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Influence of Photoperiod, Green Food, and Water Availability on Reproduction in Male California Mice *(Peromyscus californicus)*

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NELSON, R. J., D. J. GUBERNICK AND J. M. C. BLOM. *Influence of photoperiod, green food, and water availability on reproduction in male California mice (Peromyscus californicus).* PHYSIOL BEHAV **57(6)** 1175–1180, 1995.—California mice *(Peromyscus californicus)* breed primarily during the winter rainy season and generally terminate breeding during the dry summer months. This pattern of reproduction could be regulated by day length, availability of green vegetation, or water availability. The effects of photoperiod and green vegetation on reproduction were examined in Experiment 1 by housing adult male *P. californicus* either in long (LD 14:10) or short (LD 8:16) photoperiods for 10 weeks with ad lib food and water availability. A subset of animals in each photoperiod treatment group also received supplements of fresh spinach thrice weekly. The effects of water availability were examined in Experiment 2 by housing adult males in long day length conditions for 10 weeks with ad lib or restricted (50% of ad lib) water availability. Neither photoperiod nor availability of green plant food significantly affected reproductive function in male California mice, although animals in long days with green food supplements displayed elevation of some reproductive organ masses. Short days did not suppress plasma LH or prolactin levels. Male *P. californicus* provide extensive care of the young during the short days of winter. The absence of photoperiod-induced changes in prolactin levels is consistent with the observation that elevated plasma prolactin titers are associated with male parental care in this species. In contrast, water restriction (simulated summer drought) reduced reproductive organ masses, as well as plasma levels of prolactin, and may act as an environmental cue to terminate breeding. Thus, water availability may regulate breeding in this species independently of photoperiod and food availability.

Seasonal cycles Photoperiodism Testis function Prolactin Breeding cycles Water intake Luteinizing hormone

PHOTOPERIOD is an environmental factor employed by many individuals of nontropical rodent species to restrict breeding to a particular season of the year (2,24). All rodent species thus far studied have been categorized as "long-day" breeders; that is, rodents breed when day lengths are greater than those during the equinox (5). Other mammals, particularly ungulates, are considered "short-day" breeders because their mating activities are stimulated or maintained by day lengths that are generally less than 12 h of light per day.

The California mouse *(Peromyscus californicus)* differs from most other nontropical rodent species because it breeds during the short days of winter. *Peromyscus californicus* is found in chaparral, sage scrub, and oak-woodland habitats from San Francisco Bay south to the Baja California peninsula in western North America (10,15); this species tends to be abundant in mesic environments (15). Throughout their range, California mice breed primarily during the rainy season from November to May (10,21), which also coincides with new vegetative plant growth and relatively low ambient temperatures.

Reproduction coincident with the short day lengths of the California winter is consistent with several hypotheses: (a) these rodents may be short day breeders; that is, their reproductive systems are stimulated or maintained by short photoperiods; (b) *P. californicus* may be typical long-day breeders when examined in the lab, but in the field, some other environmental factor, such as food or water availability, overrides the inhibitory effects of short day lengths; and (c) these mice may not be reproductively responsive to day length and some other factor(s) regulates their seasonal breeding.

One of the physiological sequelae to chronic maintenance in short photoperiods common to both long- and short-day breeders is a significant reduction in blood plasma levels of prolactin (5). Prolactin has been associated with maternal behavior in many species (19); however, prolactin levels are insufficient to support

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maternal behavior in Syrian hamsters *(Mesocricetus auratus)* maintained in short days (20). Short-day induced reductions in plasma prolactin levels would seem inconsistent with observed parental behavior in *P. californicus* because these mice normally breed during the short days of winter. Prolactin is associated with the maintenance of paternal behavior in *P. californicus*; fathers have higher levels of plasma prolactin than nonfathers (7). Thus, blood plasma prolactin titers might be expected to be elevated in *P. californicus* exposed to short day lengths. However, the vast majority of research suggests that plasma prolactin levels should be depressed by short day exposure and that some other environmental factor, such as the availability of green food or water, overrides the photoperiod-induced suppression of prolactin. A factorial analysis of photoperiod, green food, and water availability will allow assessment of the role of each environmental factor alone and in combination with others in regulating reproduction in *P. californicus.*

If the reproductive system of *P. californicus* is stimulated by short day lengths, then mice in short days will have functional reproductive systems. Mice in long days should display regressed reproductive systems comparable to the extent observed in the field (21). However, if breeding in this species is similar to all other nontropical rodents thus far examined and is maintained in long day lengths, then reproductive regression will occur in short day animals despite ad lib food and water availability.

