

State-dependent life history and senescence of white-footed mice¹

Douglas W. MORRIS, Centre for Northern Studies, Department of Biology and Faculty of Forestry, Lakehead University, Thunder Bay, Ontario P7B 5E1, Canada, e-mail: douglas.morris@lakeheadu.ca

Abstract: The application of a state-dependent approach to life-history evolution is assessed by determining the state variables, and their interactions, that influence litter-size distributions produced by a free-living population of white-footed mice. State-dependent theory explains why the most productive litter size is not as frequent in the population as expected by the number of recruits. Yet female age, size, and body condition interact with reproductive season in ways that defy a simple state-dependent approach to the life history of this species. Maternal age and reproductive season are confounded by the inability of young females to reproduce in spring. The biased production of small litter-size classes by large-bodied females in autumn appears to be a senescent effect resulting from old, large females in poor condition relative to young, small ones. Senescence implicates long-term cumulative reproductive costs in this, and perhaps other, populations of small mammals.
Keywords: body size, evolution, life history, litter size, *Peromyscus*, senescence.

Résumé: L'application d'une approche basée sur la condition des individus à l'étude de leur développement est évaluée à l'aide de variables et des interrelations entre ces variables qui influencent la distribution de la taille des portées d'une population de souris à pattes blanches en liberté. Cette théorie sur la condition des individus arrive à expliquer pourquoi les portées de grande taille ne sont pas aussi fréquentes dans la population que ne l'aurait suggéré le nombre de recrues. Malgré tout, l'âge, la taille et la condition corporelle des femelles interagissent avec la saison de reproduction selon des modalités qui défient cette approche basée simplement sur la condition des individus pour rendre compte du développement chez cette espèce. L'influence de l'âge de la mère ainsi que celle de la saison de reproduction sont masquées par celle de l'incapacité des jeunes femelles de se reproduire au printemps. Le biais dans l'obtention à l'automne de petites portées par des femelles de grande taille semble constituer un effet de la sénescence chez ces femelles âgées et en piètre condition par comparaison aux jeunes femelles de petite taille. La sénescence entraîne des coûts reproductifs, cumulatifs à long terme, dans cette population et peut-être d'autres populations de petits mammifères.
Mots-clés: taille corporelle, évolution, développement, taille des portées, *Peromyscus*, sénescence.

Introduction

Models of state-dependent life history (the optimal life history depends upon an individual's state, McNamara & Houston, 1992) offer hope of a general theory that can be fine-tuned to the biology of a diverse array of organisms. This is possible because many components of life history such as brood and offspring size, offspring survival, and the timing of reproduction are likely to depend upon the parent's state (e.g. age, size, energy reserves, habitat). Studies on white-footed mice (*Peromyscus leucopus*) provide an example of the value of a state-dependent approach. The distribution of litter sizes and the optimum number of offspring depends upon maternal body size (Morris, 1996). Females that produce litters larger than their body-size optimum leave few descendants from those large litters. Small females have a lower optimum litter size than large ones.

The utility of a general theory is compromised by difficulties in selecting appropriate state variables and by complex interactions that occur among them (Morris, 1996). State-dependent theory assumes that

$$LH_i = f(S) \quad [1]$$

where LH_i represents the i th life history trait and S is an appropriate state variable. To avoid circularity, one must

obtain an estimate of S , call it S_1 , to study the functional relationship between state and life history. The problem is that any one state variable depends upon others and their potential interactions, e.g.

$$S_1 = F(g[S_2] + h[S_3] + \dots + k[S_i] + l[S_2S_3] + \dots + m[S_2 \dots S_i]) \quad [2]$$

This paper attempts to assess the implications of equation [2] to our study of life history. First, I review an empirical example of the role of complex interactions in state-dependent litter size of white-footed mice. Second, I test alternative state-dependent hypotheses that can account for the interactions. Third, I solve equations [2] and [1] and evaluate their implications to life-history evolution.

Complex interactions and litter sizes of white-footed mice

The most productive litter size produced by female white-footed mice in forest and fencerow habitats in south-western Ontario, Canada, is five offspring (Morris, 1986; 1992a). Yet litters of size five are less frequent than expected on the basis of the number of recruits that they produce (Morris, 1992a; 1996), primarily because litters of size six and greater have extremely low recruitment success. Litter size is heritable, but variable, and females with an expected litter of the most productive size (five) will also produce a disproportionate number of even larger

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litters with very low recruitment (Mountford's hypothesis, Mountford, 1968). Females that produce a smaller mean litter size will have fewer offspring recruited from their small litters than from litters with five offspring, but will also produce few of the very large and even less productive litters. Variation in litter size creates an optimum litter that is smaller than the size that produces the greatest number of recruits because small litters yield more recruits than very large ones (Morris, 1996).

