

PROXIMATE AND ULTIMATE CONTROLS ON LIFE-HISTORY VARIATION: THE EVOLUTION OF LITTER SIZE IN WHITE-FOOTED MICE (*PEROMYSCUS LEUCOPUS*)

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Abstract.—Recruitment of litter-mates of nest-box-inhabiting white-footed mice was monitored to study the evolution of litter size. The frequency distribution of litter sizes was non-symmetrical, and the most frequent litter size was less than the optimum. This was not the result of differential parental survival, which was independent of litter size produced. Recruitment remained constant or increased slightly to a peak in litters of five young, and then dropped precipitously for larger litters. The single optimum litter size of five did not appear to have any physiological correlates. Instead, the equally low probability of successful recruitment of any young from any given litter may have given rise to a bet-hedging strategy of frequent iterated reproductions. A theoretical analysis of optimal parental investment in offspring was initiated under the assumption that optimal brood size represents a maximization of differences between age-specific costs and benefits of reproduction, both of which should be measured in constant currency of inclusive fitness. In the past, benefit has been measured by current fecundity, and cost by residual reproductive value. However, reproductive value is an appropriate estimate of inclusive fitness only for organisms in which parental investment has little effect on the subsequent survival of offspring to reproductive age. Reproductive value weighted by offspring survival and devalued by the degree of genetic relatedness defines a new currency, replacement value, which is more appropriate for evaluating the costs and benefits of parent-offspring conflict over parental investment in current as opposed to future young. Total parent-offspring conflict intensifies with increases in current brood size. For species with severe reproductive constraints, such as post-partum estrus in white-footed mice, such conflict may force parents to curtail investment in current offspring at or near parturition of subsequent litters, even if that means reducing the survival of current young.

Received January 7, 1985. Accepted September 23, 1985

Parents should, on average, produce broods of that size which maximizes the recruitment of offspring to the breeding population (Lack, 1947, 1948). This will generally be less than the maximum brood size because of a variety of physiological and behavioral constraints on reproduction, and because of opposing selective pressures favoring increased or decreased numbers of young (e.g., Cody, 1966; Mountford, 1968; Ricklefs, 1970, 1977; Smith and Fretwell, 1974; Brockelman, 1975; Morris, 1985). The optimal brood size will strike a balance of trade-offs between the benefit of maximizing the production of young, and associated costs in terms of reduced juvenile and adult survival (Charnov and Krebs, 1974; Stearns, 1976) (Fig. 1).

The most productive clutch for a given level of parental survival is that which

maximizes the recruitment of young into the breeding population. In general,

$$R_b = bJ_b \quad (1)$$

where R_b is the number of recruits for broods of size b , b is brood size and J_b is juvenile survival of broods of size b . With a monotonic decrease in juvenile survival with brood size, as illustrated in Figure 1, brood b is the most productive brood if and only if

$$R_{b-1} < R_b > R_{b+1}. \quad (2)$$

Note that b is more productive than $b + 1$ if and only if

$$bJ_b > (b + 1)(J_{b+1})$$

and

$$J_{b+1} < J_b \frac{b}{b + 1}. \quad (3)$$

Similarly, litters of size b are more productive than those of size $b - 1$ if and only if

$$J_{b-1} < J_b \frac{b}{b-1}. \quad (4)$$

Then, the most productive brood size is that in which one additional young reduces juvenile survival by a factor greater than the ratio of the brood sizes, and one fewer offspring increases juvenile survival less than the ratio of the increase in brood size from $b - 1$ to b .

This powerful prediction raises several questions. How close is the modal brood size in natural populations to the theoretical optimum? What proximate and ultimate mechanisms are responsible for variation around the predicted optimum? What is the empirical relationship of juvenile survival with increasing brood size?

It should be noted that the optimum is attained by a reduction in average offspring survival with increased brood size. The theory does not differentiate between the alternatives of reduced survival probabilities of individual offspring with increasing brood size as opposed to variation in the success of different brood-size classes in recruiting any offspring into the breeding population. In both cases, average offspring survival declines as brood size increases, but these alternatives represent key differences in overall life history. For example, if large broods result in low reproductive success as a result of predation on entire broods, then selection may be operating primarily on the ability of parents to secure safe nest sites. If, on the other hand, individual survival probabilities decrease with increasing brood size, selection is likely to be operating on the differential abilities of parents to care for and nourish young.