Reduced water availability or green food supplements may suppress reproductive function regardless of photoperiod, indicating that the presence of one or both of these cues act to trigger breeding. Alternatively, reduced water availability or green food supplements may suppress reproductive function in only long or short days, suggesting an interactive effect among these environmental factors. Experiment 1 examines the effects of day length and green food availability on reproductive function, including blood plasma luteinizing hormone (LH) and prolactin levels. LH stimulates testosterone production and thus, indirectly, stimulates sperm production. Mice were housed either in long or short days for 10 weeks; half of the animals in each photoperiodic treatment group received fresh spinach supplements. Short days and green food availability most closely simulates the environmental conditions associated with breeding in the natural habitat of this species. Thus, animals in this experimental treatment group should have large, functional reproductive systems. Long day lengths and no green food availability closely mirrors the environmental conditions associated with the seasonal cessation of breeding in this species. Mice in this group should possess regressed, nonfunctional reproductive systems. Because the reproductive systems remained functional in all of the experimental groups in Experiment 1, a second study was designed to assess directly a third environmental factor, namely, water availability, on breeding. *P. californicus* typically do not breed during the dry summer months (15,22), and it is possible that reduced water availability causes the cessation of reproductive function. In Experiment 2 the effects of simulated drought were examined in *P. californicus* maintained in simulated California summer day lengths.

METHOD

Experiment 1

Animals. Adult, virgin male *Peromyscus californicus*, descendants of animals captured in the Santa Monica Mountains near Los Angeles, CA, were maintained in one of two environmentally controlled rooms for 10 weeks. The long-day group consisted of 14 mice housed in one room that was programmed to be illuminated for 14 h/day (LD 14:10; lights on 0600 h Eastern Standard Time (EST)), whereas the short-day group consisted of 30 animals housed in a separate room that was illuminated for 8 h/day (LD 8:16; lights on 10.00 h EST). Both environmental rooms maintained a constant temperature of 21 ± 2°C and relative humidity of 50 ± 2%. Animals were individually housed in polypropylene cages (27.8 × 7.7 × 13 cm), and food (Agway Prolab 1000; Syracuse, NY) and tap water were available ad lib. Half of the males in each photoperiodic treatment condition received thrice weekly supplements of fresh spinach (3.5 g/day).

Autopsy and determination of spermatogenesis. A blood sample was obtained under methoxyflurane anesthesia (Metofane; Pitman-Moore, Washington Crossing, NJ) from the retro-orbital sinus (23) of all males after 10 weeks in their respective photoperiodic treatment condition. Blood was centrifuged, plasma was separated, and stored frozen at −80°C until hormone assays were conducted. Animals were weighed prior to blood collection, then killed by cervical dislocation. Testes, epididymides, seminal vesicles, epididymal fat pads, and intrascapular fat pads were removed, cleaned of connective tissue, and weighed. The average age of animals at autopsy was 7 ± 0.3 months.

Paired testes (after capsules were removed) and epididymides were finely minced with iris scissors, separately transferred to an Eberbach blender, and homogenized for 30 and 45 s, respectively (4). The number of sperm-shaped cells resistant to homogenization was determined in duplicate for each homogenate. The average of these two values was used to calculate the final number of sperm per paired testes or epididymides for each male.

Fur development. To assay a nonreproductive function, fur development was assessed. Fur depth and length of underhair and guard hair were measured with calipers to the nearest 0.1 mm. Pelage density was obtained by shaving and weighing (±0.01 mg) a 1-cm^2 patch of fur obtained from the posterior dorsal surface of animals fitted with a 1-cm^2 template.

