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Social, but Not Photoperiodic, Influences on Reproductive Function in Male *Peromyscus aztecus*[1]

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ABSTRACT

Nontropical rodents rely on environmental factors to restrict breeding to a specific time of the year. Among these factors, photoperiod appears to be the primary environmental cue used for predicting optimal breeding conditions. The purpose of the present study was to characterize reproductive function, as well as photoperiodic and social responsiveness in male *Peromyscus aztecus*, which occupy low-latitude, high-altitude habitats. In experiment 1, adult male *P. aztecus* were individually housed in either long (16L:8D) or short days (8L:16D) for 10 wk. Short-day mice did not differ from long-day mice on any reproductive or nonreproductive parameter. Comparisons to related *Peromyscus* species suggested that relative reproductive organ size and function were reduced in both long- and short-day males. Because ad libitum food and water were available, we reasoned that males in both photoperiodic conditions lacked social stimuli. To test this hypothesis, adult male *P. aztecus* were housed in long days either individually or with a female conspecific in experiment 2. Mice housed with females had significantly larger relative paired testes and epididymal masses, and higher testicular sperm counts and serum testosterone levels compared to those of individually housed mice. Taken together, these results suggest that social factors may play a more prominent role than photoperiod in stimulating reproductive development in laboratory-housed *P. aztecus*. These results are consistent with the results found for other low-latitude rodent species and suggest that *P. aztecus* uses a flexible rather than obligatory breeding strategy.

INTRODUCTION

Individuals of many nontropical rodent species rely on environmental cues to restrict breeding to a specific time of the year. Among these factors, daily photoperiod (day length) provides a precise temporal cue to estimate the time of year [1]. Photoperiodic information (i.e, change in day length across the year) is used to phase energetically demanding activities to coincide with adequate energy availability. Day length has been reported to be the most commonly used environmental cue for predicting optimal breeding conditions among nontropical mammals [2–4]. However, most species of rodents live in the tropics, where photoperiodic information is less useful as a predictive cue [3]. Although some tropical mammals respond reproductively to changes in day length [5–8], others show little or no reproductive response to photoperiod [9, 10]. For example, males of a tropical *Peromyscus* species, cloud forest mice (*Peromyscus nudipes*), display slight seasonal changes in testes and epididymal mass during the dry season in Costa Rica; however, epididymal sperm counts remain high throughout the year [9]. When examined in the laboratory, individuals of this species fail to display any photoperiodic changes in reproductive morphology [9].

Photoperiodic responsiveness varies both between and within species. Individuals within the genus *Peromyscus* display a range of reproductive responsiveness to photoperiod depending on their latitude of origin [3, 4, 11, 12]. For example, a higher proportion of white-footed mice (*P. leucopus*) inhabiting high latitudes have inhibited reproduction in short days than do mice from low latitudes [3]. A likely functional explanation for this phenomenon is that individuals inhabiting high latitudes are faced with longer, more severe winters than mice inhabiting low latitudes, placing a premium on precise timing of behavioral, physiological, and morphological adaptations at higher latitudes. Development of winter-coping strategies is less critical in low-latitude mice because they typically experience mild winters that can support year-round breeding [1].

Male *P. californicus*, a low-latitude *Peromyscus* species, also breed seasonally, restricting breeding to the short days of the California winter, a time coincident with the rainy season from November to May [13]. In this species, breeding is coincident with new plant growth. However, in controlled laboratory settings with ad libitum access to food and water, *P. californicus* do not inhibit reproductive function in either short or long days [14]. Thus, reproductive function can be uncoupled from photoperiodic regulation in *P. californicus*.

P. aztecus is another *Peromyscus* species inhabiting low latitudes; however, the extent of seasonal breeding or reproductive responsiveness to photoperiod has yet to be determined for this species. The range of *P. aztecus* is restricted to below 20°N latitude. *P. aztecus* inhabit the humid, mountainous regions of southeastern Mexico through the highlands of Guatemala to Honduras and northern El Salvador [15]. Traditional taxonomic classification has placed *P. aztecus* as a subspecies of brush mice (*P. boylii*) [16]. *P. boylii* populations are typically large but tend to fluctuate seasonally, with a peak in late summer and a nadir in late winter or spring [17]. Wild brush mice, in common with other *Peromyscus* species, may cease reproductive activities during the winter or during other times of unfavorable environmental conditions [17]; however, this remains to be determined. In captivity, female brush mice are polyestrous with an estrous cycle lasting ~5 days [17]. To our knowledge, no studies have been published investigating the regulation of reproduction in *P. boylii*.

