GENETIC VARIATION IN PHOTOPERIODISM IN
PEROMYSCUS LEUCOPUS: GEOGRAPHIC VARIATION IN AN
ALTERNATIVE LIFE-HISTORY STRATEGY

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Phenotypic variation in reproductive response to photoperiod is typical of many temperate-
zone populations of rodents. This variation could be due either to genetic variation in
photoresponsiveness or phenotypic plasticity within populations genetically homogeneous
for photoresponsiveness. At least some of this variation has been shown to be genetic in
single populations of three species of rodents and in one laboratory population of another
species of rodent. Neither the latitudinal range over which this genetic variation occurs nor
the frequency with which populations contain this kind of genetic variation is known. To
test for genetic variation in reproductive photoresponsiveness in a population of Peromyscus
from a mid-temperate latitude, a population of P. leucopus from Williamsburg, Virginia
(37°16'N, 76°42'W), was subjected to artificial selection either for reproductive response
or lack of reproductive response to photoperiod, with a control line that was not subject to
selection. Reproductive photoresponsiveness was significantly heritable (narrow sense \( h^2 \)
ranging from 0.54 to 0.74 in the first laboratory generation). Three generations of selective
breeding yielded one line of mice with 80% of individuals responding strongly to photo-
period (regression of gonads under short day length, 8L:16D) and a nonresponsive line
with only 16% strongly responsive individuals. There were significant responses to selection
in each generation in one or both selected lines, while a control line changed significantly
only in one sex in a single generation. These results are similar to those from a population
from Michigan (43°N) but are different from a population from Georgia (34°N). These data
are consistent with the hypothesis that genetic variation in photoresponsiveness is present
in a mosaic pattern rather than a latitudinal cline. Presence of genetic variation in repro-
ductive photoresponsiveness in two widely separated populations of P. leucopus provides
support for the hypothesis that genetic variation in reproductive photoresponsiveness is
likely to be a common life-history feature of populations of this species between 37 and
45°N, and probably further north as well.

Key words: Peromyscus leucopus, white-footed mouse, photoperiod, reproduction, sea-
sonal breeding

Strategies for maximizing successful re-
production vary in time and space. Seasonal
fluctuations in physical factors such as food
or climate are ultimate factors that favor sea-
sonal reproduction in mammals (Bronson
and Heideman, 1994), and synchronization
of reproductive attempts with seasonal pe-
riods of abundant food and moderate weath-
erer is a common component of reproductive
strategies. The seasonal cycle of changes in
day length is the proximate cue that most
temperate-zone mammals use to regulate re-
productive timing (Bronson and Heideman,
1994). However, the short life expectancy of
many rodents creates a strong selective pres-
ture toward reproductive attempts, even
when probability of successful reproduction is low (Bronson, 1989).

Phenotypic variation in reproductive response to photoperiod is typical of many temperate-zone populations of rodents (Blank, 1992; Bronson and Heideman, 1994). This variation could be due either to genetic variation in photoresponsiveness or phenotypic plasticity within populations that are genetically homogeneous for photoresponsiveness. Even if populations are genetically homogeneous for this trait, environmental factors such as small body size, poor physical condition, low temperatures, or maternal effects might affect probability of winter maturation and breeding attempts in young rodents born in autumn (Hayes and Jenkins, 1997). These phenotypically plastic responses could underlie some or all of the phenotypic variation in reproductive condition observed in wild and laboratory populations. It has been hypothesized that fluctuating selection in the wild is important in the dynamics of natural populations of rodents (Nelson, 1987), but this hypothesis assumes that variability within populations is due to genetic variation.

At least some of the phenotypic variation in photoresponsiveness has been shown to be genetically based in single populations taken from the wild in three species of rodents (P. maniculatus, 44°N, 103°W—Desjardins et al., 1986; P. leucopus, 43°N, 84°W—Heideman and Bronson, 1991; Microtus agrestis—Spears and Clarke, 1988), and similar results have been obtained in one laboratory population of another species of rodent (Phodopus sungorus—Lynch et al., 1989). Neither the latitudinal range over which this genetic variation occurs within a species nor the frequency with which populations contain this kind of genetic variation is known. Thus, it is unknown if this kind of genetic variation is a common feature of populations of rodents in temperate zones.

