensive areas in its north-central geographic range

have been converted to intensive agricultural landscapes where *P. leucopus* lives predominantly in residual forests, tree-covered field margins, and in old fields abandoned from active agriculture. White-footed mice are semi-arboreal and their occupation of artificial nest boxes (Nicholson 1941, Goundie and Vessey 1986, Morris 1986, 1992a, b, 1996a, b, Wolff 1986) greatly simplifies the study of their life history. In the north, most litters are produced in spring and autumn reproductive seasons.

My assistants and I have used nest boxes to monitor reproduction and subsequent recruitment of white-footed mice since 1981. Most litters that we marked were unsuccessful at recruiting even a single offspring to the nest-box population, and the vast majority of those that were successful produced only a single recruit. The probability of successful recruitment (litter success) is low and variable among seasons, and functions as a lottery (Morris 1986) that accounts for the white-footed mouse bet-hedging strategy of frequent iterated reproduction (like any lottery, the probability of winning increases with the number of tickets an individual holds).

Litter sizes observed in white-footed mice are consistent with state-dependent optimal investment. Litter size is smallest, and recruitment greatest, in the preferred forest habitat, though this effect is influenced strongly by population density during the previous reproductive season (Morris 1989, 1992b, 1996c). Litters of five offspring yield the most recruits, but they are not as frequent as one would expect on the basis of their recruitment of offspring to the population. Litters of six offspring have dramatically lower recruitment than do all smaller litter-size classes (Morris 1986, 1992a, 1996a).

Large, experienced females tend to produce larger litters than small ones (Morris 1992a, b, 1996a). Body size can thus be used as a composite or summary state variable influencing litter size in this population of white-footed mice. The litter-size distribution of white-footed mice of different body sizes is consistent with the state-dependent explanation of Mountford's hypothesis. Females that produce litters larger than their body-size optimum have very low mean recruitment (Morris 1996a). Competing hypotheses related to reproductive costs and annual and spatial variation in recruitment are insufficient explanations for the distribution of litter sizes produced by this population of white-footed mice (Morris 1992a).

Contrary to theory, offspring from small litters produced by females larger than the median body length of 93 mm did not have high mean survival. The apparently anomalous result also has a state-dependent explanation. Large-bodied females, and especially those that are one-year-old or older, produced the majority of their small litters in autumn when recruitment from all litter sizes was low (Morris 1996a, b). The mass of old,

large-bodied females was similar between spring and autumn reproductive seasons, but mean body length was greater in autumn than in spring. Old, large females in autumn are in a lower reproductive state (mass per unit body length) than similar sized females in spring.

The importance of body size as a composite state variable will vary among populations and species depending on how much of the variance in a particular life-history trait it explains. One might expect that the importance of body size as a useful summary variable would be relatively low in species such as many small mammals that obtain resources for reproduction by increased ingestion rather than through mobilizing stored reserves (e.g., Millar 1978, 1979, Sikes 1995). In deer mice (*Peromyscus maniculatus*), for example, maternal mass accounted for a maximum of 21% of the variance in litter size (Myers and Master 1983, but the analyses were based on the body sizes and litter sizes produced by individual females where we expect maximum variance, not on mean values for classes of females). Body size may also be an insufficient state variable in northern grasshopper mice (*Onychomys leucogaster*) where mean maternal mass on the day of parturition accounted for only 26% of the variance in litter sizes, (Sikes 1995; sample sizes for many litter sizes were small). Body mass is a highly variable measure of maternal body size and it would be interesting to know whether other metrics yield higher correlations. For the white-footed mice that I have worked with, mean maternal body length accounts for nearly 80% of the variation in mean litter size (Morris 1996a). In white-footed mice the composite state-variable of body size captures much of the otherwise confusing interdependence among state variables.

But it is implicit in, and one of the main strengths of, state-dependent theory that the state of the parent may affect the state of offspring. An example is found in northern populations of the European kestrel where female body size, responding to cyclical small-mammal prey, varies significantly among years (Korpimäki and Rita 1996). Fledgling mass also varies among years, but in an apparently complex way that depends on prey density, the density of kestrels, and the effects of both factors on clutch size.