Plasma LH ELISA. Blood plasma levels of immunoreactive LH were measured by ELISA techniques using reagents obtained from the NIAMD. This ELISA has been completely validated for use in *Peromyscus* (J. M. C. Blom, L. Tamarkin, and R. J. Nelson, unpublished manuscript); inhibition curves obtained with serial dilutions of serum and pituitary homogenates were parallel to inhibition curves derived from increasing amounts of NIAMD sheep-LH-RP3. Briefly, the manner by which LH is detected is similar to that of a radioimmunoassay in that a specific amount of conjugated LH is in competition with LH either in the sample or standard for a limited number of antibody sites. In the first step of the assay, a rabbit polyclonal antibody that recognizes many epitopes on the LH molecule was adsorbed to the bottom of a well on an ELISA plate. This antibody (captured antibody) was then used to bind the conjugated as well as the unconjugated LH in the standard or sample. After washing, conjugated alkaline-phosphatase was incubated with the antibody-LH complex. After removing unbound alkaline-phosphatase, an enzyme substrate p-nitrophenyl disodium phosphate was added and converted by the alkaline-phosphatase into a colored product. The amount of color that developed per unit time is inversely proportional to the amount of LH present in the sample. Color (wavelength) was determined on a 96-well microplate reader (Biorad Model 3550; Richmond, CA). Colors of unknown samples were then compared with the colors of known standard amounts of LH, and a value for each unknown was computed in duplicate. The mean of the these two values was computed to provide an LH value for each animal.

Plasma prolactin RIA. Details of this RIA have been published previously (7,13). Briefly, blood plasma prolactin concentrations were determined in duplicate 10 μl aliquots with a double antibody RIA developed with a sensitive first antibody (rabbit) raised against deer mouse *(P. maniculatus bairdii)* prolactin (13).

TABLE 1

MEAN (±SEM) REPRODUCTIVE ORGAN MASS AND SPERM COUNTS FOR CALIFORNIA MICE HOUSED IN LONG (LD 14:10) OR SHORT (LD 8:16) PHOTOPERIODS WITH (S^+) OR WITHOUT (S^-) SPINACH SUPPLEMENTS

Group	Paired Testes Mass (mg)	Paired Epididymal Mass (mg)	Seminal Vesicles (mg)	Epididymal Sperm Count ($\times 10^6$)	Testis Sperm Count ($\times 10^6$)	Epididymal Fat Pad (mg)
LD 14:10 (S^+)	11.0 ± 0.8*	2.4 ± 0.1	2.7 ± 0.4	248.0 ± 39.1	88.9 ± 21.6*	9.6 ± 3.0
LD 14:10 (S^-)	8.5 ± 0.5	1.9 ± 0.1	1.9 ± 0.3	220.7 ± 27.4	42.3 ± 8.5	9.3 ± 2.3
LD 8:16 (S^+)	8.9 ± 0.5	1.9 ± 0.1	2.0 ± 0.3	198.7 ± 24.1	66.8 ± 10.6	7.5 ± 1.3
LD 8:16 (S^-)	10.0 ± 0.6	2.5 ± 0.2	2.4 ± 0.3	246.5 ± 27.6	114.4 ± 39.9	8.9 ± 1.3

*$p < 0.05$ when compared to mean value in same photoperiodic condition.

The second antibody was a sheep antirabbit gamma-globulin obtained from Antibodies, Inc. (Davis, CA). Final hormone concentrations are expressed as nanogram equivalents of a purified deer mouse prolactin per milliliter (ml) of California mouse blood plasma. Additional details of this RIA have been published previously (7,13).

Statistical analyses. A two-way analysis of variance (ANOVA) was used to detect differences between groups on each dependent measure. Individual pair-wise comparisons were analyzed with independent two-tailed *t*-tests. All comparisons were planned so no posthoc corrections were employed (8). The treatment effects were considered statistically significant if $p < 0.05$.