Studies on birds have tended to confirm the idea that there is an optimum brood size caused by the trade-offs between early juvenile survival and increased numbers of young (e.g., Lack, 1954; Lack et al., 1957; Perrins, 1964,

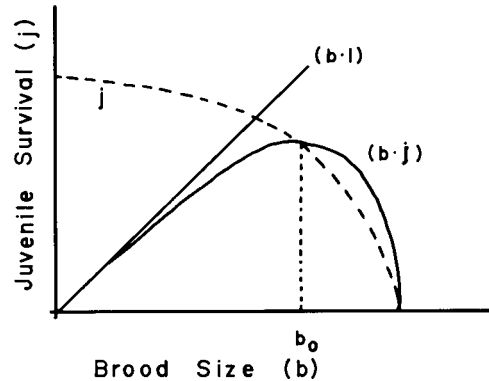


FIG. 1. When juvenile survival decreases as brood size increases (dashed line), the optimum number of young (b_0) is less than the maximum. The straight line reference is the production of young with zero juvenile mortality ($j = 1$). If parental survival also decreases as brood size increases, the optimum is reduced even further (after Charnov and Krebs, 1974).

1977). These results need confirmation from comparative studies on other organisms. Tests should include more detailed estimates of possible trade-offs between brood size and recruitment of reproductive individuals into the breeding population.

This paper examines the relationship between litter size and the recruitment of marked young into a free-ranging population of the white-footed mouse, *Peromyscus leucopus*. Most previous studies of litter-size variation in mammals have concentrated instead on environmental, size and phylogenetic effects (Lord, 1960; Dunmire, 1960; Millar, 1977, 1981). Exceptions include Millar (1973), who noted a reduction in litter size at weaning in free-living pikas relative to that at ovulation and birth in autopsied animals. Fleming and Rauscher (1978) experimentally examined several possible factors which may lead to trade-offs in litter size in *P. leucopus*. Litter size was related to parity, but neonatal size and early growth rates were not related to the number of nursing young. Fleming and Rauscher (1978) suggested that litter-size variation in *Peromyscus* may reflect variation in age-structure among populations.

My objective is to determine whether there is an optimum litter size in a wild population of *P. leucopus* as a result of reduced recruitment with increased numbers of young. Second, if there is an optimum litter size, what is the shape of the trade-off function between increased young and reduced survival? Third, if there is an optimum, does it coincide with the most frequent litter size? Fourth, is there an additional cost of reproduction in terms of reduced parental survival with increased litter size? Fifth, what are the relative influences of proximate and ultimate mechanisms on these patterns?

MATERIALS AND METHODS

Small wooden nest boxes (internal dimensions 14 × 15 × 22 cm with one 2.5 cm entrance hole) were placed at approximately 30 m intervals along overgrown fencerows and in second growth deciduous forest in Essex County, Ontario (42°10'N, 83°30'W). In 1981, each of the 79 boxes was examined once monthly from April to December. In 1983, each box was checked once during April, May, September, and October. The data for 1982 were excluded due to very low *P. leucopus* population density in that year. During each check, all mice over one week old were removed from the boxes, aged, sexed, measured (body length and tail length), and individually marked with metal ear tags. The age of immature and juvenile mice was estimated based on literature reports of developmental stages (Layne, 1968), and all adult females were weighed. Soiled nests were replaced with fresh mattress stuffing, the mice placed back in the box, and the box returned to its original position. Except during my examinations, mice were free to come and go at will. All nest box checks were made between 9:00 A.M. and 7:00 P.M.

For all analyses that follow, valid litters are only those cases in which a) similar aged immature (eyes closed) or not fully coordinated juvenile mice were observed nursing an adult female, or were

in the same box with only one lactating female, or b) immature mice at the same stage of development were found alone in a nest box. If more than one litter was found in the same box, they were included in the data set c) only if I could be certain of sib relationships by developmental differences. Fully coordinated juvenile mice were not included even if in the presence of a lactating female because they may have been near the age of weaning. For the analyses of data on mother-litter size comparisons, I included only those mothers satisfying criterion (a) above. Recruitment of young was based on the capture in any nest box of adult mice originally marked as littermates satisfying criterion (a), (b), or (c). This is a minimum estimate, because it excludes animals which may not have returned to the nest boxes but which nevertheless may have successfully reproduced elsewhere. My purpose is not to estimate recruitment for the entire population; rather, it is to evaluate how recruitment varies among litters treated in exactly the same way. Many analyses are restricted to the spring 1981 litters because the monthly nest box checks during the summer of 1981 resulted in more data on successful recruitment and parental survival than did the two fall checks in 1983.