To determine if this genetic variation is widespread in populations of rodents and test for geographic patterns (and especially for latitudinal clines—Carlson et al., 1989; Desjardins and Lopez, 1980, 1983; Gram et al., 1982; Lynch et al., 1981) in its distribution, it is necessary to assess multiple populations of rodents in a single species over a broad geographic range. We tested for genetic variation in reproductive photoresponsiveness in a population of Peromyscus from Williamsburg, Virginia, from a mid-temperate latitude (37°16’N, 76°42’W) to compare it to populations from Michigan (43°N) and Georgia (34°N) tested previously. We measured heritability and the response to artificial selection either for strong reproductive response or a lack of reproductive response to photoperiod, with a control line that was not subject to selection.

**MATERIALS AND METHODS**

The founder population of mice was trapped February–April 1995 in Sherman live traps provided with nesting material and baited with rolled oats. Mice were caught at three sites separated by 500–1,000 m in forest owned by the College of William and Mary. Forest and forest-edge cover was continuous between sites, except that one trapping site was separated from the others by two single-lane roads.

Mice were housed in polyethylene cages (27 by 16 by 13 cm or 28 by 13 by 16 cm) with wire tops, provided with pine shavings to a depth of 3 cm, given tap water ad lib., and maintained at 23 ± 2°C. Larger fluctuations (23 ± 7°C) occurred for periods of 12–24 h in spring and autumn during routine servicing of the heating-cooling system, and fluctuations of 12–25°C occurred during 4 periods of 1–3 days in October and November 1997, during rearing of the F_2 generation, due to failures of the heating/cooling system. After weaning at age 21–23 days, mice were housed singly. Breeding mice and lactating females were given cotton nesting material and a high-fat diet (Prolab 3000—Southern States Cooperative, Inc., Williamsburg, VA) ad lib.; all other mice were maintained on a mouse-maintenance diet (Prolab 2000—Southern States Cooperative, Inc., Williamsburg, VA) provided ad libitum. Light was provided from overhead fluorescent lights, with light intensity at the cages of 100–1,000 lux. The wild-caught mice were paired on a photoperiod of...
16L:8D (LD), yielding a parental generation to serve as the stock for the selection experiments.

All litters were separated within 72 h of birth from their father and transferred with the mother to either 8L:16D (SD) or left in LD. At 70 ± 3 days of age, mice were weighed and ear-tagged (Size 1 Monel—National Band and Tag Co., Newport, KY), and their reproductive status was assessed. Males were lightly anesthetized with methoxyflurane (Pitman-Moore, Inc., Mundelein, IL), and width and length of right testis were measured through the scrotum with calipers. Width of testis was multiplied by length to give a testis index. All testis measurements were taken by one individual (P. D. Heideman), blind with respect to treatment in all but a few cases in which knowledge of treatment was unavoidable. Females were deeply anesthetized with methoxyflurane, and reproductive organs were examined through a small lateral incision. Females were assigned a reproductive index of 1–5 on the basis of size of ovary, uterine diameter, and presence or absence of macroscopically visible follicles and corpora lutea. Ranks were assigned as follows: 1, tiny ovaries (usually <2 mm in greatest length) lacking visible follicles or corpora lutea and a uterine diameter of ≤0.5 mm; 3, ovaries intermediate in size (usually 2.5–3.5 mm) with small visible follicles or corpora lutea and a uterine diameter >0.5 but <1.0; 5, large ovaries (usually >3.5 mm) with large visible follicles or corpora lutea and a uterine diameter >1.0. Scores of 2 or 4 were assigned to individuals not fully meeting the criteria for the extremes or intermediate categories. On the basis of those ranks, photoperiod responsiveness of all mice was assessed as nonresponsive, responsive, or intermediate. Females with a rank of 1 or 2 were classified as responsive, those with a 4 or 5 rank were classified as nonresponsive, and ranks of 3 were classified as intermediate. Males with a testis index <24 mm² were classified as responsive, those with testis index >32 mm² were classified as nonresponsive, and all others were classified as intermediate (Heideman and Bronson, 1991). Males also were assigned ranks based on testis index (adapted from Heideman and Bronson, 1991) to provide a means of comparing males and females. Ranks were as follows: 1, 8–15 mm²; 2, 15.1–24 mm²; 3, 24.1–32 mm²; 4, 32.1–39 mm²; 5, >39.1 mm².