Environmental networks

It appears, and especially so for white-footed mice and European kestrels, that state-dependent explanations for life history may often involve a variety of state variables and their interactions. The degree of complexity that one wishes to include will often depend on the intent of the study. For white-footed mice one can do a very good job of predicting litter size simply from maternal body size. That relationship alone may be
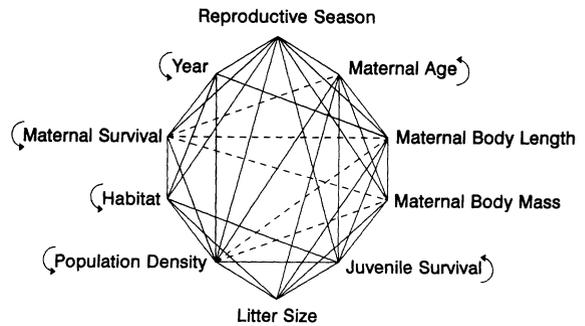
Fig. 4. The environmental network among state variables known to influence various aspects of white-footed mouse life history. Some interactions are inferred (dashed lines), some others, including many higher-order effects, have not yet been tested. Main effects are indicated by loops (from results in Morris 1986, 1989, 1991, 1992a, b, 1996a, b, c).

good enough for many applications. One may or may not be able to reduce residual variation by including additional state variables. But that is not quite the point. To understand the factors influencing white-footed mouse litter size one must look to the effects of density (possibly with time lags), seasonality, habitat, and the relationship between body mass and body length as it is modified by maternal age.

Regardless of whether life history typically involves many or few state variables, it would be quite helpful to have a standard method of displaying and interpreting the interactions among them because interactions always reveal exceedingly interesting biology. One simple method is to draw the web of interactions as an environmental network (Morris 1992b). Each factor is represented as a point or node arranged as the vertices of a polygon. A factor can be either a dependent life-history variable or an independent state variable, and depending on context, can change from one to the other (e.g., litter size may depend on maternal body size, juvenile survival may, in turn, depend on litter size). Two-way interactions are represented by straight lines between any pair of nodes, higher-order interactions are represented by enclosed polygons among sets of factors. Main effects are graphed as loops at each vertex (e.g., more litters observed in one habitat than another, more litters produced in some years than in others).

Fig. 4 documents some of the most significant interactions that influence litter size in white-footed mice (Morris 1986, 1989, 1991, 1992a, b, 1996a, b, c). Large-bodied female white-footed mice produce larger litters than do smaller females (line between litter size and maternal body length). More large litters are produced in fencerow habitat than in nearby forest (line between litter size and habitat). The number of litters produced in different habitats varies between seasons and years (line between reproductive season and year), as does maternal body size (triangle joining maternal body

length, reproductive season and year). Litter size in this population of white-footed mice does not vary significantly between seasons or years and the web of interactions is less complicated than it could be (Fig. 4).

Some rather complicated interactions might affect litter size if we were able to generate sample sizes large enough to examine them (it would be most unlikely to obtain sample sizes large enough to evaluate the 10-way interaction traced around the entire network). First, litter size is modified by a variety of variables including population density and the mass of large females in autumn (quadrangle joining litter size, maternal body mass, reproductive season and population density) that one may not include in an initial analysis of state-dependent life history. Second, it is possible for complicated multi-way interactions to modify litter size with virtually no empirical ability to detect them (even highly ambitious field designs are limited to the simultaneous analysis of perhaps five factors). Third, a variety of life-history traits interact in different ways with the suite of environmental variables (e.g., population density [often with a time lag of at least one reproductive season {Morris 1996c}], habitat, seasonal and annual temporal effects). The network for white-footed mice suggests that much of this species' life history may be understood by the pattern of interactions among a relatively small set of spatial and temporal environmental variables. Progress in theories of density-dependent habitat selection illustrate that we may often be able to predict the interactions, including some of the higher-order effects, and thereby their consequences on life history and its evolution.