RESULTS

The 137 litters recorded during this study described a unimodal but negatively skewed frequency distribution of litter size in *Peromyscus* (Fig. 2). The data for 1981 and 1983 gave a similar distribution of litter sizes, and there was no significant difference in the distribution between the two years (Kolmogorov-Smirnov test, $z = 1.19$, $P = 0.12$). Nest-box litters consistently described a negatively skewed distribution of litter sizes with a mode of four.

Did parity effects influence the observed distribution of litter-size classes?—I answered this question with the fall 1981 data by selecting out the 21 litters for which I had reasonable estimates of dif-

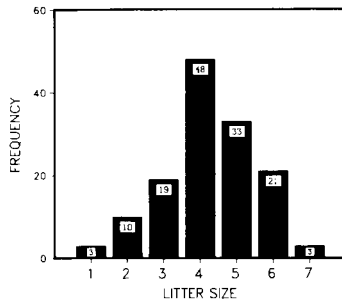
DISTRIBUTION OF *Peromyscus* LITTER SIZES IN ONTARIO

FIG. 2. The empirical distribution of litter sizes of *Peromyscus leucopus* living in nest boxes in Essex County, southern Ontario.

ferences in parity among the mothers. I grouped the fall mothers into two classes, those that I knew had overwintered in 1980–1981 (7 animals), and those that I knew were born in the spring or summer of 1981 (14 animals). The overwintered females would have had the opportunity to produce at least one more litter (spring 1981) than those females born in 1981. There was no significant difference in average litter size between the two parity classes (Kruskal-Wallis nonparametric analysis of variance; $\chi^2 = 0.349$; $P = 0.55$).

Did the success of a litter in recruiting at least one offspring to the adult nest-box population vary as a function of litter size?—I analyzed differences in the proportion of successful litters (spring 1981 data) relative to that expected if all litters had an equal probability of recruiting at least one offspring. There was no significant difference in the success of various litter-size classes in contributing one or more recruits (single classification goodness-of-fit test; Sokal and Rohlf, 1981 pp. 704–716; G with Williams' correction for small samples = 2.981; $0.1 < P < 0.5$; Table 1).

Perhaps large litters recruit, on average, more young to the population than smaller litters?—I analyzed the spring 1981 data for this effect by nonparametric correlation of litter size and total re-

TABLE 1. Observed and expected numbers of successful litters in four litter-size classes (spring 1981 litters). Expected values were generated by correcting the proportion of successful litters out of the entire sample by the frequency of a particular litter-size class. Note that only one-half of all litters observed were successful at recruiting one or more adults to the nest-box population.

Litter-size class	Frequency of litters	Observed successful litters	Expected successful litters
1–3	9	6	4.5
4	14	7	7
5	8	5	4
6	7	1	3.5
Total	38	19	19.0

$G(\text{Williams}) = 2.981$; $0.1 < P < 0.5$

ruits, $\tau = 0.67$, $N = 19$, $P = 0.001$. The number of recruits increased with litter size.

Did individual survival rates vary as a function of litter size?—I answered this question by a single classification goodness-of-fit test on the observed versus expected number of recruits relative to the total production of young in a particular litter-size class (Table 2). The analysis was significant (G with Williams' correction = 9.03, $0.01 < P < 0.025$) and showed that litters of size six contributed far fewer recruits than expected. The probability of any given offspring being recruited increased from 0.3 in litters sized one to three, to 0.375 for litters of size five, and then dropped sharply to only 0.095 for litters of six young (Table 2).

Why should litters of size six contribute fewer recruits than all other size classes?—One possibility is that young in these large litters grow at a slower rate than those in small litters and, as a result, are weaned at a smaller size, with concomitantly lower survival probabilities. A second possibility is that they grow at about the same rate but are in poorer physical condition. A good estimate of physical condition would be body weight corrected by body size (length). I tested both of these possibilities on randomly sampled individ-

TABLE 2. Observed and expected numbers of recruits in four litter-size classes (spring 1981 litters). Expected values were generated by correcting the proportion of recruits out of all young produced by the total production of young in a particular litter-size class.