Experiment 2

Animals. A separate group of adult male virgin California mice ($n = 27$) remained housed in long day conditions (LD 16:8; lights on at 0700 h EST) at 21 ± 2°C for the entire study. Animals were housed individually in polypropylene cages (27.8 × 7.7 × 13 cm) and were provided with ad lib food (Agway Prolab 1000; Syracuse, NY) and tap water. Individual daily water consumption measurements were recorded for these animals over 10 days and the mean water intake was calculated. Nine males continued to receive ad lib water throughout the study, whereas daily water availability was reduced by 50% for the remaining 18 mice. Animals were examined at necropsy after 10 weeks of their respective experimental treatment. The average age of the male mice at the end of the study was 6 ± 0.3 months.

A blood sample was obtained via the retro-orbital sinus (23) prior to lethal injection of sodium pentobarbital, and blood plasma levels of LH and prolactin were assayed as in Experiment 1. Body mass, as well as reproductive organ and nonreproductive tissue masses (i.e., paired testes, paired epididymides, seminal vesicles, epididymal fat pads, and intrascapular brown fat pads), were recorded. Spermatogenic activity was determined by the method described in Experiment 1. The number of sperm per paired testes or epididymides was calculated as above. Fur characteristics were not obtained in Experiment 2.

TABLE 2

MEAN (±SEM) BODY MASS, BROWN FAT MASS, METABOLIC RATE, AND FUR PARAMETERS FOR CALIFORNIA MICE. SYMBOLS AND OTHER CONVENTIONS AS IN TABLE 1

Group	Body Mass (g)	Intrascapsular Brown Fat Pad Mass (mg)	Pelage Density (mg/cm^2)	Pelage Depth (mm)
LD 14:10 (S^+)	53.2 ± 3.2	6.5 ± 1.4	1.66 ± 0.02	5.8 ± 0.3
LD 14:10 (S^-)	52.5 ± 1.8	6.1 ± 0.7	2.85 ± 0.03*	5.8 ± 0.3
LD 8:16 (S^+)	51.9 ± 1.7	6.3 ± 1.0	1.64 ± 0.02	4.9 ± 0.2
LD 8:16 (S^-)	51.8 ± 1.8	5.2 ± 0.5	1.86 ± 0.02	5.2 ± 0.1

* $p < 0.05$ when compared to mean value in same photoperiodic condition.

RESULTS

Experiment 1

Paired testes, epididymides, seminal vesicles, epididymal white or intrascapular brown fat depots (absolute or adjusted for body mass), testicular or epididymal sperm numbers, pelage development, and body mass of long-day and short-day males did not differ (Tables 1 and 2) ($p > 0.05$ in each case). There was also no main effect of green food supplements on reproductive organ size or function, body mass, or development of fur (Tables 1 and 2).

However, in some cases, spinach availability interacted with long days. Long-day mice with access to green supplements had larger testes ($p < 0.01$) and epididymides ($p = 0.055$) than long-day males without spinach (Table 1). Spinach did not affect reproductive organ mass in short-day males ($p > 0.05$; Table 1), but long-day mice lacking spinach supplements had significantly reduced testicular sperm counts ($p < 0.05$). Supplemental green food seemed to suppress fur development in long-day, but not short-day mice ($p < 0.05$; Table 2). Blood plasma prolactin concentrations were unaffected by day length or spinach availability ($p > 0.05$; Fig. 1). In contrast, plasma LH titers were elevated in short-day males as compared to long-day males whether green food was available or not ($p < 0.01$; Fig. 1). The plasma LH levels of long-day and short-day males did not change significantly with spinach supplements ($p > 0.05$; Fig. 1).