Density-dependent habitat selection and litter size

Individual habitat selectors should distribute themselves across habitats in a way that maximizes their fitness (Fretwell and Lucas 1970, Rosenzweig 1974, 1981). Assuming that fitness varies with density, an evolutionarily stable strategy (ESS) of habitat selection will occur when the density of individuals in each habitat is adjusted such that no individual can increase its fitness by changing habitats. The solution to the ESS is given by habitat isodars (Morris 1988), plots of the density of individuals in pairs of habitats such that the expected (not necessarily the mean) fitness is the same in both (Fig. 5). Since we know that both habitat and density influence the litter size produced by white-footed mice (Fig. 4), we should be able to use isodars to interpret their joint influence on litter size.

Consider the environmental network for white-footed mice (Fig. 4). How might we interpret the three two-way interactions between litter size, population density and habitat (lines between litter size and population density, between litter size and habitat, and between population density and habitat)? An obvious conclu-

sion is that habitat's influence on litter size occurs independent of the effects of density. A significant three-way interaction (triangle joining litter size, population density and habitat) might reasonably lead us to conclude that the relationship between litter size and population density varies between habitats. If the species is a density-dependent habitat selector, both conclusions may be incorrect.

Imagine that litter size in a population is a negative and linear function of population density (Fig. 6; see also Slade et al. 1996). Imagine, as well, that the same population has an ESS of habitat selection yielding a linear isodar with a slope of one. Linear isodars with unit slope occur only when the difference in density between occupied habitats is constant regardless of overall population size (Fig. 6). The result is that litter size will be greater in the habitat with low density, and that the difference in litter size will be constant at all population sizes (the two-way interactions between litter size and population density, between litter size and habitat, and between population density and habitat are significant). Do we conclude that density-dependent habitat selection has no effect on litter size? No. The density of individuals in the two habitats, and thus the litter size, is determined by the two-way interaction between density and habitat (density-dependent habitat selection). The influence of density on litter size is not independent of habitat.
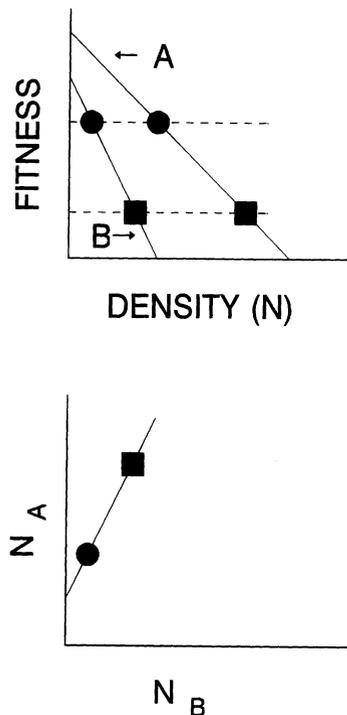

Fig. 5. An evolutionarily stable strategy of density-dependent habitat selection (top) and its isodar solution graphed as the respective density (N_i) in each habitat (bottom). Symbols correspond to equilibrium densities where the fitness in habitat A is equivalent to that in habitat B.
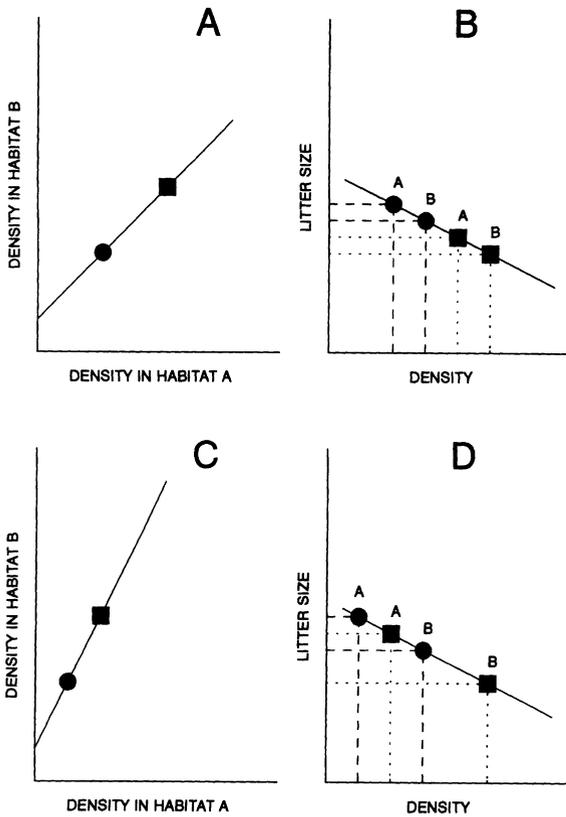
Fig. 6. An illustration of how density-dependent habitat selection can effect changes in state-dependent life history. Symbols represent two different samples of population density along the isodar (e.g., two different population sizes). A. A linear isodar with slope 1 yields a constant difference in density between habitats A and B. B. Litter size declines linearly with increased population density. Litter size will be larger in habitat A by a constant amount (the interaction between litter size and habitat is redundant with the interaction between litter size and density). C. A linear isodar with slope greater than one yields a unique difference in density between habitats at every population size. D. Even if the relationship of litter size with density is identical to that above, and identical in both habitats, the actual litter size observed will depend on density-dependent habitat selection (a three-way interaction).