Within the past 30–40 yr, *P. aztecus* has become recognized as a species distinct from *P. boylii* [18–20]. However, despite their use as an experimental animal, virtually no data exist regarding reproductive physiology in *P. aztecus*. For example, it is not known whether these animals display seasonal patterns in reproductive function (e.g., *P. maniculatus, P. californicus*) or, alternatively, exhibit year-

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round breeding in the wild. Thus, the present study provides the first characterization of the effects of photoperiod on reproductive function in male *P. aztecus* in the laboratory. Because *P. aztecus* occupy low latitudes, we predicted that a high proportion of individuals within this species should be reproductively unresponsive to photoperiod.

Our results indicated that photoperiod had no effect on reproductive parameters in *P. aztecus*. Despite the lack of a photoperiodic effect on gonadal size or sperm counts in experiment 1, it was observed that the relative reproductive organ masses and sperm counts in *P. aztecus* were considerably lower than values typically reported for other *Peromyscus* species under similar conditions [14, 21, 22]. For example, relative testes masses and testicular sperm counts were roughly half of the values reported for *P. maniculatus* maintained in long days and mild ambient temperatures in the laboratory [22]. Compared to California mice (*P. californicus*), *P. aztecus* had ~40% smaller relative seminal vesicles, as well as ~30% lower sperm counts [14]. Because *P. aztecus* were maintained in constant laboratory conditions with ad libitum food and water, we reasoned that individual males in both photoperiodic conditions may have lacked social cues, which can be critical for the onset of reproduction. To test this hypothesis, adult male *P. aztecus* were housed in long days with or without the presence of a female conspecific in experiment 2. If social cues from females are important for stimulating reproductive development in *P. aztecus*, then animals housed with a female should have larger reproductive organ masses, as well as higher testosterone concentrations and sperm counts.

MATERIALS AND METHODS

Experiment 1

Twenty adult (> 60 days of age) male *Peromyscus aztecus* were obtained directly from the Peromyscus Genetic Stock Center at the University of South Carolina, Columbia, SC. These animals are descendants of animals originally trapped near Michoacan, Mexico (latitude, 20.0°N). The colony was established in 1986, and there have been approximately 10 generations bred in captivity (W. Dawson, personal communication). Animals were individually housed in polypropylene cages (27.8 × 7.5 × 13.0 cm) in a colony room with a 24-h 16L:8D light cycle (lights-on 0600 h Eastern Standard Time [EST]). Temperature was kept constant at 20 ± 1°C, and relative humidity was maintained at 50 ± 5%. Food (Agway Prolab 1000, Syracuse, NY) and tap water were provided ad libitum throughout the experiment.

Mice were randomly divided into one of two photoperiodic conditions. Half of the animals (n = 10) were housed in a short-day photoperiod (8L:16D), while the other half (n = 10) were housed in long days (16L:8D). Animals were maintained in their respective photoperiodic conditions for 10 wk. At the end of this time they were brought into the surgery room and lightly anesthetized with methoxyflurane vapors, and a blood sample was collected from the retroorbital sinus. Animals were then killed by cervical dislocation, and paired testes and epididymides, seminal vesicles, epididymal white adipose tissue (EWAT), and intrascapular brown adipose tissue (BAT) were removed and cleaned of connective tissue. Seminal vesicles were compressed with a glass vial to remove seminal fluid. All organs and fat pads were weighed by laboratory assistants who were uninformed of the treatment assignments. Tissue masses were corrected for total body mass, and both absolute and relative masses were used in all subsequent statistical analyses.

Fur development was assessed as an index of a photoperiod-dependent nonreproductive function [21]. Fur depth was measured with hand-held calipers to the nearest 0.1 mm. Pelage density was determined by shaving and weighing a 1-cm^2 patch of fur taken from the posterior dorsal surface of mice fitted with a 1-cm^2 template.

Capsules were removed from paired testes and finely chopped with iris scissors. Testes were then transferred to an Eberbach blender (Waring; New Harford, CT) and homogenized for 30 sec with sperm grinding solution [21]. The number of sperm-shaped cells resistant to homogenization was determined in duplicate for each homogenate, using a hemocytometer. The mean of the two values was used to calculate the final number of sperm per paired testes for each experimental animal.