Litter-size class	Frequency of litters	Production of young	Observed recruits	Expected recruits	Proportion recruited
1-3	9	20	6	5.70	0.30
4	14	56	20	15.95	0.36
5	8	40	15	11.39	0.375
6	7	42	4	11.96	0.095
Total	38	158	45	45.00	

$G_{\text{(Williams)}} = 9.03; 0.01 < P < 0.025$

uals from 52 litters for which I had body length, body weight, and age estimates of litter-mates. Analysis of covariance evaluated differences in body length among litter-size classes while controlling for age and weight effects. I included only those litters aged between three and 18 days because I did not measure mice less than three days old, and after about 18 days post-partum, aging on the basis of developmental characteristics becomes progressively less precise. I am assuming in this analysis that litter size should have more of an effect on growth rate than on the diagnostic developmental criteria used for aging. Once age was taken into account, neither body weight nor litter size added significantly to the observed variation in body length (Table 3). There seemed to be no simple physiological growth-rate-related explanation as to why litters of size six contributed fewer recruits than litters of all other size classes.

TABLE 3. Analysis of covariance evaluating differences in body length among litter sizes after correcting for age and weight effects (52 litters). Body length and weight were log-transformed prior to analysis.

Source of variation	F	P
Covariate age	53.46	<0.001
Covariate weight	0.37	0.54
Litter size	0.40	0.85
Explained	12.93	<0.001

TABLE 4. Observed and expected numbers of surviving mothers as a function of litter size produced (spring 1981 litters). Expected values were generated by correcting the proportion of known survivors out of all mothers by the frequency of different litter-size classes. Total litters are different from those in Tables 1 and 2 because very young litters in which litter-mates were unmarked could not be used for recruitment estimates but can be used to evaluate parental survival.

Litter-size class	Frequency of litters	Known survivors	Expected survivors
<4	12	9	8.09
4	15	11	10.12
5	8	4	5.39
>5	8	5	5.39
Total	43	29	28.99

$G_{\text{(Williams)}} = 0.589; 0.5 < P < 0.9$

Did parental survival decrease with increasing litter size?—Using mothers which gave birth in the spring of 1981, I calculated minimum survival as the proportion of these females which were recaptured in nest boxes at least one month after parturition. There was no effect of litter size on known survival of mothers (single classification goodness-of-fit test; G with Williams' correction = 0.589; $0.5 < P < 0.9$; Table 4).

DISCUSSION

The most productive litter size in this population of *P. leucopus* was five young, contributing on average about 1.9 young per litter produced (Fig. 3). This was larger than the most frequent litter size (four) and less than the largest litters observed, which on average contributed fewer recruits than any other litter-size class. The empirical production curve was unimodal and juvenile survival of the most productive litter satisfied the predictions of inequalities (3) and (4). There were no obvious physiological reasons for the poor recruitment of young from large litters. Yet it is reasonable to assume that reduced growth-rates in large litters would occur only when the combined energetic demands of the litter exceed some thresh-

old. This demand would be greatest near weaning and might not be detectable until littermates are beyond my cut-off age of 18 days.

The unimodal production curve in *P. leucopus* is reinforced because the probability of offspring survival increased slightly among intermediate litter sizes. This increase was not great, but that it occurred at all, or that juvenile survival did not decrease monotonically over all litter-size classes, argued that it was most unlikely for different sized litters to be equally productive. Though life-history models predict the stable coexistence of multiple optima (Schaffer, 1974; Schaffer and Rosenzweig, 1977), these may seldom be realized.

One possible explanation for an initial increase in offspring survival with litter size in *P. leucopus* is that mothers of smaller litters were less experienced than those of larger litters. Fleming and Rauscher (1978) provided some data which showed this trend for 28-day survival in a laboratory colony of *P. leucopus*, but only for females which had produced three or more litters. This prediction was not borne out by my weak test of parity effects on litter size. My test did not include the actual ages of the overwintered females, some of which may have been past the peak reproductive age when litter size begins to decrease with age (Drickamer and Vestel, 1973). In laboratory colonies of *P. leucopus* the peak litter size generally occurs in females between litters 5 and 8 (Drickamer and Vestel, 1973). To observe depressed parity effects in my population of *P. leucopus* which typically produce one or two litters in the spring (April–June) and another one or two in the autumn (September–November), the overwintered females would have had to be two years old or older, which is well beyond the usual age at death of free-living *Peromyscus* (Terman, 1968; the oldest mouse of known age in my study was a 12-month-old May-born female). It is unlikely that parity effects alone have caused increased recruitment in intermediate-sized litters.