Experiment 2

Reduced water availability significantly impaired the size of some reproductive organs in male California mice. Paired epi-

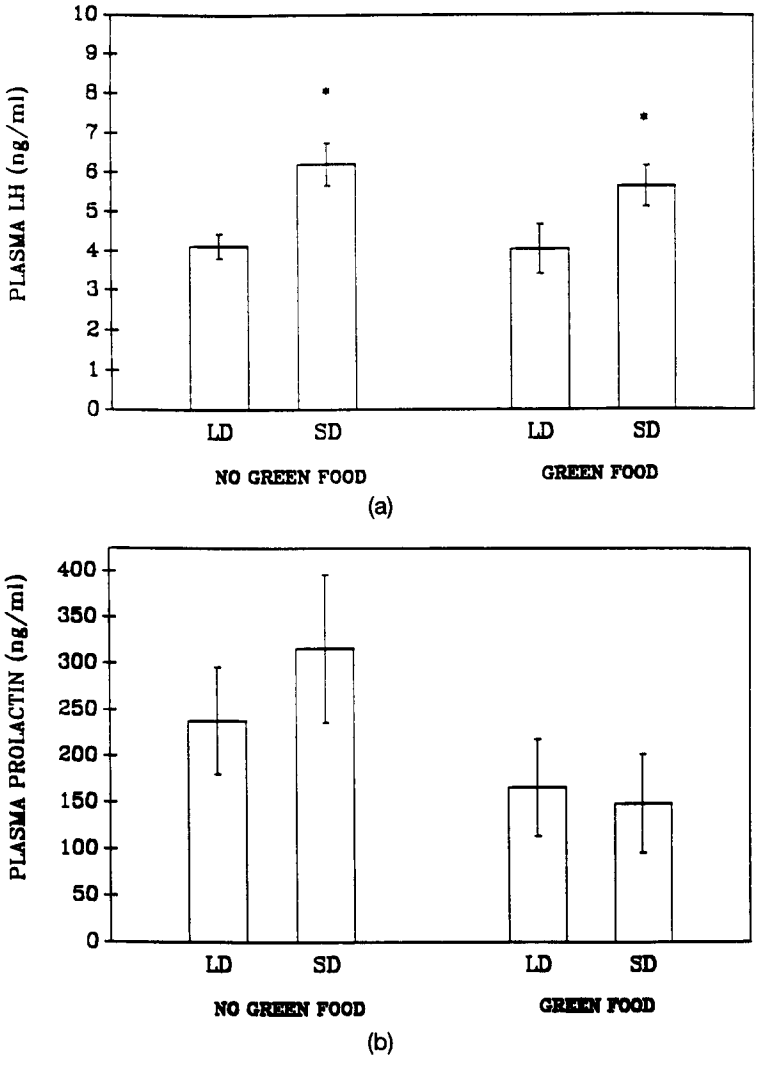

FIG. 1. (a) Mean (± SEM) blood plasma luteinizing hormone (LH) levels (ng/ml) in male California mice housed in long (LD)(LD 14:10) or short (SD) (LD 8:16) days. Animals in each photoperiodic condition were either supplemented or not supplemented with thrice weekly rations of spinach. Asterisks indicate significant differences in LH levels between long day and short day animals. (b) Mean (± SEM) blood plasma prolactin levels (ng/ml) in male California mice housed in long (LD) or short (SD) days. Other symbols and conventions as above.

didymides and seminal vesicle masses were significantly reduced in water restricted mice ($p < 0.05$ in each case; Table 3). Reduced water consumption did not suppress body mass or paired testes mass ($p > 0.05$; Table 3). Neither testicular nor epididymal sperm numbers were affected by water restriction ($p > 0.05$; Table 3).

TABLE 3

MEAN (±SEM) REPRODUCTIVE ORGAN MASS, BROWN FAT MASS, AND SPERM COUNTS FOR CALIFORNIA MICE MAINTAINED IN LONG DAYS WITH AD LIB OR RESTRICTED WATER AVAILABILITY

	Body Mass (g)	Paired Testes Mass (mg)	Paired Epididymal Mass (mg)	Seminal Vesicles Mass (mg)	Epididymal Sperm Count ($\times 10^6$)	Testis Sperm Count ($\times 10^6$)	Epididymal Fat Pad Mass (mg)	Brown Fat Mass (mg)
Restricted Water	41.8 ± 1.9	8.3 ± 0.6	0.9 ± 0.2*	1.7 ± 0.4*	291 ± 25.0	74 ± 20.0	8.3 ± 1.0	6.4 ± 0.9
Ad Lib Water	46.0 ± 2.5	9.4 ± 1.4	3.2 ± 0.5	3.9 ± 0.8	264 ± 15.2	97 ± 5.4	11.3 ± 1.9	7.7 ± 1.4

*$p < 0.05$.