Mice for a control line were selected randomly from the parental generation (the offspring of the wild mice). To establish a photoperiod-responsive line, responsive males and females from the parental generation were paired. To establish a photoperiod-nonresponsive line, nonresponsive males and females from the parental generation were paired. Pairings were random within lines, except that sibling-sibling pairings were excluded. Only responsive mice were retained as breeders in subsequent generations in the responsive line, and only nonresponsive mice were retained as breeders in subsequent generations in the nonresponsive line. Within both of those lines, offspring from as many families as possible that met the selection criteria were used for breeding. In the control line, breeders were selected at random, except that at least one individual male or female offspring was chosen from each breeding adult in that line. Selection was carried out for three generations. Sample sizes in SD were as follows: parental generation—104 males, 104 females; F₁ control line—71 males, 67 females; F₂ control line—109 males, 106 females; F₁ control line—66 males, 58 females; F₂ nonresponsive line—102 males, 101 females; F₂ nonresponsive line—136 males, 134 females; F₁ nonresponsive line—70 males, 55 females; F₁ responsive line—78 males, 93 females; F₂ responsive line—67 males, 69 females; F₁ responsive line—39 males, 38 females.

Selection for large or small gonads could have favored faster or slower maturation in our two selected lines, rather than photoperiod-dependent maturation. In this case, the responsive line would just be slow to mature, but not necessarily more sensitive to SD. To test this possibility, we raised some individuals from the parental and F₂ generations in LD as controls. Those individuals were tested at age 70 ± 3 days as above. Sample sizes in LD were as follows: parental generation—30 males, 36 females; F₂ control line—17 males, 26 females; F₂ nonresponsive line—36 males, 20 females; F₂ responsive line—19 males, 14 females.

Data on testis index for males and body weight for sexes were analyzed by two-tailed t-test, analysis of variance, or linear regression (Feldman et al., 1992; Roth et al., 1995). Distributions of size of testis deviated from normal in some of our datasets (Fig. 2), and in those cases we carried out randomization tests (Simon, 1995) and parametric tests. In no case did results of tests differ, and we have presented only re-
Table 1.—Reproductive characteristics and body weight of males and females in the parental generation (X ± 1 SD).

<table>
<thead>
<tr>
<th></th>
<th>SD</th>
<th>LD</th>
<th>t</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Males</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Testis index</td>
<td>27.9 ± 10.8</td>
<td>45.6 ± 8.3</td>
<td>69.03</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Reproductive index</td>
<td>2.9 ± 1.4</td>
<td>4.7 ± 0.5</td>
<td>47.17</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Body weight</td>
<td>20.1 ± 3.8</td>
<td>22.6 ± 4.1</td>
<td>9.91</td>
<td>0.002</td>
</tr>
<tr>
<td><strong>Females</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Reproductive index</td>
<td>3.1 ± 1.7</td>
<td>4.7 ± 0.9</td>
<td>29.56</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Body weight</td>
<td>19.5 ± 4.5</td>
<td>21.3 ± 5.0</td>
<td>4.15</td>
<td>0.044</td>
</tr>
</tbody>
</table>

results of parametric tests. The reproductive index of females had a strongly bimodal distribution, and randomization tests were carried out to assess differences in reproductive index. Narrow-sense heritability (h²) was calculated by single-parent regression (mean value for offspring of one sex on the value for the parent of that sex), because mid-parent values can be biased by maternal effects (Falconer, 1989).

When all generations and all lines were considered together, males were ca. 5% heavier than females (males, 20.4 g ± 0.2 SE: females, 19.5 g ± 0.2. t = 4.39, P < 0.001). Similar differences in bodyweight were observed in most lines in most generations, but usually those differences were not statistically significant.