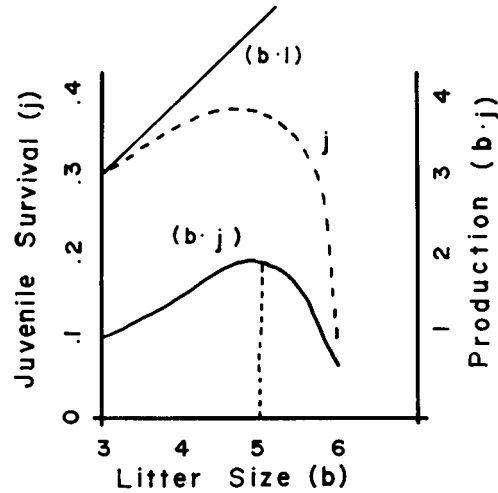


FIG. 3. The empirical production curve for different sized litters of *P. leucopus*. Litter-size class three also includes data for litters sized one and two. The production curve ($b \cdot j$) was generated as the product of litter size times the proportion of all young recruited in litters of that size. Note that the production curve rises more rapidly than the survival curve and that litters of size six are less productive than all others. Compare with Figure 1 to note similarities in the theoretical and empirical curves. All curves are really step functions but are drawn as smooth lines to ease interpretation.

The success of recruiting one or more young to the population was independent of litter size. The proportion of successful litters of a particular size class corresponded to the proportion of those litters produced, and the chance of producing a successful litter was a lottery in which each litter had an equally low (50%) chance of success. This may actually be an overestimate, because I could not detect litters which may have been lost prior to my discovering them. The low success rate may be the ultimate explanation why *P. leucopus* (and probably most small mammals) have evolved a life-history strategy of several iterated reproductions. The low success rate also means that whatever is responsible for the high recruitment rate for smaller litters, and for the low recruitment rate of litters of size six, it acts through variation in the survival of litter-mates, not through variation in the survival of entire litters.

Most discussions of optimal brood size related to decreasing juvenile survival with increased numbers of young (e.g., Williams, 1966; Gadgil and Bossert, 1970; Charnov and Krebs, 1974; Goodman, 1974; Pianka and Parker, 1975) tacitly assume that large broods are more poorly nourished than smaller ones because parents are optimizing reproductive effort, but my field data showed that age, and not litter size, was primarily responsible for differences in body size. Millar (1977, 1978) has also documented constant growth rates independent of litter size in laboratory studies on *P. leucopus*, and in general, small mammals tend to wean young at a constant weight (Millar, 1975, 1977, 1978). This makes good sense if nursing females are carrying a second litter in the uterus. A successful strategy to optimize between the conflicting demands of nursing and developing young would seem to be to nurse the current litter as long as possible without interfering with the success of the subsequent litter, but no longer.

Consider a female white-footed mouse at parturition with a given litter size. In the spring of the year, and with post-partum estrus, mothers are faced with the conflicting demands of nursing young and those undergoing development in the uterus. Post-partum estrus can be viewed as an adaptation to the lottery of litter success. With only one-half of the litters recruiting any young at all, female *P. leucopus* should produce as many litters as possible, and they have a short time in which to do so. To the mother, the decision of how much to invest in the current litter is an optimization between the costs of the current offspring and the benefits of the developing litter. The expected size of the developing litter is the population mode of four. How much should the mother invest in post-partum care in the current litter in order to maximize her long-term reproductive success?

Pianka and Parker (1975) addressed this problem by considering the costs and benefits of current reproduction versus future expected reproductions, or resid-

ual reproductive value. In a stationary population with discrete age classes, reproductive value of a female aged x is given by

$$V_x = b_x + \sum \frac{l_t}{l_x} b_t \quad (5)$$

where b_x is the current fecundity of a female aged x , and (l_t/l_x) is the probability of survival of that female to age t . During the spring of the year when *P. leucopus* generally produce two litters prior to the summer cessation of breeding, reproductive value can be approximated by

$$b_x + \frac{l_t}{l_x} b_t$$

where the expected value of b_t is four. It seems reasonable to assume that a given female has a limited amount of energy and risk to devote to reproduction. It also seems reasonable to assume that above some threshold, additional resources to the current litter will reduce the chances of parental survival to care for that developing in the uterus. Given that the expected litter size in this study was four, then, all other things being equal, we would expect females in which $b_x < 4$ to invest less in post-partum parental care per offspring than those for which $b_x > 4$. Females with small litters would be expected to save their investment for the larger litter in utero, whereas females with large litters would be expected to invest more in the current litter. This would in turn be translated into lower juvenile survival rates for litters less than four, and higher rates for larger litters. Females should devote equal investment to both litters when

