Differential Response of Female Deer Mice to Short Photoperiod[1]

James L. Blank, Andrew I. Korytko, and Sabrina Weber, Department of Biological Sciences, Kent State University, Kent, OH 44242

ABSTRACT. Individual male deer mice (*Peromyscus maniculatus*) respond to inhibitory (short) photoperiod with gonadal responses that range from azoospermia to normal spermatogenesis. We undertook the present study to determine if female deer mice exhibit similar variation in reproductive response to inhibitory daylength. Following 8 wk exposure to short days, reproductive tract weights of 25% of all individual females did not differ from those displayed by mice housed on stimulatory (long) photoperiod; reproductive tracts of all remaining short day mice weighed significantly less. Short photoperiod also significantly reduced body weight, albeit only in those mice with regressed reproductive tracts. These results demonstrate that female deer mice respond differentially to the inhibitory effects of short photoperiod. Taken together with previous results, the present findings indicate that populations of deer mice are composed of subsets of males and females that differ in reproductive response to short daylength.

INTRODUCTION

Many rodents that live at north temperate latitudes frequently forgo reproduction during the winter months (Millar 1984a,b). A winter nonbreeding season is obligated in most species by gonadal regression and the concomitant reduction in steroidogenesis and gametogenesis. Typically, cessation of reproductive function occurs during the fall months in response to one or more environmental cues (Blank and Desjardins 1986, Bronson 1987). Short photoperiod is widely argued to be the primary proximate cue causing gonadal regression under natural conditions (Turek and Campbell 1979, Lincoln 1980, Goldman and Darrow 1983), although in deer mice cold ambient temperature and reduced food availability also have been implicated (Desjardins and Lopez 1983, Blank and Desjardins 1983). The inhibitory effects of short photoperiod on gonadal function can be reproduced in the laboratory by exposing animals to a short daylength (Turek and Campbell 1979, Goldman and Darrow 1983, Blank and Desjardins 1986). While the physiological pathways and mechanisms by which short daylength causes gonadal regression have not been fully described, studies generally show that inhibitory photoperiod exerts its effect by modifying neuroendocrine mechanisms governing the release of one or more anterior pituitary gonadotrophins known to support gonadal function (Turek and Campbell 1979, Lincoln 1980, Goldman and Darrow 1983, Blank and Desjardins 1986).

Early laboratory research on photoperiodic inhibition of reproduction used animal models in which individuals responded uniformly to short daylength with gonadal regression (Turek and Campbell 1979). However, more recent studies using individuals derived from outbred or wild animal stocks demonstrate that species exhibit significant individual variation in the extent to which photoperiod inhibits reproductive function (Lynch and Gendler 1980, Blank and Desjardins 1986). Differential gonadal responses are particularly noteworthy in laboratory populations of deer mice (*Peromyscus maniculatus*) derived from natural breeding populations. Individual males of this species respond to short photoperiod with a broad range of testicular responses (Blank and Desjardins 1983, 1985, 1986). Spermatogenesis is completely suppressed in about one-third of all individuals exposed to short daylength. In contrast, an equal number of mice exhibit normal spermatogenesis following short day exposure and are fertile. Differences in gamete production reflect differences in plasma concentrations of testosterone (T) and luteinizing hormone (LH), the putative gonadotrophin thought to regulate testicular function (Blank and Desjardins 1986). Plasma concentrations of both hormones are significantly reduced in males found to be azoospermic following short day exposure, while short-day housed males with normal spermatogenesis have T and LH levels equal to fertile males maintained under long photoperiod. It is unlikely that these findings are laboratory artifact since breeding individuals have been observed in winter in natural populations of deer mice (Turner 1974) and each disparate testicular response to short photoperiod can be genetically selected (Desjardins et al. 1986).

Field studies showing the presence of winter breeding in north temperate populations of deer mice provide indirect evidence that females of this species also exhibit differential ovarian responses to inhibitory environmental cues. The present study was designed to determine the extent to which individual female deer mice exhibit differential responses to short photoperiod.

MATERIALS AND METHODS

Female deer mice derived from the F_2 generation of an outbred F_1 breeding stock were used in this study. The parents of the F_1 generation were captured in Wind Cave National Park, Hot Springs, SD (lat 43°30' N; long 103°34' W). All animals were housed two per cage and maintained under 16 hours of light per day (LD 16:8) and warm ambient temperature (23° C). Food (Formulab®, Ralston-Purina, St. Louis, MO) and water were available at all times.