When all generations and lines were considered together, there were statistically significant correlations between body mass and reproductive status for both males (F = 11.35, P < 0.001, r² = 0.01) and females (F = 21.61, P = 0.001, r² = 0.026). The extremely low values for r² indicated that body mass accounted for little of the variation in reproductive status. We did not adjust for body size in our analyses because we were interested in the actual stage of reproductive development. For example, we did not consider a fat mouse to be reproductively less developed because its mature reproductive tract was a relatively low proportion of body mass. Similarly, we did not consider a light mouse with small gonads to be more reproducively mature because its reproductive tract was a relatively high proportion of body mass. Finally, given the low values for r², it was unlikely that adjustments for body mass would have affected the result of any analysis.

**Results**

Many adult mice (defined as those having molted into the brown pelage of adults) captured in the wild in mid-winter were reproductively active. Of males captured in the wild in midwinter, 79% (15 of 19) had large testes typical of nonresponsive mice, and only 21% had small testes that met the criteria for fully responsive mice. While we did not conduct surgeries to assess ovarian status, 25% (4 of 16) of wild-caught adult females gave birth to litters conceived in the wild. None of the mice were lactating, and 60% had an imperforate vaginal opening, suggesting that ≥50% of the females were reproductively inactive.

The parental generation, the offspring of wild-caught mice raised in SD (the first generation in the laboratory), were highly variable in reproductive development. In the parental generation, 42% of mice were considered strongly responsive to photoperiod. Males raised in SD had testis indices ranging from 12 to 55 mm²; 41% of those males had a testis index <24 mm² and were considered strongly responsive to photoperiod. Males raised in SD had significantly smaller testes than mice raised in LD (Table 1). All LD males had testis indices >30 mm², and all had testes above the threshold for nonresponsive mice. Of females (48 of 112) raised in SD, 43% had not begun their pubertal ovulation at 70 days of age and were classed as strongly responsive. Females raised in SD had significantly lower reproductive indices than those raised in LD (Table 1). In contrast, 94% (34 of 36) of females raised in LD had reached their pubertal ovulation by 70 days. Photoperiod also affected body weight. Both males and
females were ca. 10% lighter in SD than in LD (Table 1).

There were significant responses to selection for and against reproductive photo responsiveness (Fig. 1). Within males, the mean testis index decreased by 10 mm$^2$ in the responsive line ($F = 16.52, P < 0.001$) and increased by 8 mm$^2$ in the nonresponsive line ($F = 7.52, P < 0.001$; Fig. 2) after three generations of selection. In the control line, in contrast, there was no significant change in testis index after three generations ($F = 0.36, P = 0.780$). In the responsive line, the percentage of strongly responsive mice increased from 42 to 90% by the F$_3$ generation. In the nonresponsive line, the percentage of strongly responsive mice decreased from 42 to 15% by the F$_3$ generation. In the F$_1$, F$_2$, and F$_3$ generations, both selected lines differed significantly from the control line ($F = 17.12, P < 0.001$; $F = 29.25, P < 0.001$; $F = 32.97, P < 0.001$, respectively), and all pairwise comparisons in each generation also were significant ($P < 0.05$ for all).

Within females in the responsive line, the mean reproductive index decreased from $3.07 \pm 0.16$ in the parental generation to $2.05 \pm 0.26$, in the F$_3$ generation ($P < 0.001$; Fig. 3). In the nonresponsive line, the reproductive index increased to $3.98 \pm 0.17$ in the F$_3$ generation ($P < 0.001$; Fig. 3). In the control line, in contrast, there was no significant change in reproductive index in the first three generations ($P = 0.386$), but there was a significant change in the F$_3$ generation ($P = 0.031$; Fig. 3). In the responsive line, the percentage of responsive mice increased from 43 to 71% by the F$_3$ generation. In the nonresponsive line, the percentage of responsive mice decreased from 43 to 17% by the F$_3$ generation. In each of the F$_1$, F$_2$, and F$_3$ generations, the three lines differed significantly in reproductive index of females ($P < 0.001$ for all). In each generation, pairwise comparisons of reproductive index of the responsive and nonresponsive line were all highly significant ($P < 0.001$ for all), but females in the two selected lines were not always significantly different from those in the control line.