$$b_x = \frac{l_t}{l_x} b_t$$

and should invest more in the current litter if and only if

$$b_x > \frac{l_t}{l_x} b_t$$

that is, only when

$$\frac{l_t}{l_x} < \frac{b_x}{b_t}$$

When all females survive to reproduce again, $l_t/l_x = 1$. So females should always invest more in the current litter whenever $b_x > b_t$, that is, whenever $b_x > 4$. Eight of eleven mothers captured in late April and early May 1981 were subsequently recaptured, whereas four of eight similar mothers in May 1983 were recaptured. This gives a combined minimum estimate of survivorship to next reproduction of $l_t/l_x = 12/19 = 0.63$ and implies that the investment in first litters of size three may exceed the investment in second litters of size four ($0.63 < 3/4$). In any case, for first spring litters, this simple argument predicts increasing post-partum investment and juvenile survival with increasing litter size, which is what I observed for litters of size five and smaller.

But the young as well as the female parent have a vested interest in the degree of parental investment, and this inevitably leads to conflict over the parent's investment in current or future reproductions (Trivers, 1974). The overall intensity of the conflict should increase with increasing litter size. The conflict is intensified further still in polygamous species because the coefficient of relatedness of current to future young is relatively small (Trivers, 1974).

We can show these relationships more clearly by considering the advantage to individual offspring of parental reproduction and investment in some common currency of inclusive fitness. Define replacement value of a female parent aged x (RV_x) as her reproductive value weighted by the survival probability of offspring to age of first reproduction (l_1) and devalued by the mother's coefficient of relatedness to offspring (r_o). Then

$$RV_x = V_x l_1 r_o \quad (6)$$

and for a stationary population of a sexual diploid species where $r_o = 1/2$

$$RV_x = \frac{b_x l_1}{2} + \frac{1}{2} \sum \frac{l_i}{l_x} (b_i l_i)$$

where the two right hand terms represent current (RV_x^c) and residual replacement value (RV_x^*), respectively. Replacement value for any current offspring is given by

$$RV_o = l_1 + l_1 r_s (b_x - 1) + r_s \sum \frac{l_i}{l_x} (b_i l_i) \quad (7)$$

where r_s is the coefficient of relatedness to sibs. That is, replacement value for an offspring is equal to its own chances of survival to breeding age plus its expected inclusive fitness obtained by present and future sibs also living to that age.

But r_s = some ratio, say k/c where $k \leq c$, and

$$RV_o = l_1 + l_1 \left(\frac{k}{c}\right) (b_x - 1) + \frac{k}{c} \sum \frac{l_i}{l_x} (b_i l_i)$$

Multiplying through, RV_o^c equals

$$l_1 - l_1 \left(\frac{k}{c}\right) + l_1 b_x \left(\frac{k}{c}\right)$$

which is the same as

$$(c - k) \left(\frac{l_1}{c}\right) + l_1 b_x \left(\frac{k}{c}\right)$$

In sexual diploid species, k always equals 1, so

$$RV_o^c = (c - 1) \left(\frac{l_1}{c}\right) + l_1 \left(\frac{b_x}{c}\right)$$

And for monogamous sexual diploids,

$$RV_o^c = \frac{l_1}{2} + RV_x^c \quad (8)$$

Assuming that current parental investment acts to increase l_1 , each offspring by itself stands to gain a constant increment more by a particular investment than does the parent. Furthermore,

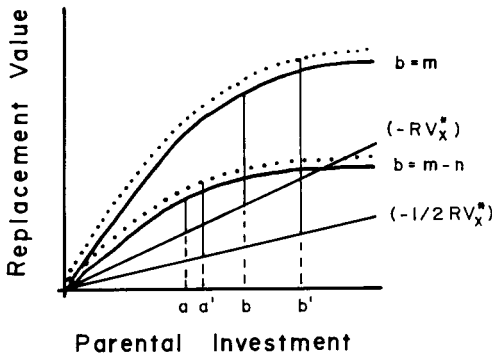


FIG. 4. The relationship between parental investment for parent (solid lines) and offspring (dotted lines) for two litter sizes in terms of replacement value. Individual offspring always gain more by a particular investment than does the parent. Optimal investment occurs when reproductive profit (current replacement value [RV_x^c and RV_o^c] minus residual replacement value [RV_x^* and RV_o^*] for the parent and offspring, respectively, shown here as the distance between the upper benefit and lower cost curves) is maximized. The optimal parental investment for the offspring always exceeds that of the parent. With decreasing genetic relatedness of current offspring with future sibs (in this example, shown by polygamy; $RV_o^* = 1/2RV_x^*$), parent-offspring conflict intensifies with increasing brood size ($a' - a < b' - b$). The intensity of the conflict will depend on the actual shapes of the benefit and cost curves. Note that this argument assumes equal parental investment among all current offspring. There will also be conflict over that investment within broods (Trivers, 1974), but for most of the period of investment, parents should be able to capitalize on the size, strength and age asymmetry with young to force equal investment among progeny (Alexander, 1974).