Now imagine that the isodar has a slope greater than one (diverging fitness functions). The difference in density between habitats is no longer constant (the three-way interaction among litter size, population density and habitat is significant), *even though the relationship between litter size and density is constant in both habitats*. Density-dependent habitat selection appears to play such a predominant role in determining the litter size of white-footed mice occupying agricultural landscapes. Litter size declines linearly with increasing population density (Morris 1996a; Fig. 7) and the white-footed mouse isodar between forest and fencerow habitats appears linear with a slope significantly greater than one (Morris, 1996c; Fig. 7).

Density-dependent habitat selection does not preclude the possibility that the relationship between litter

size and density also varies with habitat. My point is that the state-dependence of litter size may occur by rather circuitous routes that defy simple statistical explanations. In the case of density-dependent habitat selection, higher-order state-dependent interactions with life history can occur because individuals (and their states) react to the overall currency of fitness, rather than to the separate components of life history in the environmental network.

Future directions

Environmental networks, as we now know them, are but a hint of the wealth of state-dependent interactions that influence life history and its evolution. The apparent dependence of life history on habitat selection suggests new insights into the density-dependent evolution
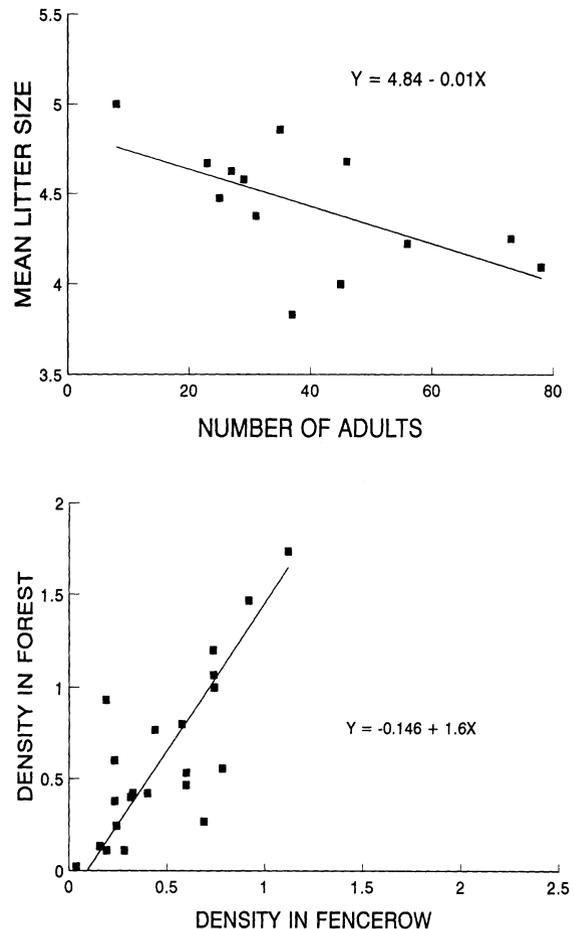