Both males and females in the nonresponsive line were ca. 1 g heavier than mice in the other two lines, but the difference was statistically significant only within females (males, $F = 2.25, P = 0.110$). There was no significant difference among generations.

In the F$_2$ generation, some mice from each line were raised in LD to test for inadvertent selection on rate of maturation independent of photoperiod. Males from the nonresponsive and control lines had significantly larger testes in LD than mice from the parental generation or the responsive line ($F = 5.16, P = 0.002$; $P < 0.05$ for pairwise comparisons). In all three lines, mice raised in LD had significantly higher testis indices or reproductive indices than mice in the same line raised in SD ($P < 0.05$ for all comparisons). As in the parental generation, mice were significantly lighter, by an average of 1.4 g, in SD than in LD ($F = 8.74, P = 0.003$).

Narrow-sense heritability was determined for all mice in the first generation and in the control line thereafter. The reproductive response to photoperiod was
Fig. 2.—Distribution of testis indices in each line, photoperiod, and generation. Circles represent the testis index for an individual. Boxes show $\bar{X} \pm 1 \text{SE}$, and the lines extending above and below boxes are $\pm 1 \text{SD}$. Two horizontal lines through each panel show the boundaries set for strong photoresponsiveness ($<24 \text{ mm}^2$) and nonresponsiveness ($>32 \text{ mm}^2$).

significantly heritable (Table 2). There was significant heritability of reproductive photoresponsiveness in the control line through the F$_2$ generation, and that also was present as a trend in the smaller sample for the F$_3$ generation (Table 2).

**Discussion**

In this population, there was phenotypic variation in reproductive status in mid-winter as well as in SD in the laboratory, a finding similar to that of Kerbeshian et al.
Fig. 3.—Reproductive index (X ± 1 SE) in each line, photoperiod, and generation (open circles, control line; solid squares, responsive line; solid circles, nonresponsive line). Symbols lacking error bars are means for which the symbol is larger than the error bar. Symbols not connected by lines are from mice raised in LD; those connected by lines are from mice raised in SD.

(1994) in a study on Microtus pennsylvanicus (41°N)—the only other field and lab comparison of this kind. In our study, however, the apparent difference between proportion of males and females in reproductive condition in the wild may not be accurate, as we did not examine ovaries of wild-caught females for evidence of estrus cycling. In addition, because we could not age young wild mice accurately, our results from the wild population (adult mice) are not strictly comparable with those from the laboratory (young mice).

Two types of evidence show that there is selectable genetic variation in reproductive responses to photoperiod in this population of P. leucopus. First, there was a significant response to selection in both selected lines, with little or no change in a control line. Second, there was significant heritability of photoresponsiveness. Heritability values in the F1 generation were not significant, which may be due in part to the smaller samples in that generation (Table 2). The three generations of selection we carried out produced one selected line that was responsive to short photoperiod, in which almost all individuals had failed to begin the pubertal transition by age 70 days; in LD, however, almost all individuals had completed puberty by this age. The nonresponsive line, in which mice were selected to mature despite being held in short photoperiod, included some responsive individuals. About one-half of mice in that line were truly nonresponsive, equivalent in reproductive development to mice raised in long photoperiods, and ca. 15% of mice were still strongly responsive to photoperiod. Thus, three generations of selection did not produce lines of mice fixed for one of the two extreme phenotypes.

Our results suggest that much of the variation in photoresponsiveness in the wild population is genetic in origin. By the F3 generation, there was little overlap in size of testis between the two lines. Nevertheless, substantial variation in reproductive development remained, especially in the nonresponsive line. This remaining variation could represent environmental variation, non-selectable genetic variation due to epistasis or pleiotropy, or residual additive genetic variation.