The low survival of offspring in large litters relative to smaller ones demanded by Mountford's hypothesis can be explained by a state-dependent approach to optimal life history. The theory, like Mountford's original model, assumes natural variation about the optimum litter size. Females that produce litters greater than the optimum will have low recruitment success. But females in a "low-quality" state will have lower success from litters of that size than will females in a "high-quality" state (Morris, 1996; see also Smith & Fretwell, 1974; Pettifor, Perrins & McCleery, 1988; Lalonde, 1991; Aparicio, 1993). Both high- and low-quality females producing litters less than their respective optima should have exceptionally high recruitment. The resulting survival distribution will be biased toward high survival in small litters, and low survival from large ones.

In white-footed mice, and many other mammals, litter size is related to a female's body size (Eisenberg, 1981; Myers & Master, 1983; Stearns, 1983; Boyce, 1988; Harvey & Read, 1988; Morris, 1992a, b), and body size can thus be used as a surrogate variable reflecting a female's state. Consistent with state-dependent life history, small white-footed mouse females (low quality) that produced large litters had significantly lower recruitment from those litters than did larger females (high quality) that produced litters of the same size (Morris, 1996). But large females that produced small litters also had low recruitment. This unusual result is caused by a complex interaction between female body size, the litter size that a given female produces, the time of year that a female reproduces and subsequent recruitment (Morris, 1996). Disproportionate numbers of litters near the body-size optimum of five offspring are produced in spring when overall recruitment from all litters is high (Morris, 1992a, b). In autumn, when recruitment from any litter size is low, many large females produce small litters (Morris, 1996). Thirteen percent of all litters produced by large females belong to the 1-3 litter-size class in spring compared with 26% in autumn. There also appear to be more large litters produced in autumn but the difference is not as great (28% in spring, 36% in autumn). There is no similar interaction for small females (Figure 1).

One should be able also to develop a state-dependent explanation for the peculiar interaction between female body size, time of reproduction, litter size, and subsequent recruitment in white-footed mice. The explanation must demonstrate why large females have seasonal differences in the distribution of litter sizes while small females do not. Two state-dependent hypotheses have been proposed (Morris, 1996): 1) Large females that produce small litters in the autumn represent senescent animals that are no longer capable of producing large litters; 2) Large females producing small autumn litters represent rapidly growing high quality

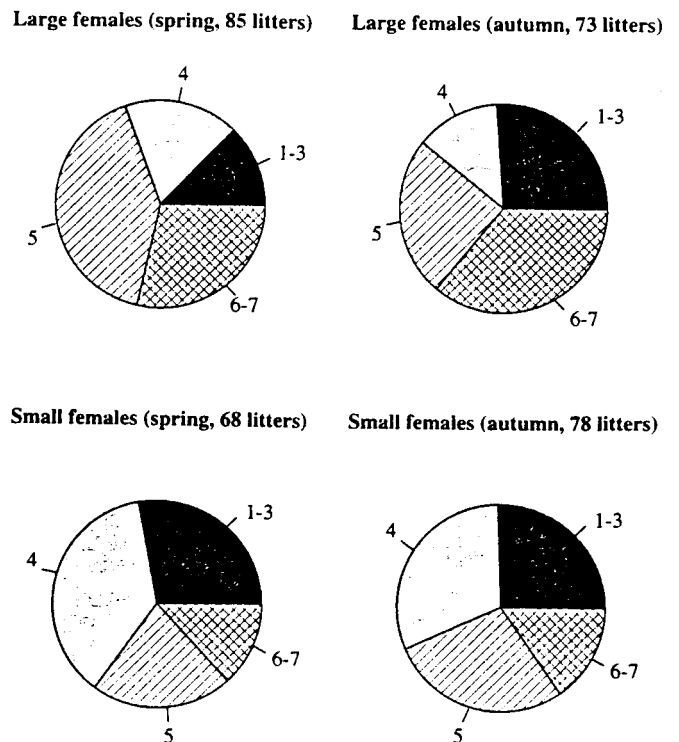


FIGURE 1. The distribution of litter-size classes produced by large-bodied female white-footed mice varies significantly between spring and autumn reproductive seasons. There is no significant difference in the seasonal production of litter-size classes produced by small-bodied females (data from Morris, 1996).

spring-born females whose "inexperience" limits litter size (litter size in *Peromyscus* is known to vary with parity [Drickamer & Vestal, 1973; Fleming & Rausher, 1978; Myers & Master, 1983]). A third alternative is that the relationship between litter size and body size is curvilinear with small females producing a smaller range of litter sizes than large ones.