Serum testosterone concentrations were determined by RIA with the use of a ^{125}I kit (ICN Biomedicals, Carson, CA). All instructions furnished by ICN were followed. Each sample was assayed in duplicate. The testosterone assay was highly specific; cross-reactions with other androgenic hormones were less than 0.3%. Serum testosterone values were determined in a single RIA for each experiment. The sensitivity of the assay was 0.1 ng/ml.

Experiment 2

Male *P. aztecus* (n = 12) were randomly assigned to one of two housing conditions. Half of the animals were paired with a female for 8 days while the other half remained individually housed. All animals were maintained on long days (16L:8D). Six stimulus female *P. aztecus* (> 60 days of age) with no prior mating experience were purchased from the Peromyscus Genetic Stock Center and individually housed for 7 days before being paired with a male. On Day 8 after pairing, a blood sample was taken from male mice; mice were then killed, and reproductive organs and fat pads were removed, cleaned of connective tissue, and weighed. Sperm counts and serum testosterone concentrations were determined as in experiment 1. Females were examined daily beginning 21 days after onset of pairing. The incidence of pregnancy, number of young born, and initial pup size were recorded.

Statistical Analyses

Reproductive organ and fat pad masses, serum testosterone levels, sperm numbers, and pelage measurements were analyzed by independent Student's *t*-tests (SigmaStat; Jandel Scientific, San Rafael, CA). Serum samples below the sensitivity of the testosterone assay were recorded as 0.1 ng/ml for purposes of statistical analyses. Differences between groups were considered statistically significant at $p < 0.05$.

RESULTS

Experiment 1

Photoperiod did not affect any reproductive parameter in male *P. aztecus*. There were no differences in absolute or relative reproductive organ masses between long- and short-day *P. aztecus*. Body mass, absolute and relative paired testes and epididymides, seminal vesicles, and testicular sperm counts did not differ between long and short days ($p > 0.05$ in all cases; Fig. 1 and Table 1). There were no significant differences in either EWAT or BAT between

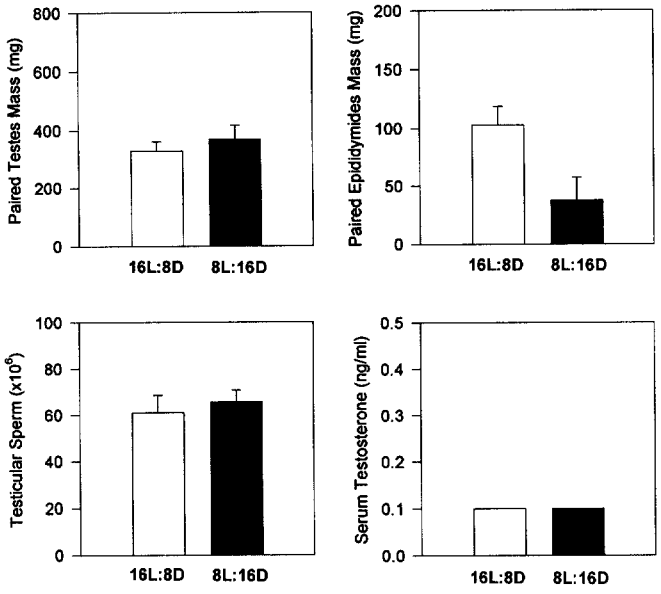

FIG. 1. Mean (± SEM) reproductive organ masses of male *P. aztecus* housed in long (16L:8D) or short (8L:16D) days.

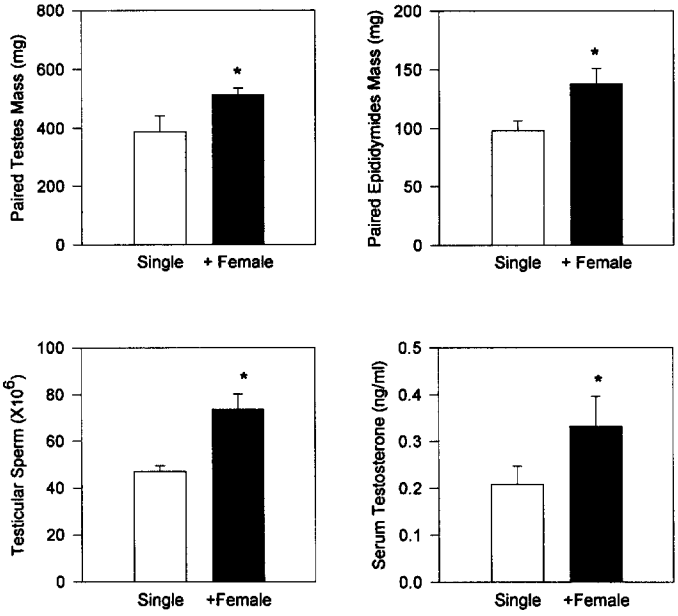

FIG. 2. Mean (± SEM) reproductive organ masses of male *P. aztecus* housed individually or paired with a female.

experimental groups ($p > 0.05$ in both cases; Table 1). Long- and short-day animals did not differ in pelage depth or density ($p > 0.05$ in both cases; Table 1). Serum testosterone levels were below the lower limit of detectability of 0.1 ng/ml for all mouse samples.