Lynch et al. (1981) and Gram et al. (1982) tested adult mice from the same population used in this study but using an older laboratory stock of P. leucopus developed by R. Terman. Lynch et al. (1981) found that adult males placed in SD or LD for 12 weeks had indistinguishable phenotypes, but in a longitudinal study, mice from Virginia were intermediate in photoresponsiveness between mice from Connecticut (41°N) and Georgia (34°N—Gram et al., 1982). These studies suggest that the population in Virginia had few individuals that were reproductively photoresponsive as adults, but it is possible the mice studied by Lynch et al. (1981) and Gram et al. (1982) would have been more strongly photoresponsive during the pubertal transition. Greater photoperiodic sensitivity of peri-pubertal animals, relative to adults, is suggested by theory (Horton and Rowsemitt,
TABLE 2.—Heritability ($h^2$) of testis index (for the male offspring on father comparison) or reproductive index (all others) over three generations. Sample size is given for families.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Generation</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>F₁</td>
</tr>
<tr>
<td>Male offspring on fathers</td>
<td></td>
</tr>
<tr>
<td>$n$</td>
<td>67</td>
</tr>
<tr>
<td>$h^2$</td>
<td>0.74 ± 0.14</td>
</tr>
<tr>
<td>95% CI for $h^2$</td>
<td>0.48, 1.00</td>
</tr>
<tr>
<td>$t$</td>
<td>5.59</td>
</tr>
<tr>
<td>$P$</td>
<td>0.001</td>
</tr>
<tr>
<td>Female offspring on fathers</td>
<td></td>
</tr>
<tr>
<td>$n$</td>
<td>69</td>
</tr>
<tr>
<td>$h^2$</td>
<td>0.73 ± 0.16</td>
</tr>
<tr>
<td>95% CI for $h^2$</td>
<td>0.41, 1.06</td>
</tr>
<tr>
<td>$t$</td>
<td>4.495</td>
</tr>
<tr>
<td>$P$</td>
<td>0.001</td>
</tr>
<tr>
<td>Female offspring on mothers</td>
<td></td>
</tr>
<tr>
<td>$n$</td>
<td>71</td>
</tr>
<tr>
<td>$h^2$</td>
<td>0.54 ± 0.17</td>
</tr>
<tr>
<td>95% CI for $h^2$</td>
<td>0.20, 0.88</td>
</tr>
<tr>
<td>$t$</td>
<td>3.144</td>
</tr>
<tr>
<td>$P$</td>
<td>0.003</td>
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<tr>
<td>Male offspring on mothers</td>
<td></td>
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<tr>
<td>$n$</td>
<td>69</td>
</tr>
<tr>
<td>$h^2$</td>
<td>0.63 ± 0.14</td>
</tr>
<tr>
<td>95% CI for $h^2$</td>
<td>0.36, 0.91</td>
</tr>
<tr>
<td>$t$</td>
<td>4.588</td>
</tr>
<tr>
<td>$P$</td>
<td>0.001</td>
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1992; Kaitala et al., 1997) and has been reported in several species of rodents (Donham et al., 1989; Johnston and Zucker, 1979; Rivest et al., 1986; Stanfield and Horton, 1996).

To date, two populations of *P. leucopus* have been tested for genetic variation in reproductive photoresponsiveness (Michigan, 43° N—Heideman and Bronson, 1991; Virginia, 37° N—this study). Populations in Michigan and Virginia were similar in amount of variation in photoresponsiveness at the pubertal transition and also were similar in the response to selection. The major difference between these two populations was that the population in Michigan responded more rapidly to selection (Heideman and Bronson, 1991). The parental generation of our population in Virginia was similar in level of phenotypic variation in size of testis to a population from Connecticut described by Carlson et al. (1989). In contrast, a population from Georgia (34°N) appears to lack phenotypic variation in photoresponsiveness (Carlson et al., 1989).