I test the curvilinear hypothesis by plotting the relationship between litter size and body size. I differentiate between the senescence and parity hypotheses by contrasting the distribution of litter sizes produced in autumn by large females that have survived at least one winter with those in their first reproductive season. I test the senescence hypothesis directly by evaluating the relationships between a female's weight and her body mass (body condition = "quality"). Senescent females are predicted to be in poorer condition than young ones, and should have a different mass-body length relationship than do younger animals.

Materials and 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 fencerow habitats in southwestern 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 three days of age and older were removed from the boxes, measured (body length, mass), sexed, and assessed for reproductive condition (males, testes descended or scrotal; females, lactating or pregnant, vagina perforate or imperforate). All animals older than seven days were given a unique ear tag for identification. 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. Further details of the field protocols can be found in Morris (1986; 1989; 1991; 1992a).

Tests of the three hypotheses require precise estimates of maternal body size. Field estimates 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. I constructed two maternal body-length classes, one less than, and one equal to or greater than the population median (93 mm, see Morris 1992a for additional details), tested for observer heterogeneity and deleted any heterogeneous subsets (Morris, 1995). The final set of unbiased data was used in all subsequent analyses. Similarly, I created two maternal age classes corresponding to reproductive females known to be born during the same year that they reproduced, *versus* those known to have survived over winter. Many of the females reproducing in autumn are of uncertain age (they were adult when first captured). Young-of-the-year and overwintered females only are used in analyses requiring estimates of maternal age.

I tested the hypothesis of a curvilinear relationship between litter size and maternal body length by regressing mean litter size, produced by females in a given body-length class, against mean maternal body length of that class for all adjacent body-length classes. I partitioned litters into four size classes (≤ 3 , 4, 5, ≥ 6) and contrasted the autumn litter-size distributions of spring-born *versus* overwintered females to differentiate between the parity and senescence hypotheses (log-linear analysis, Norušis, 1992).

I searched for evidence of senescence by examining female body mass for different classes of females among spring and autumn reproductive seasons and among fencerow, edge and forest habitats (season and habitat treated as fixed effects) with body length as a covariate (analysis of variance, procedure GLM, MINITAB, release 8). I included habitat because it has a strong influence on recruitment (Morris, 1986; 1989). Female body mass varies with time since parturition (estimated by the age of nursing offspring), which I added as a second covariate.

I solved equation [2] with a similar analysis on all females. I grouped females into sequential classes, substituted the mean predicted values into equation [1] and solved it by linear regression predicting mean litter size. This smoothing technique was designed to reduce individual error about the regression while maintaining a general state-dependent explanation for litter size.

Results

THE RELATIONSHIP BETWEEN LITTER SIZE AND BODY SIZE

There was no evidence of a curvilinear relationship between mean litter size and mean female body length in this population of white-footed mice (Figure 2). The curvilinear hypothesis is rejected.

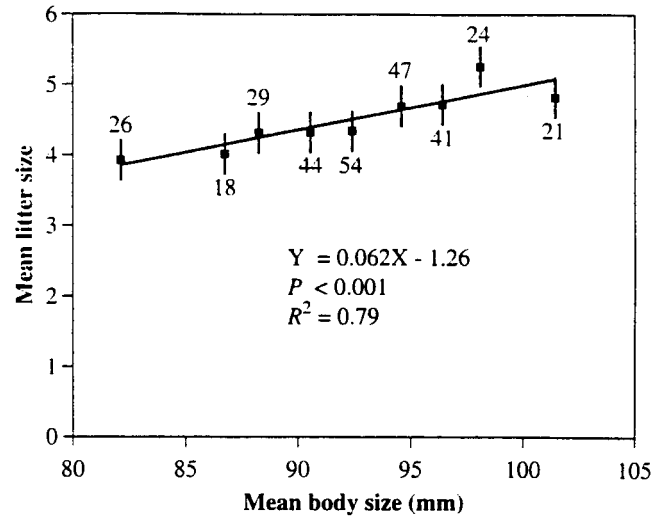


FIGURE 2. Mean litter size of white-footed mice depends upon mean maternal body length (vertical lines correspond to standard errors, numbers refer to sample sizes of females in adjacent body-size classes, from Morris, 1996).