At 90-120 days of age, females (N=36) were transferred from long (LD 16:8) to short (LD 8:16) daylength for 8 weeks. All females used in the experiment possessed perforate vaginae, indicating estrous cyclicity, as assessed

for a 1 wk period prior to onset of experimental conditions. Body weight was measured prior to short day exposure and weekly thereafter. At the end of the 8 wk treatment period, females were sacrificed by pentobarbital overdose. The reproductive tract (ovaries, oviducts, and uterus) was removed and weighed (wet weight; mg); uterine width (mm) was also measured. A separate group of similarly-aged females (N=10) maintained on long photoperiod (LD 16:8) served as a longitudinal control group. Comparisons were made between the experimental and longitudinal control groups (Fig. 1), and between experimental group females prior to and after short day exposure (Table 1).
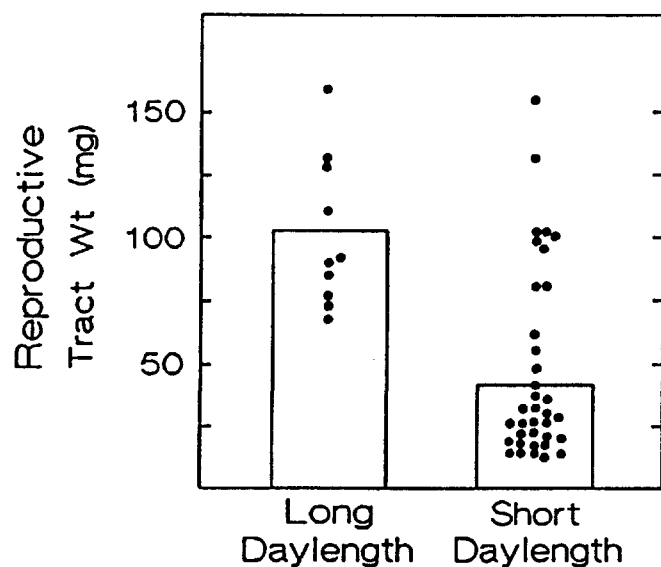

FIGURE 1. Distribution of reproductive tract weights among groups of female deer mice exposed to either long photoperiod (LD 16:8) or short photoperiod (LD 8:16). Short daylength induces a broad range of individual reproductive responses. Among 36 females exposed to short photoperiod, 9 (25%) possessed reproductive tract weights equal to or greater than those displayed by mice maintained on stimulatory long daylength. Reproductive tracts consist of ovary, oviduct, and uterus following removal of fat and connective tissue. Bars indicate mean and closed circles indicate individual values.

Mean body weights of longitudinal control mice ($\bar{x}$=20.0 ± 0.84) and all mice eventually exposed to short days ($\bar{x}$=19.8 ± 0.50) were not significantly different (P>0.05, N=46) before exposure to experimental conditions.

Values are expressed as mean ± standard error or range for each treatment. Comparisons of treatment effects on body weight, reproductive tract weight, and uterine width were evaluated using a one-way ANOVA. Comparisons of body weights during long and short day exposure for mice exhibiting the same reproductive response to short days were made using a paired t-test.

RESULTS

Short days had a suppressive effect on reproductive tract weight of female deer mice (Fig. 1). Mice exposed to short days exhibited a significant decline (P<0.05, N=46) in reproductive tract weight relative to the long day control group ($\bar{x}$=47.6 ± 1.3 mg (N=10) vs. $\bar{x}$=101.7 ± 0.8 mg (N=36), respectively). Uterine width among short day exposed mice ($\bar{x}$=0.9±0.05 mm, N=36) was also significantly (P<0.05, N=46) reduced compared to controls ($\bar{x}$=2.09 ± 0.03 mm, N=10). Further inspection of the reproductive responses of individual females revealed an array of adjustments evoked within the short photoperiod exposed population. Of 36 short-day mice, the reproductive tract weight of 9 (25%) females fell within the range exhibited by long day controls. All remaining mice exhibited tract weights less than the minimum displayed by controls.

Mean body weight of all short day exposed mice was not significantly different (P<0.07, N=46) from that of long day controls (Table 1). However, comparison of individual body weights among experimental mice before and after exposure to short photoperiod showed that the effect of short photoperiod varied according to each individual's reproductive response to inhibitory daylength (Table 1). Mean body weight of short day mice with reduced reproductive tract weights (Reduced RT) was significantly (P<0.05, N=27) less than mean body weight observed in these mice during long photoperiod exposure. In contrast,

TABLE 1

Mean body weight of female deer mice during long day exposure and for the same mice after exposure to short photoperiod.