this increased benefit to individual offspring increases as r_s declines, whereas the parent's rewards are constant ($r_o = 1/2$ for sexual diploids). Thus with polygamy,

$$RV_o = \frac{l_i}{2} + RV_x^c + 1/2RV_x^*.$$

These relationships can be shown by plotting the components of replacement value against parental investment where RV_o^c and RV_x^c are the benefits of current investment, and subtracting RV_o^* and RV_x^* represents costs in terms of future reproduction (Fig. 4). Both offspring and

parent are in agreement over increased parental care with current litter size. The conflict is related only to residual replacement value. Then why, in my study, did litters of size six have the lowest recruitment rate?

Three possibilities exist: 1) above some threshold, increasing parental care actually reduces juvenile survival (this is unlikely); 2) litters of size six may be beyond the optimum investment by female parents; 3) natural selection may not be operating on the probability of any given juvenile's survival to adult age. Both of these latter alternatives are probably the case for *P. leucopus*. The lottery of litter success dictates both an upper maximum in parental investment which does not seriously hinder the parent's chances of future reproduction and a minimum investment which insures that the current litter is weaned before or at the time of next reproduction. *Peromyscus leucopus* appears to have adopted a bet-hedging strategy (Schaffer, 1974; Schaffer and Gadgil, 1975; Stearns, 1976) in response to variation, not just in terms of juvenile survival but, rather, in terms of low probabilities of any recruitment from any given litter.

At some point, the conflict must reach a breaking point in the female's willingness to sacrifice future reproduction to current offspring. She should cease providing parental care and may either emigrate or force the dispersal of her young. Female *Peromyscus* usually stop nursing older litters and force them out of the nest on the birth of subsequent litters (Svihla, 1932). The breaking point will tend to occur earlier in large than in small litters, with the result that individuals in large litters are relatively less experienced and more prone to risks of starvation, predation, and other forms of mortality. Yet as long as some young are, on average, recruited from large litters, the strategy serves to maximize the parent's fitness whose expected next litter size (four) is close to the optimum.

Low recruitment of young from large

litters of free-living white-footed mice may be a reflection of asymmetry in parent-offspring optima, an asymmetry which is resolved by intense conflict over parental investment. Such behavioral control of life-history evolution leads to an interesting prediction. If parent-offspring conflict accounts for reduced recruitment in large litters, this effect should be greatly reduced in mothers which do not breed post-partum. I have too few data on individual females to perform such a test. An easier test would simply be to compare the success of recruitment of young from different litter-size classes of fall-born young when the female has only her own and current litter's survival at risk (winter reproduction is relatively rare in *P. leucopus*). For fall-born animals, the behavioral-control hypothesis predicts that differences in recruitment among litter-size classes should be reduced.

A tentative solution to the conflict would seem to be mechanisms which delay either post-partum breeding or implantation of subsequent litters with increases in current litter size. Early work (Svihla, 1932; Layne, 1968) hinted at delayed implantation in *Peromyscus*, and recent laboratory studies by Lackey (1978) and Myers and Master (1983) have shown that the length of gestation is more variable in lactating than in non-lactating female *Peromyscus* and may be related to the size of the nursing litter. These results confirm the existence of the mother's dilemma over parental care, but may not reflect realities of natural populations. Wild females may not have the option of prolonged gestation because they must also consider the associated costs of delayed reproduction in terms of the seasonal availability of resources. Millar (1984) and Millar and Innes (1985) have documented an inverse relation between the incidence of post-partum breeding and length of the breeding season. Thus, we can also predict that for *Peromyscus*, parent-offspring conflict should intensify with increasing latitude and elevation.

With an optimum parental investment at some intermediate brood size, broods should have associated maxima in juvenile body size or weight gain. Such is apparently the case in at least one recent study of life-history evolution in the blue tit (Nur, 1984). In both years of Nur's study, the relationship of mean nestling weight at ten days of age with brood size was parabolic, implying a maximum parental investment per offspring at less than the maximum clutch size. These relationships were not standardized by parental age and are open to counterinterpretation. Nevertheless, the results are suggestive enough to encourage more detailed and standardized studies of parental investment (Morris, 1985).