COMPARISON OF LITTER-SIZE DISTRIBUTIONS PRODUCED BY YOUNG *VERSUS* OLD FEMALES

Large young-of-the-year females produced an autumn litter-size distribution that was not different from that of large females known to have survived over winter (likelihood ratio $\chi^2 = 1.16$, $df = 3$, $P = 0.76$, Table I; analysis based on two litter-size classes yields a similar outcome, but both analyses are based on relatively small samples). Using this test alone, neither the parity nor senescence hypothesis can be rejected as explanations for biased autumn production of small litters by large females.

TABLE I. The distributions of autumn litter sizes produced by large bodied young-of-the-year and overwintered female white-footed mice

Age of female	Litter-size class			
	≤ 3	4	5	≥ 6
Young-of-the-year	2	2	5	3
Overwintered	4	5	6	9

BODY CONDITION: THE RELATIONSHIP BETWEEN BODY MASS AND BODY LENGTH

There was a highly significant difference in the relationship between body mass and body length for overwintered females reproducing in spring (175 females) *versus* those that reproduced in autumn (33 females) (season \times body length interaction, $F = 9.77$, $P = 0.002$, Table II). Female mass, after adjustment for covariates and other terms varied between seasons (reproductive season main effect, $F = 11.5$, $P = 0.0001$). The seasonal adjusted effect was caused by

TABLE II. Analysis of variance assessing the state-dependence of female mass between overwintered females producing litters in spring and autumn reproductive seasons (sums of squares adjusted for all other terms)

Source	DF	SS	F	P
Body length	1	23.37	1.84	0.18
Days since parturition	1	17.76	1.40	0.24
Reproductive season	1	145.82	11.50	0.0001
Habitat	2	0.79	0.03	0.97
Season × habitat	2	5.73	0.23	0.80
Season × body length	1	123.95	9.77	0.002
Habitat × body length	2	0.65	0.03	0.98
Season × habitat × body length	2	5.59	0.22	0.80
Season × parturition	1	48.65	3.84	0.05
Habitat × parturition	2	20.60	0.81	0.44
Season × habitat × parturition	2	8.74	0.34	0.71
Error	190	2409.82		

differences in mean overwintered female body length between spring and autumn reproductive seasons (93.33 mm and 95.48 mm, respectively, oneway ANOVA, $F_{1,206} = 6.54$, $P = 0.01$) and more or less constant mean body mass (31.15 g in spring and 31.27 g in autumn, oneway ANOVA, $F_{1,206} = 0.02$, $P = 0.88$). Overwintered females had lower mass per unit body length in the autumn than in the spring. The seasonal differences in the relationship between mass and body length also contributed to seasonally-dependent differences in mass related to time since parturition (season × parturition interaction, $F = 3.94$, $P = 0.05$, Table II).

I attempted to evaluate whether the seasonal differences represented senescent or simply seasonal effects by repeating the analysis on overwintered *versus* young-of-the-year females that reproduced in autumn (33 and 29 females respectively, seasonal comparisons are not possible, young-of-the-year females do not reproduce in spring). I excluded habitat as a grouping variable because it had no significant effect in the first analysis. When adjusted by other terms, overwintered females appeared to be slightly heavier than young-of-the-year females (age main effect, $F = 4.41$, $P = 0.04$, Table III), but tended to display a different relationship of mass with body length than did young females (age × body-length interaction, $F = 3.92$, $P = 0.05$, Table III). These results reflect slight differences in body mass (mean mass = 31.27 g and 29.66 g for overwintered and young-of-the-year females, respectively, oneway ANOVA, $F_{1,60} = 2.36$, $P = 0.13$) but major differences in body length between the two age-classes of females (overwintered = 95.48 mm, young-of-the-year = 91.76 mm, oneway ANOVA, $F_{1,60} = 7.43$, $P = 0.008$).