What regulates reproductive state in white-footed mice during winter? Available data suggest that in many northern populations some mice are under a genetically determined strategy of obligate suppression of reproduction by short photoperiods. Other mice within these populations have genotypes that permit breeding in winter. It seems likely that our photoperiodically nonresponsive mice could be phenotypically plastic in their reproductive response to winter. Mice that are nonresponsive or weakly responsive to photoperiod alone might be reproductively suppressed instead
by restricted availability of food acting via neuroendocrine mechanisms that are photoperiod independent. In the laboratory, the combination of restriction of food, low temperature, or both, with short photoperiod may induce responses to short photoperiods in P. leucopus (Blank, 1992; Blank and Desjardins, 1985; Demas and Nelson, 1998; Desjardins, 1981; Nelson et al., 1997). Thus, P. leucopus in northern populations probably contain some individuals that are phenotypically plastic in their reproductive response to winter, while others follow a genetically determined strategy in winter of obligate reproductive inhibition. More southern populations also may vary in reproductive responses to photoperiod or may be exclusively nonphotoperiodic (Carlson et al., 1989).

Our results do not provide support for a broad latitudinal cline in genetic variation in reproductive photoresponsiveness, because populations in Michigan (Heideman and Bronson, 1991) and Virginia (this study) were similar. Our results are consistent with either a sharp latitudinal gradient between 34 and 37°N in Georgia and Virginia, respectively, or with a mosaic pattern of genetic variation in reproductive photoresponsiveness. Because populations in both Michigan and Virginia were able to change rapidly in response to artificial selection, our results support previous suggestions that populations may undergo temporal fluctuations over relatively short time periods (Blank, 1992; Desjardins et al., 1986; Nelson, 1987). One or few consecutive winters that are either unusually harsh or unusually favorable for reproduction could produce large changes in frequency of alleles for or against obligate photoresponsiveness. As with the population in Michigan (Heideman and Bronson, 1991), even three generations of strong artificial selection failed to eliminate either phenotype from selected lines (Fig. 1). This suggests that populations would be unlikely to become fixed for either genotype except during periods of strong selection continu-

ing for five or more generations. In many northern populations, geographic variation in habitat or severity of winter would be likely to maintain genetic variation in reproductive photoresponsiveness. Thus, our results suggest that genetic variation in reproductive photoresponsiveness is a common feature of populations of P. leucopus between 37 and 45°N and possibly at more northern and southern latitudes.

Finally, it seems likely that genetic variation in reproductive photoresponsiveness is typical of populations of small rodents in these latitudes of the north-temperate zone (Desjardins et al., 1986; Heideman and Bronson, 1991; Lynch et al., 1989; Spears and Clarke, 1988; Wichman and Lynch, 1991). If so, selective conditions over recent winters will be an important historical component contributing to life-history strategies and population regulation of mice in this large region of the temperate zone, supporting a hypothesis proposed by Nelson (1987) in reference to population cycles of rodents. Thus, a particular mild winter that favors breeding may be followed by a large population of rodents in late winter, if the penultimate winter favored nonresponsive mice, or by a small population of rodents in late winter, if the penultimate winter favored responsive mice, which were then obligately inhibited even during the mild winter.

A genetic basis to variation in photoresponsiveness has been found in every study addressing this question (Desjardins et al., 1986; Heideman and Bronson, 1991; Lynch et al., 1989; Spears and Clarke, 1988; Wichman and Lynch, 1991; this study). Numbers of studies and species are still small, however, and predictions above should be tested in more populations of P. leucopus and other species. We suggest that short selection experiments would be sufficient to screen wild populations for genetic variation in reproductive photoresponsiveness. Field capture of 20-40 pairs of mice, with ca. 80 mice of each sex raised in SD, and another 20 of each sex in LD,
would provide data to test for reproductive responses to photoperiod and characterize variation in those responses. Assortative mating of ca. 40–60 pairs of mice (the extreme phenotypes) and production of a second generation of 80 mice of each sex raised in SD would provide data for a test for a response to selection and for heritability. Our data suggest that these sample sizes would provide high statistical power in populations with considerable genetic variation (e.g., those reported to date) and would be adequate to detect genetic variation in many populations that contain less variation. Smaller samples, about one-half the sizes above, would provide sufficient statistical power to detect genetic variation in populations that contain as much variation as the population we studied. Because fluctuating selection on photoperiodic responsiveness may have large effects on size of populations and the timing of annual variation in size of populations, it would be valuable to understand the geographic range and pattern of phenotypic and genetic variation in reproductive photoresponsiveness in *P. leucopus* and other species of small mammals.

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