Limited water availability also did not inhibit blood plasma LH titers ($p > 0.05$; Fig. 2). However, plasma prolactin concentrations were significantly reduced by water restriction ($p < 0.01$; Fig. 2).

DISCUSSION

Exposure either to short or long day lengths did not inhibit reproductive function in male *P. californicus*. Animals in long or short photoperiod conditions had equivalent reproductive organ masses and plasma prolactin concentrations, as well as body masses, fat depot masses, and pelage development. Availability of green food also did not substantially affect reproductive function. Although fecundity was not assessed directly in the present study, sperm counts were generally equivalent among the treatment groups and were consistent with fertility in all animals (4). Blood plasma levels of LH were elevated in short day length conditions, but neither plasma LH nor prolactin concentrations were affected by the availability of green food. In contrast to photoperiod and green food availability, water availability significantly affected reproductive function. Reduced water availability decreased epididymal and seminal vesicle masses. Water restriction did not affect body mass, paired testes mass, spermatogenic activity, or plasma LH titers, but reduced water availability did reduce plasma prolactin levels.

The reduction of ad lib water availability by half did not affect body mass and did not appear to affect pelage quality or the general health of the mice. This indicates that water availability acts as a specific cue affecting reproductive function and that reproductive regression in *P. californicus* is not a generalized reaction to the stress of water restriction. The extent of water restriction among these animals during the annual summer drought in their natural habitats is unknown. However, other species living in similar habitats reduce water intake by 70–90% during the dry California summer (reviewed in 12).

Short days did not cause reproductive regression in male *P. californicus*. Thus, the regulation of seasonal breeding in this species differs from the California vole *(Microtus californicus)*, which also displays a similar pattern of winter breeding during short day lengths. Male California voles regress reproductive