	Body Weight (g)		
	All Mice Combined	Normal RT	Reduced RT
Long Photoperiod	19.8 ± 0.5[a] N=36	20.7 ± 1.2 N=9	19.5 ± 0.6[c] N=27
Short Photoperiod	18.2 ± 0.5 N=36	20.7 ± 1.1[b] N=9	17.4 ± 0.5[a,b,c] N=27

Values are expressed as mean ± (S.E.).
*RT = reproductive tract weight
For each photoperiod, mice are combined into one group (All Mice Combined) and also categorized according to their reproductive response to short photoperiod (Normal RT* or Reduced RT). Identical superscripts denote significantly different values.

mean body weight of short day females with tract weights falling within the range of controls (Normal RT) was not significantly different ($P >0.05$, N=9) from the mean observed in these same mice during long day exposure. Mean body weights of females falling into each of the short day reproductive response groups were not significantly different ($P >0.05$, N=36) under long day conditions. However, following short-day exposure, mean body weight of females with reduced reproductive tract weights was significantly less ($P <0.05$, N=36) than that of mice with normal reproductive tract weights.

DISCUSSION

The present findings demonstrate that individual female deer mice respond to short photoperiod with variable reproductive responses. Among all females exposed to short days, 25% maintained reproductive tract weights within the range of long-day exposed controls. Earlier investigations showed that 30% of all male deer mice obtained from the same natural breeding population exhibited normal spermatogenesis following short day exposure, a number concordant with that observed for females in the present study (Blank and Desjardins 1986).

From a physiological perspective, these data indicate that short days can serve as an environmental signal suppressing reproduction in female deer mice. A source of potential error in estimating the exact number of reproductively competent and incompetent mice is that variability in uterine and oviduct weights exists during the course of a normal estrous cycle (Feder 1981). In other words, some short-day exposed females may have been autopsied during a period of the estrous cycle when reproductive organ weights were at a minimum size. However, because this assertion also applies to the control group, reproductive tract weight is likely a reliable indicator of reproductive competency.

Short daylength caused a significant reduction in body weight only among mice with reduced reproductive tract weights; short day females with normal reproductive tracts showed no change in body weight. Further, body weights of short-day exposed females with reduced tract weights were significantly less than both short day mice with normal tract weights and long-day exposed longitudinal controls. The significant decline in body weight (about 2 g, on average) cannot be accounted for by the reduction in reproductive tract weight (about 72 mg, on average). Thus, these data suggest a functional association between reproductive state and body weight. Studies of other photoperiodic species show that plasma levels of ovarian steroids, both estrogens and progestins, are lower following short-day exposure in individuals with regressed reproductive tracts (Turek and Campbell 1979, Bronson 1987). Because ovarian steroids have anabolic effects on body composition, it can be hypothesized that the reduction in body weight in reproductively-inhibited deer mice results from reduced ovarian steroidogenesis. Research on a number of photoperiodic breeders demonstrates that photoperiod exerts an inhibitory effect on pituitary-gonadal function via both steroid-dependent and independent pathways residing in the hypothalamus (Steger et al. 1986). Thus, it is also possible that short photoperiod

causes a reduction in body weight by modifying function of a neural body weight regulatory center independently of plasma steroid levels. This possibility with respect to photoperiodic regulation of body weight, or reproductive function, has not been evaluated in deer mice.

The presence of individual variability in response to short photoperiod in both sexes of this species also has important implications for the ecology of the deer mouse in its natural habitat. Deer mice generally survive about 6 months in natural populations (Howard 1949, Millar 1984a,b). Therefore, the suspension of all breeding activity for several months during the fall and winter represents a significant period in the life of an individual during which all opportunity for reproduction is eliminated. Yet, field studies in this and related species indicate that winter breeding is not uncommon, especially during mild winters and/or when food is abundant (Beer and MacLeod 1966, Fairbairn 1977, Taitt 1981, Millar 1984b, Vessey 1987). The present data suggest that one determinant of the prevalence of winter breeding may be differential reproductive responsiveness to declining daylength.

Although the physiological mechanism(s) that mediate differential reproductive responses have not been identified, this variation may represent a physiologically based "bet-hedging" life history strategy for meeting the demands of the winter environment (Stearns 1976). The number of deer mice that respond to short photoperiod with gonadal regression can be increased to 80%, or decreased to 20%, in just two generations of selection (Desjardins et al. 1986). This indicates a genetic component to phenotypic differences in gonadal response to short days that can be rapidly selected. Taken together with observations of winter breeding in this species, these findings provide strong evidence that natural populations of deer mice are composed of subsets of individuals that differ in their response to inhibitory photoperiod.