Experiment 2

Male *P. aztecus* housed with females had significantly larger relative paired testes and epididymides, seminal vesicles, serum testosterone concentrations, and testicular sperm counts than did mice housed alone ($p < 0.05$ in all cases; Fig. 2 and Table 2). Housing conditions did not affect EWAT or BAT ($p > 0.05$ in both cases). Two to four days of exposure to a female were required before male *P. aztecus* mated. Differences in reproductive organ size and function did not appear to translate into obvious differences in fertility. Among the female *P. aztecus* paired with males, 83.3% mated and became pregnant; The length of gestation was 21–22 days, the average litter size was 2.6 ± 0.4, and the initial pup body mass averaged 2.8 ± 0.1 g.

DISCUSSION

Individuals of *P. aztecus* appear to be nonresponsive to photoperiod in the laboratory. There were no significant differences in any reproductive or nonreproductive parameter between animals housed in either long or short days in experiment 1. However, relative reproductive organ size and function appeared reduced in both long- and short-day males when compared to related *Peromyscus* species. Individually housed males, although provided with ad libitum food and water, apparently lack social stimulation provided by the presence of females that may enhance reproductive development in male *P. aztecus*. Males housed with a female conspecific for 10 days mated within 2–4 days and displayed larger relative testes and epididymides, as well as higher sperm counts and serum testosterone values at autopsy compared to individually housed mice. These results suggest that social factors play a more prominent role than photoperiod in the regulation of reproductive function in *P. aztecus*. Specifically, the presence of a female can stimulate gonadal growth as well as increase steroidogenesis and spermatogenesis in males of this species. These results support and extend previous findings that demonstrated increased gonadal development in *Peromyscus* in the presence of females.

In many rodent species, seasonal patterns in reproduction may be entrained by photoperiod; short days signal the presence of winter and cause gonadal regression, while long days indicate spring and summer and stimulate gonadal recrudescence [3]. Alternatively, reproduction may be the result of an opportunistic strategy according to which breeding occurs only in the presence of an optimal climate and abundant food regardless of day length [23]. Previous research has demonstrated that photoperiodic responsiveness

TABLE 1. Mean (± SEM) body, reproductive, and fat masses and pelage parameters in male *P. aztecus* housed in 16L:8D or 8L:16D.

Parameter	16L:8D	8L:16D
Body mass (g)	40.90 ± 1.44	44.37 ± 1.42
Relative paired testes (mg/g)	7.97 ± 0.76	8.29 ± 0.11
Relative paired epididymides (mg/g)	2.43 ± 0.38	3.00 ± 0.035
Relative seminal vesicles (mg/g)	0.49 ± 0.05	1.40 ± 0.40
EWAT (mg)	100.00 ± 8.0	115.0 ± 07.0
BAT (mg)	154.5 ± 12.0	156.7 ± 31.4
Fur depth (mm)	17.48 ± 2.15	17.68 ± 1.33
Fur density (g)	0.05 ± 0.01	0.03 ± 0.01

TABLE 2. Mean (± SEM) body, reproductive, and fat pad masses in male *P. aztecus* housed individually or with a female conspecific.

Parameter	Single	+ Female
Body mass (g)	40.27 ± 1.62	43.25 ± 0.74
Relative paired testes (mg/g)	9.46 ± 1.13	11.94 ± 0.64
Relative paired epididymides (mg/g)	2.42 ± 0.15	3.19 ± 0.30
Relative seminal vesicles (mg/g)	2.90 ± 0.25	3.31 ± 0.67
EWAT (mg)	202.0 ± 23.9	206.0 ± 32.2
BAT (mg)	166.0 ± 24.9	176.0 ± 13.4

decreases with decreasing latitude (reviewed in [3]). Generally, rodent species inhabiting low latitudes (i.e., below 10°N) stop responding to day length as a reproductive cue, whereas populations of high-latitude animals (i.e., above 10°N) display varying degrees of photoperiodic responsiveness [23]. The present results add further support to this pattern. Unlike individuals of high latitude *Peromyscus* species, *P. aztecus* do not appear to rely on changes in day length to regulate reproductive function. Photoperiodic responsiveness may be less critical for *P. aztecus* because they naturally experience the mild winters typical of southeastern Mexico, which may be conducive to year-round breeding.