Fig. 7. The relationship between mean litter size and the number of adult white-footed mice captured in live traps (top, forest and forest-edge habitats, 1983–1989, 170 litters), and the isodar of white-footed mice occupying forest and fencerow habitats (bottom, from Morris 1996c). Litter size in white-footed mice occupying the agricultural landscape is determined, at least partially, by density-dependent habitat selection.

of life histories. Habitats yielding low fitness, for example, should have low densities and, perhaps, a different suite of life history traits than habitats occupied at high density. The traits in the low-density habitat may appear to be those influenced by density-independent selection (e.g., r selection) when, in fact, the entire process is clearly density-dependent.

The flux of individuals between habitats caused by habitat selection may tend to homogenize spatial differences in natural selection on life history. The degree to which habitat selection "equalizes" natural selection will depend on the fitness differential among habitats, on dispersal rates and on the relative frequencies of each habitat (e.g., Holt and Gaines 1992, Kawecki and Stearns 1993, Kawecki 1995). Thus, natural selection will be biased in favor of adaptations to the habitat occupied by the most individuals (Rosenzweig 1987). Population densities will vary among habitats, nevertheless, and much of the difference that we observe in life history among habitats may simply represent different density-dependent expressions of the same reaction norm.

The potential of numerous interacting state variables emphasizes the importance of clearly defined objectives in all studies of state-dependent life history. Otherwise, the state-dependence of life history can open a Pandora's box of complex interactions that obfuscates our understanding. Do we want to know how different state variables interact with one another, how a particularly interesting state variable influences life history, or how a consideration of parental and offspring "quality" explains and broadens our understanding of life history? Regardless of the specific question, state-dependent life history suggests new and promising lines of inquiry. What, for example, are the consequences, for organisms with different mean litter sizes, and in different states, of non-optimal litter sizes? How effectively can one life history trait compensate for non-optimal values in another (e.g., compensation for a sub-optimal litter size by increased post-partum investment)? Under what conditions does the state of offspring act as a significant contributor to evolutionary fitness? How does one obtain accurate measures and interpretations of reproductive costs when the state-dependence of the life history is spread across generations? What are the ultimate evolutionary conditions that cause some organisms to optimize their litter size with no apparent reproductive costs while the optimum litter size in others is a compromise between the benefits of increased investment and the parental costs of declining survival or future fecundity?

But perhaps we are missing the point of reproductive costs and how they influence life history. Perhaps we should rephrase our question to ask under what conditions are the costs of reproductive investment paid directly by parents in terms of their future survival and fecundity? Under what other conditions are reproduc-

tive costs paid indirectly through the reduced survival, reduced state and reduced future state-dependent reproduction by offspring?

References

Aparicio, J. M. 1993. The effect of clutch size errors on fitness: a hypothesis. – Oikos 68: 186–190.

Barber, C. A. and Evans, R. M. 1995. Clutch-size manipulations in the yellow-headed blackbird: a test of the individual optimization hypothesis. – Condor 97: 352–360.

Bradshaw, A. D. 1965. Evolutionary significance of phenotypic plasticity in plants. – Adv. Gen. 13: 115–155.

Caswell, H. 1989. Matrix population models. – Sinauer, Sunderland, MA.

Charnov, E. L. and Krebs, J. R. 1974. On clutch size and fitness. – Ibis 116: 217–219.

Cooke, F., Taylor, P. D., Francis, C. M. and Rockwell, R. F. 1990. Directional selection and clutch size in birds. – Am. Nat. 136: 261–267.

Daan, S., Deerenberg, C. and Dijkstra, C. 1996. Increased daily work precipitates natural death in the kestrel. – J. Anim. Ecol. 65: 539–544.

Dhondt, A. A., Adriaensen, F., Matthysen, F. and Kempenaers, B. 1990. Nonadaptive clutch sizes in tits. – Nature 348: 723–725.

Dhondt, A. A., Kempenaers, B. and Adriaensen, F. 1992. Density-dependent clutch size caused by habitat heterogeneity. – J. Anim. Ecol. 61: 643–648.