I repeated the analysis contrasting young-of-the-year

TABLE III. Analysis of variance assessing the state-dependence of female mass between overwintered and young-of-the-year females producing litters in autumn (sums of squares adjusted for all other terms)

Source	DF	SS	F	P
Body length	1	1.81	0.11	0.74
Days since parturition	1	0.30	0.02	0.89
Age	1	73.99	4.41	0.04
Age × body length	1	65.77	3.92	0.05
Age × parturition	1	7.00	0.42	0.52
Error	56	939.76		

females reproducing in autumn (29 animals) with overwintered females reproducing in spring (175 animals). Both covariates, but neither of the interactions, were significant (Table IV). Young-of-the-year females reproducing in autumn, and overwintered females reproducing in spring, were not different in terms of body condition.

TABLE IV. Analysis of variance assessing state-dependence of female mass between overwintered females reproducing in the spring and young-of-the-year females producing litters in autumn (sums of squares adjusted for all other terms)

Source	DF	SS	F	P
Body length	1	344.18	27.22	< 0.001
Days since parturition	1	58.26	4.61	0.03
Maternal class	1	28.10	2.22	0.14
Class × body length	1	25.89	2.05	0.15
Class × parturition	1	24.70	1.95	0.16
Error	198	2503.67		

SIZE CLASS AND AGE OF REPRODUCTIVE FEMALES

The results from the analyses of variance suggest that overwintered females are in poorer condition (mass per unit body length) in the autumn than in spring. The results also demonstrate that overwintered females are in poorer condition in autumn than are young females. Young females have a mean body length less than the median of 93 mm, overwintered females have a mean body length greater than the median. This suggests that the biased production of small litters by large females in the autumn is produced primarily by animals in poorer condition than large females that reproduce in spring. Small females do not exhibit a seasonal bias in litter-size distributions because they are of similar condition to overwintered females in spring. I confirmed this interpretation by contrasting the body-size classification of overwintered *versus* young-of-the-year females. Most overwintered females were included in the "large body-length" class, and most young-of-the-year females were in the "small body-length" class (log-likelihood $\chi^2 = 6.32$, $DF = 1$, $P = 0.01$, Table V). The biased production of small litters by large females in the autumn was confounded by female age. Many old females produced smaller litters for their body size than did young ones (senescence).

TABLE V. Most overwintered females that reproduced in autumn belonged to the "large body-length" class. Most young-of-the-year females reproducing in autumn belonged to the "small body-length" class

Age of mother	Body-length class	
	Small (< 93 mm)	Large (≥ 93 mm)
Young-of-the-year	17	12
Overwintered	9	24

A STATE-DEPENDENT SOLUTION

I repeated the first state-dependent ANOVA (minus habitat, it was not a significant predictor of maternal mass), for all 359 females for which I had sufficient and unbiased data. The analysis was highly significant (Table VI). I created nine body-mass categories based on the predicted body-masses from the analysis, calculated the mean predicted

TABLE VI. Analysis of variance assessing state-dependence of female mass between spring and autumn reproductive seasons (sums of squares adjusted for all other terms). Female mass can be predicted by the linear multiple regression equation: $Mass = 14.13(\text{season}) + .57(\text{body length}) + .33(\text{days since parturition}) - .15(\text{season} \times \text{body length}) - .14(\text{season} \times \text{parturition}) - 24.68$

Source	DF	SS	F	P
Body length	1	1077.97	77.89	< 0.001
Days since parturition	1	241.58	17.46	< 0.001
Reproductive season	1	50.69	3.66	0.06
Season \times body length	1	48.70	3.52	0.06
Season \times parturition	1	67.25	4.86	0.03
Error	353	4885.29		

mass and mean litter size of females in each category and regressed mean litter size against mean predicted mass to solve equation [1]. The analysis was significant (Figure 3). Litter size depends upon a female's state.

I attempted to explain biased litter sizes produced by overwintered females by repeating the regression on the raw data ($F_{1,357} = 7.24, P = 0.007$). I then regressed the standardized residuals from that model against the standardized residuals from the linear model. This latter regression would be significant if females that are heavier than their predicted mass tended also to produce larger litters than expected (the converse is true for females lighter than predicted). The analysis using all females was significant ($F_{1,357} = 6.72, P = 0.01$). The analysis on the 24 large overwintered females reproducing in autumn was not ($F_{1,22} = 0.07, P = 0.8$).