One must be wary of constraints imposed by a variety of morphological and life-history characters. Egg size or size of newborn young may frequently be constrained by female morphology (e.g., references in Brockelman, 1975; Leutenegger, 1979; Millar, 1981; Congdon et al., 1983). Post-partum estrus in particular, and iterated reproduction in general, place limits on the duration of parental care and modify parental options for optimal investment per offspring. Lastly, the asymmetry in parent and offspring optima frequently leads to conflict and to a parental investment which probably strikes a balance satisfying the optimality criteria of neither the parent nor offspring (see also Parker and MacNair, 1979; Charnov, 1982; Horn and Rubenstein, 1984; Parker, 1984).

That the most frequent litter size (four) is less than the most productive (five) is in agreement with at least two alternative explanations. First, if the probability of recruitment declines or is unimodal with litter size, and if there is genetic variation in mean litter size, the most frequent litter size may be smaller than the most productive (Mountford, 1968). The same prediction is made if parental mortality increases with litter size (Charnov and Krebs, 1974). I can reject the second alternative because parental survival was independent of the number of young. To

Mountford's suggestion I would add that the same pattern can occur as a result of environmental variation in litter size.

The empirical distribution of litter sizes points toward this latter possibility. The peculiar negatively skewed distribution suggests strong directional selection toward large litters, even though spring-born litters of size six have low recruitment. Of course, seasonal variation in recruitment could mean that large fall-born litters may actually be the most productive at that time and reduce the apparent penalty of the observed distribution of litter sizes. Second, the optimum litter size itself may be variable and respond to differences in habitat or productivity. Third, litter size may act primarily to optimize parental investment among offspring. The negative skew in the litter-size distribution may reflect a similar skew in reproductive effort among females.

Skeptics may argue that some of the results of this study are artifacts caused by using nest boxes to estimate fecundity and survival. This could only be the case if there were preferential colonization of nest boxes by females as a function of litter size, or if litters in nest boxes are subject to consistently different litter-size-specific selective pressures than are those occurring in natural nest sites. Both of these possibilities are unlikely. The distribution of litter sizes I have recorded is almost identical to that tabulated by Lackey (1978 table 2) for 128 lab-raised litters of *P. leucopus* from Michigan. Such an event occurring in the presence of bias would be an improbable coincidence. A second criticism could be that my use of minimal recruitment rates (animals marked as juveniles and recaptured as adults in nest boxes) somehow biases my interpretation of life-history evolution in *P. leucopus*. In fact, there may be no bias whatsoever. Alerstam and Högstedt (1983) predicted that for species with parental care, if mortality risks are proportional to brood size, recruitment rates should be regulated toward e^{-1} (37%). My field estimates for litters of size five

and smaller produced a combined rate of 35%. Nevertheless, at some point, mortality of young must increase (Ricklefs, 1983), and in my study that appeared to happen catastrophically in litters with six young. In any case, to be real, this recruitment bias would have to be consistently related to litter size, and that too seems unlikely. To those who are unconvinced, I simply suggest that known survival of free-ranging offspring to breeding age is, in my mind, a good estimate of a mother's reproductive success.

Whatever is responsible for the observed patterns, this field study adds several new wrinkles to the study of life-history evolution. First, pre-reproductive survival did not decrease monotonically with litter size. Second, even though there was an optimum litter size, it did not appear to be determined by physiological trade-offs. Third, the lack of trade-offs may be a constraint imposed by an overall bet-hedging strategy dictated by the lottery of litter success. Fourth, the most frequent litter size was less than the optimum, and the frequency distribution of litter sizes was markedly non-symmetrical. Fifth, parental survival appeared to be independent of litter size.

ACKNOWLEDGMENTS

I thank Kelly Morris for field and logistical assistance, computer programming, and for tolerating numerous field excursions of considerable distance. Thanks also to Paul Anderson for the nest boxes, to John Enright for frequent field assistance, to Monarch Mattress Company for free nesting material and to Morridell Farms Ltd. for access to research sites. Ralph Morris and Jack Millar helped clarify my thoughts on the evolution of brood size, and numerous suggestions from anonymous reviewers improved the paper. The 1981 field work was completed while I held a NSERC post-doctoral fellowship at The University of Western Ontario. This research was supported in part by NSERC grant A0411.

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