Fretwell, S. D. and Lucas, H. R. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. – Acta Biotheor. 19: 16–36.

Goundie, T. R. and Vessey, S. H. 1986. Survival and dispersal of young white-footed mice born in nest boxes. – J. Mammal. 67: 53–60.

Gupta, A. P. and Lewontin, R. C. 1982. A study of reaction norms in natural populations of Drosophila pseudoobscura. – Evolution 36: 934–948.

Holt, R. D. and Gaines, M. S. 1992. Analysis of adaptation in heterogeneous landscapes: implications for the evolution of fundamental niches. – Evol. Ecol. 6: 433–447.

Houston, A. I. and McNamara, J. M. 1992. Phenotypic plasticity as a state-dependent life-history decision. – Evol. Ecol. 6: 243–253.

Kawecki, T. J. 1995. Demography of source-sink populations and the evolution of ecological niches. – Evol. Ecol. 9: 38–44.

Kawecki, T. J. and Stearns, S. C. 1993. The evolution of life histories in spatially heterogeneous environments: optimal reaction norms revisited. – Evol. Ecol. 7: 155–174.

Korpimäki, E. and Rita, H. 1996. Effects of brood size manipulations on offspring and parental survival in the European kestrel under fluctuating food conditions. – Écoscience 3: 264–273.

Lack, D. 1947. The significance of clutch size. 1. Intraspecific variation. – Ibis 89: 302–352.

Lack, D. 1948. The significance of litter size. – J. Anim. Ecol. 17: 45–50.

Lalonde, R. G. 1991. Optimal offspring provisioning when resources are not predictable. – Am. Nat. 138: 680–686.

Lloyd, D. G. 1987. Selection of offspring size at independence and other size-versus-number strategies. – Am. Nat. 129: 800–817.

Mangel, M. and Clark, C. W. 1988. Dynamic modelling in behavioral ecology. – Princeton Univ. Press, Princeton, NJ.

Mappes, T., Koskela, E. and Ylönen, H. 1995. Reproductive costs and litter size in the bank vole. – Proc. R. Soc. Lond. B 261: 19–24.

McNamara, J. M. and Houston, A. I. 1986. The common currency for behavioral decisions. – Am. Nat. 127: 358–378.

McNamara, J. M. and Houston, A. I. 1992. State-dependent life history theory and its implications for optimal clutch size. – Evol. Ecol. 6: 170–185.

McNamara, J. M. and Houston, A. I. 1996. State-dependent life histories. – Nature 380: 215–221.

Mertens, J. A. L. 1969. The influence of brood size on the energy metabolism and water loss of nestling great tits Parus major. – Ibis 111: 11–16.

Millar, J. S. 1978. Energetics of reproduction in Peromyscus leucopus: the cost of lactation. – Ecology 59: 1055–1061.

Millar, J. S. 1979. Energetics of lactation in Peromyscus maniculatus. – Can. J. Zool. 57: 1015–1019.

Morris, D. W. 1985. Natural selection for reproductive optima. – Oikos 45: 290–292.

Morris, D. W. 1986. Proximate and ultimate controls on life-history variation: the evolution of litter size in white-footed mice Peromyscus leucopus. – Evolution 40: 169–181.

Morris, D. W. 1987. Optimal allocation of parental investment. – Oikos 49: 332–339.

Morris, D. W. 1988. Habitat-dependent population regulation and community structure. – Evol. Ecol. 2: 253–269.

Morris, D. W. 1989. Density-dependent habitat selection: testing the theory with fitness data. – Evol. Ecol. 3: 80–94.

Morris, D. W. 1991. Fitness and patch selection by white-footed mice. – Am. Nat. 138: 702–716.

Morris, D. W. 1992a. Optimal brood size: tests of alternative hypotheses. – Evolution 46: 1848–1861.

Morris, D. W. 1992b. Environmental networks, compensating life histories, and habitat selection by white-footed mice. – Evol. Ecol. 6: 1–14.

Morris, D. W. 1994. Habitat matching: alternatives and implications to populations and communities. – Evol. Ecol. 8: 367–406.