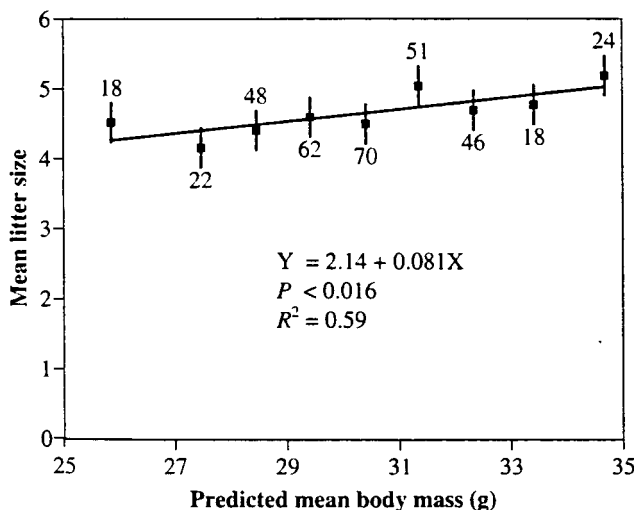


FIGURE 3. Mean litter size of white-footed mice depends upon mean body mass predicted from the state-dependent linear equation including reproductive season, female body length plus its interaction with reproductive season, and days since parturition plus its interaction with reproductive season (359 females, vertical lines correspond to standard errors, numbers refer to sample sizes of females in adjacent body-mass classes).

Discussion

Female age is an important state-variable that influences the size of litter that a white-footed mouse produces. In at least this population of white-footed mice, a female's body size is inextricably linked to her age, and to the season in which she reproduces. Many old and large females that

reproduce in the autumn produce a litter-size distribution biased toward smaller sizes than they produce in the spring. This pattern occurs despite old females being larger in the autumn than they are in spring (the weights are similar). Young and small females produce similar distributions of litter size in spring and autumn, even though the relationship between mass and body length is similar to that of large females. Thus, it appears that many old females reproducing in the autumn are incapable of producing the same litter-size distribution for their mass and size as one expects on the basis of their ability in spring, or of the ability of young and smaller females in autumn (senescence). Other large females produce very large litters in autumn that cannot, as yet, be explained by state-dependent theory. Young, large females that reproduce in autumn apparently also produce a litter-size distribution biased toward small litters caused, perhaps, by parity's influence on litter size. Complete data on the reproductive histories of individual females would be especially valuable in assessing autumn reproduction.

Age-dependent differences in mass-length regressions, and the link to the litter-size distribution produced by white-footed mice, are consistent with both antagonistic pleiotropy and disposable soma theories of senescence (Williams, 1957; Kirkwood, 1977; Charlesworth, 1980; Kirkwood & Rose, 1991; Promislow, 1991). Genes that are deleterious late in life may accumulate if they are advantageous early in life (antagonistic pleiotropy, *i.e.* if they increase early survival or reproduction). Senescence will also occur when resources are diverted away from somatic maintenance and toward reproduction (disposable soma).

Previous attempts searching for tradeoffs between both survival and future fecundity with current litter-size failed to detect reproductive costs in white-footed mice (Morris, 1992a). Senescence in this population of white-footed mice suggests that reproductive costs are cumulative rather than related strictly to any given reproductive episode. This interpretation is consistent with the suggestion that the expected litter size produced by white-footed mice is their state-dependent optimum (Morris, 1985; 1986; 1987; 1992a; 1996). Females of a closely related species (*Peromyscus maniculatus* [deer mouse]) are also suspected of reproductive senescence (Millar, 1994). Female deer mice that survive until a second breeding season tend to have poorer breeding success in their first year than females that do not survive until a subsequent reproductive period.

The intent of any state-dependent explanation of life history must be made clear prior to analysis. In the case of white-footed mice, mean litter size is highly predictable if one has data on a female's mass and how that varies with season, body length, and parity. But if the purpose is simply to predict mean litter size, one can do very well by using a female's body length alone (Figure 2). If the intent is, as here, to understand the life history, both prediction equations give but a superficial hint of underlying complexity. Age, size, body condition and reproductive season are all important state-variables influencing the distribution of litter sizes produced in this population of white-footed mice. Interactions among age, condition and season demonstrate a role for senescence. The interaction between

maternal age and reproductive season is difficult to test because the separate and joint contributions of the two variables are confounded. Young-of-the-year females do not typically mature and reproduce in spring (some reproduction by young females may occur following unusually mild winters). Additional analyses of state-dependent life history will be necessary before we know how general this sort of problem may be.

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