From the above perspectives, two important questions deserve further attention. First, what is the neuroendocrine basis for phenotypic-level differences in reproductive response to inhibitory photoperiod? Second, what are the respective costs and benefits of maintaining reproductive function during the winter months in a short-lived species? In certain individuals, suppression of reproductive function by short days may obligately eliminate the probability of producing offspring for an extended time period, thereby reducing individual fitness. Yet, foregoing reproduction not only eliminates the significant energy costs associated with rearing offspring, but also allows the allocation of available resources to activities such as metabolic adjustments that may serve to increase survivorship in a cold climate. On the other hand, eliminating reproductive function for several months also eliminates investment in offspring for a significant time period, possibly decreasing an individual's fitness. Thus, year-to-year variability in winter breeding activity may depend not only upon available resources but also upon relative numbers of reproductively active and quiescent mice as determined by their neuroendocrine responses to short photoperiod. These numbers may further depend upon differential selection pressure on individuals of either response type. This variability in photoperiodic response of both sexes

provides a large opportunity for selection (Arnold and Wade 1984) and, thereby, may afford a physiologically-based life history tactic directing an individual's reproductive success (Stearns 1976). Taken together with previous studies, these results have a number of potentially important physiological and ecological implications for seasonally-breeding species.

LITERATURE CITED

Arnold, S. J. and M. J. Wade 1984 On the measurement of natural and sexual selection: theory. Evolution. 38: 709-719.

Beer, J. R. and C. F. MacLeod 1966 Seasonal population changes in the prairie deer mouse. Am. Mid. Nat. 76: 277-289.

Blank, J. L. and C. Desjardins 1983 Spermatogenesis is modified by food intake in mice. Biol. Reprod. 30: 410-415.

——— 1985 Differential effects of food restriction on pituitary-testicular function in mice. Amer. J. Physiol. 248: R181-R189.

——— 1986 Photic cues induce multiple neuroendocrine adjustments in testicular function. Amer. J. Physiol. 250: Rl99-R206.

Bronson, F. H. 1987 Environmental regulation of reproduction in rodents. In: D. Crews (ed.), Psychobiology of reproductive behavior: an evolutionary approach. Prentice-Hall, Englewood Cliffs, NJ. pp. 204-230.

——— 1983 Environmental cues evoke differential responses in pituitary-testicular function in deer mice. Endocrinology. 112: 1398-1406.

Desjardins, C., F. H. Bronson, and J. L. Blank 1986 Genetic selection for reproductive photoresponsiveness in deer mice. Nature. 322: 172-173.

Fairbairn, D. J. 1977 Why breed early? A study of reproductive tactics in Peromyscus. Can. J. Zool. 55: 862-871.

Feder, H. H. 1981 Estrous cyclicity in mammals. In: N. T. Adler (ed.), Neuroendocrinology of Reproduction: Physiology and Behavior. Plenum Press, New York, NY. pp. 279-329.

Goldman, B. D. and J. M. Darrow 1983 The pineal gland and mammalian photoperiodism. Neuroendocrinology. 46: 48-53.

Howard, W. E. 1949 Dispersal, amount of inbreeding, and longevity in a local population of prairie deer mice on the George Reserve, southern Michigan. Contrib. Lab. Vert. Biol., University of Michigan. 43: 1-52.

Lincoln, G. A. 1980 Seasonal breeding: Nature's contraceptive. Rec. Prog. Horm. Res. 36: 1-52.

Lynch, G. R. and S. L. Gendler 1980 Multiple responses to a short day photoperiod in the white-footed mouse, Peromyscus leucopus. Physiol. Zool. 51: 289-295.

Millar, J. S. 1984a Reproduction and survival in Peromyscus in seasonal environments. In: J. Merritt (ed.), Winter Ecology of Small Mammals. Carnegie Mus. Nat. Hist. Spec. Publ. No. 10. pp. 253-266.

——— 1984b Life cycle characteristics of Peromyscus maniculatus nebracensis. Can. J. Zool. 63: 1280-1284.

Stearns, S. C. 1976 Life-history tactics: a review of the ideas. Quart. Rev. Biol. 51: 3-47.

Steger, R. W., K. S. Matt, and A. Bartke 1986 Interactions of testosterone and short photoperiod exposure on the neuroendocrine axis of the male hamster. Neuroendocrinology. 43: 69-74.

Taitt, M. J. 1981 The effects of extra food on small rodent populations: I. Deermice (Peromyscus maniculatus). J. Anim. Ecol. 50: 111-124.

Turek, F. W. and C. Campbell 1979 Photoperiodic regulation of neuroendocrine-gonadal activity. Biol. Reprod. 20: 32-50.

Turner, R. W. 1974 Mammals of the Black Hills of South Dakota. University of Kansas Museum of Natural History Publications, Manhattan, KS.

Vessey, S. H. 1987 Long-term population trends in white-footed mice and the impact of supplemental food and shelter. Amer. Zool. 27: 879-890.