Morris, D. W. 1996a. State-dependent life histories, Mountford's hypothesis, and the evolution of brood size. – J. Anim. Ecol. 65: 43–51.

Morris, D. W. 1996b. State-dependent life history and senescence of white-footed mice. – Ecoscience 3: 1–6.

Morris, D. W. 1996c. Temporal and spatial population dynamics connected by habitat selection. – Oikos 75: 207–219.

Mountford, M. D. 1968. The significance of litter-size. – J. Anim. Ecol. 37: 363–367.

Myers, P. and Master, L. L. 1983. Reproduction by Peromyscus maniculatus: size and compromise. – J. Mammal. 64: 1–18.

Nicholson, A. J. 1941. The homes and social habits of the wood mouse, (Peromyscus leucopus novaboracensis) in southern Michigan. – Am. Midl. Nat. 25: 196–223.

Perrins, C. M. and Moss, D. 1975. Reproductive rates in the great tit. – J. Anim. Ecol. 44: 695–706.

Pettifor, R. A. 1993). Brood manipulation experiments. I. The number of offspring surviving per nest in blue tits (Parus caeruleus). – J. Anim. Ecol. 62: 131–144.

Pettifor, R. A., Perrins, C. M. and McCleery, R. H. 1988. Individual optimization of clutch size in great tits. – Nature 336: 160–162.

Price, T. and Liou, L. 1989. Selection on clutch size in birds. – Am. Nat. 134: 950–959.

Price, T., Kirkpatrick, M. and Arnold, S. J. 1988. Directional selection and the evolution of breeding date in birds. – Science 240: 798–799.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. – Am. Nat. 132: 652–661.

Riddington, R. and Gosler, A. G. 1995. Differences in reproductive success and parental qualities between habitats in the Great Tit Parus major. – Ibis 137: 371–378.

Rockwell, R. F., Findlay, C. S. and Cooke, F. 1987. Is there an optimal clutch size in snow geese? – Am. Nat. 130: 839–863.

Roff, D. A. 1992. The evolution of life histories. – Chapman and Hall, New York.

Rosenzweig, M. L. 1974. On the evolution of habitat selection. – Proc. 1st Int. Congr. Ecol. Centre for Agricultural Publishing and Documentation, The Hague, pp. 401–404.

Rosenzweig, M. L. 1981. A theory of habitat selection. – Ecology 62: 327–335.

Rosenzweig, M. L. 1987. Habitat selection as a source of biological diversity. – Evol. Ecol. 1: 315–330.

Royama, T. 1966. Factors governing feeding rate, food requirement and brood size of nestling great tits Parus major. – Ibis 108: 313–347.

Sikes, R. S. 1995. Costs of lactation and optimal litter size in northern grasshopper mice (Onychomys leucogaster). – J. Mammal. 76: 348–357.

Sikes, R. S. 1998. Unit pricing: economics and the evolution of litter size. – Evol. Ecol. 12: 179–190.

Sikes, R. S. and Ylönen, H. 1998. Considerations of optimal litter size. – Oikos this issue.

Slade, N. A., McMurry, S. T. and Lochmiller, R. L. 1996. Habitat differences in mass-specific litter sizes of hispid cotton rats. – J. Mammal. 77: 346–350.

Smith, C. C. and Fretwell, S. D. 1974. The optimal balance between size and number of offspring. – Am. Nat. 108: 499–506.

Smith, H. G., Källander, H. and Nilsson, J.-Å. 1989. The trade-off between offspring number and quality in the great tit Parus major. – J. Anim. Ecol. 58: 383–401.

Tannerfeldt, M. and Angerbjörn, A. 1998. Fluctuating resources and the evolution of litter size in the arctic fox. – Oikos 83: 545–559.

Via, S. and Lande, R. 1985. Genotype-environment interaction and the evolution of phenotypic plasticity. – Evolution 39: 505–522.

Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's hypothesis. – Am. Nat. 100: 687–690.

Wolff, J. 1986. Life history strategies of white-footed mice (Peromyscus leucopus). – Virginia J. Sci. 37: 208–220.