P. aztecus examined in the present study were maintained under standard laboratory conditions with ad libitum food and water, and mild ambient temperatures. It is possible that these controlled conditions masked any degree of photoperiodic responsiveness that may be present in the wild. For example, individuals of *P. californicus* display seasonal patterns in reproduction in the wild, but fail to respond to photoperiod in a laboratory setting [14]. Furthermore, photoperiodic effects were tested under two constant photoperiods; it is possible that *P. aztecus* require a more natural pattern of changing day length (i.e., gradually increasing or decreasing photoperiods) to affect reproductive status. Gradually changing photoperiods can differentially affect reproductive development relative to abrupt changes in day length [24]. Alternatively, photoperiodic responsiveness may have been lost by unintentional selection against this characteristic at the Peromyscus Genetic Stock Center. Although the colony has only been in captivity for approximately 10 generations, photoperiodic unresponsiveness in *Peromyscus* species can be selected for in only two generations [25]. Field studies of breeding patterns in *P. aztecus* should be conducted to address these issues.

Males of several rodent species display increased gonadal development in the presence of conspecifics of the opposite sex [26–28]. Consistent with this idea, the presence of a female conspecific increases both paired testes and epididymal masses in deer mice (*P. maniculatus*) and can override the inhibitory effects of short days on reproduction [27]. Deer mice maintained in short days with a female had significantly larger testes than did individually housed deer mice [26]. In fact, by 5 mo of age, testis size in these animals was indistinguishable from that of animals maintained on long days. Similar results have been demonstrated in hopping mice (*Notomys alexis*) [28] and golden hamsters (*Mesocricetus auratus*) [29]. The increases in reproductive organ mass, sperm counts, and testosterone concentrations are consistent with the present findings.

It is important to note that male *P. aztecus* in the present study mated shortly after initial pairing with a female; additionally, sperm counts in individually housed mice, although below those of mice paired with females, were above the levels typically reported for infertile mice [22]. Thus, individually housed animals appear to maintain reproductive function in the absence of females. Exposure to females increases reproductive parameters above the levels seen in individually housed mice. Additional parametric studies are required to isolate the contributions of several other extrinsic factors (e.g., availability of food and water) to the regulation of reproduction in this species. Although increases in reproductive organ mass have traditionally been used by reproductive biologists as an index of reproductive function [1, 21, 30], the extent to which these results reflect changes in reproductive success in *P. aztecus* remains an important empirical question.

An alternative hypothesis to explain the enhanced reproductive development in male mice paired with females is that the smaller reproductive parameters in individually housed *P. aztecus* represent the "stress of isolation," which suppressed reproductive function. Highly social rodents, including prairie voles (*Microtus ochrogaster*), live in extended family groups and engage in social bonding [31, 32]. When prairie voles are individually housed, the hypothalamo-pituitary-adrenal (HPA) axis is activated and corticosterone is released, a traditional indicator of stress; no similar activation of the HPA axis is seen in voles housed with conspecifics [33]. Stress-induced corticosterone secretion can, in turn, suppress reproductive physiology [34, 35]. The degree of sociality is not established for *P. aztecus*; however, it has been noted that individuals of *P. aztecus* are "rather tolerant of one another," with several individuals occupying the same nest [17]. It is possible that the smaller reproductive parameters in individually housed *P. aztecus* are due to isolation stress-induced activation of the HPA axis. Future studies need to be conducted to determine the role of the HPA axis and specifically corticosterone responses in reproductive function in *P. aztecus*.

The results of the present study suggest that individuals of *P. aztecus* are reproductively unresponsive to photoperiod in the laboratory. However, the presence of females can stimulate increased reproductive function in long-day males. It remains unspecified what effect the presence of a female has on the reproductive physiology of *P. aztecus* maintained in short days. Taken together, these results suggest that *P. aztecus* engage in flexible breeding in the wild, with the presence of fertile females acting as an extrinsic factor capable of stimulating increased reproductive function, presumably at times when other environmental cues such as food and water are abundant. However, these results should be interpreted cautiously until adequate field studies are conducted in this species.

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