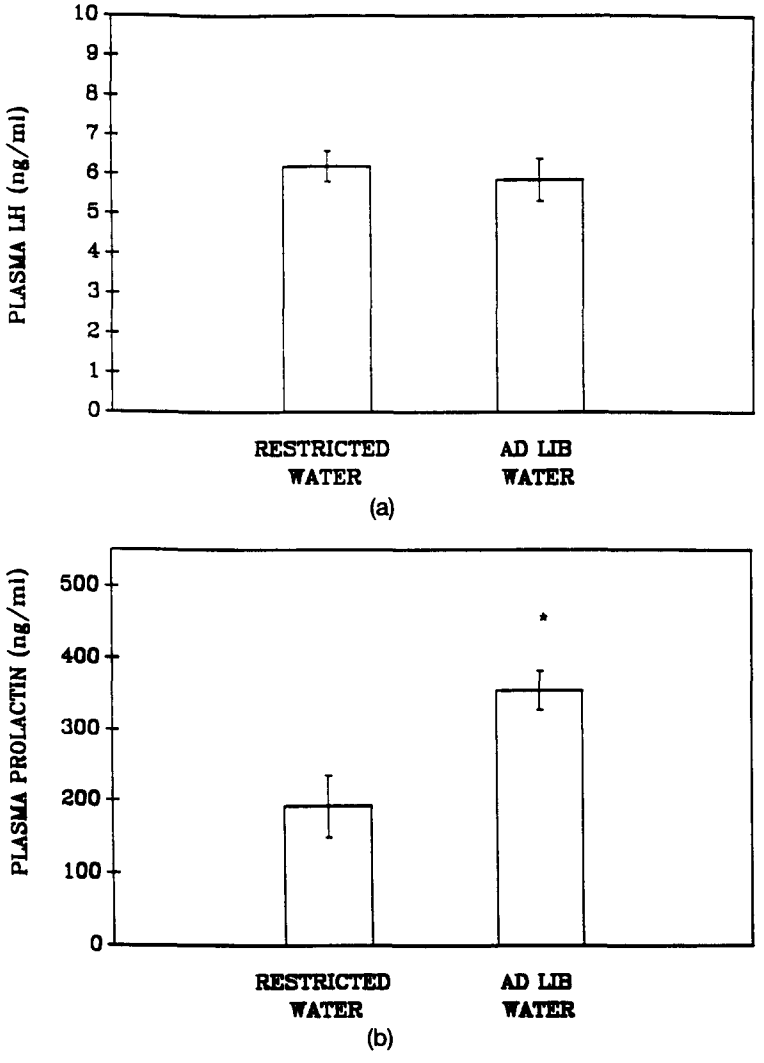

FIG. 2. (a) Mean (± SEM) blood plasma LH levels (ng/ml) in male California mice maintained in long day conditions with restricted or ad lib access to water. (b) Mean (± SEM) blood plasma prolactin levels (ng/ml) in male California mice maintained in long day conditions with restricted or ad lib access to water. Other symbols and conventions as in Fig. 1.

function when housed in short day lengths in the laboratory, but the availability of spinach overrides the photoperiod-induced reproductive regression (18). Water restriction under long day conditions inhibits reproductive function in California voles. Thus, the breeding season in nature is regulated by food and water availability (18). As revealed in laboratory studies, California voles are typical long-day breeders and respond to short days with reproductive regression; the winter availability of green vegetation apparently overrides short-day induced regression. Breeding is normally turned off by lack of potable water during the summer. Supplemental water availability can stimulate reproduction during the summer breeding hiatus in this species (9).

P. californicus is neither a typical long-day breeder nor a typical short-day breeder. The present data suggest that the maintenance of reproductive function in *P. californicus* has been uncoupled from photoperiodic regulation. The lack of photoperiodic effect on fur development in *P. californicus* also suggests that these animals are not responsive to day length in general. Exposure to short days reduces blood prolactin concentrations in all species examined (5). Thus, the lack of effect of short days on prolactin secretion in *P. californicus* further suggests that these mice may not be responsive to short day lengths.

However, the elevation of plasma LH among short-day mice raises the possibility that short days are stimulatory to reproductive function. It is possible that reproduction in this species is stimulated by short days, but similar to stallions (5), neither prolonged short-day nor long-day exposure would inhibit reproductive competence. Rather, some other factor would serve to end the breeding season. In this study, water restriction compromised reproductive function of *P. californicus*. Thus, reduced water availability coincident with the annual summer drought could terminate the breeding season of *P. californicus*. This organization and environmental regulation of the breeding season would be unique among temperate zone rodents thus far examined (3).

One of the issues that motivated this study was to understand how breeding could occur during the short days of winter. *P. californicus* provides substantial parental care to the young (6). Male parental care is associated with elevated prolactin levels (7). Because short day lengths inhibit prolactin concentrations in all other rodent species examined (5), the maintenance of parental behavior in short days was enigmatic. The present data reveal that prolactin levels are not suppressed in short days, but only after water restriction, a finding that is consistent with the natural breeding season. Whether water restriction directly affects male parental care of young remains to be determined. Water availability is an important environmental factor mediating reproduction (2), and is used as a specific cue to time breeding in several rodent species including *M. californicus* (18), *Mus musculus* (16), and *P. maniculatus* (17).

In summary, neither long nor short day lengths inhibit breeding in adult male *P. californicus*. The lack of green plant food does not inhibit reproductive function regardless of photoperiod. It is possible that short days stimulate breeding, but further experiments that examine reproductive responses to transitory photoperiods are required to assess this possibility. Restricted water availability significantly inhibits reproductive function in the laboratory, and may serve as an important cue in nature to suppress reproduction in male *P. californicus* during the annual summer drought.

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