POTENTIAL AND REALIZED REPRODUCTION IN A TROPICAL POPULATION OF *PEROMYSCUS* (RODENTIA)

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Data from a laboratory colony of *Peromyscus nudipes* founded with individuals trapped at 10°N latitude near Monteverde, Costa Rica, were compared with published and new data on the same population in the wild as a basis for assessing phenotypic plasticity in life-history characteristics. Mean litter size was almost identical in the wild and in the laboratory (2.8 ± 0.1 and 2.9 ± 0.2, respectively). In the laboratory, females matured at 6-8 weeks of age and males had matured by ca. 9-11 weeks of age. The available evidence suggests that first reproduction is delayed in the wild relative to the laboratory. The frequency with which litters were produced was much higher in the laboratory than in the wild. Females averaged 7.4 ± 0.8 litters/year in the laboratory, with a maximum of 11 litters/year, whereas females in the wild produced no more than 5 litters/year and may average about one-half that many. These results suggest that phenotypic plasticity in age at first reproduction and reproductive rate is high. In the wild, these mice evidently realize only a small fraction of their reproductive potential. The difference apparently is due to delay of first reproduction and less-frequent production of litters in the wild, and not to differences in litter size or the frequency of ovulation, mating, and conception.

Key words: ***Peromyscus nudipes,*** **reproduction, life-history, breeding, growth, tropical, Costa Rica**

The broad array of comparative and experimental research on the rodent genus *Peromyscus* has played a vital role in developing an understanding of the evolution of reproductive strategies in mammals (Bronson, 1989; Glazier, 1980; Layne, 1968; Millar, 1989; Modi, 1984; Myers and Master, 1983). Reproductive tactics of this genus are well known (e.g., Millar, 1989), but there are two notable gaps. First, few studies relate data from a wild population to data from laboratory stocks derived from that wild population (Millar, 1989). The comparison of data arising from both field and laboratory implicitly assumes that phenotypic plasticity is inconsequential. Because laboratory conditions vary so dramatically from field conditions, particularly in the provision of unlimited food and water, characteristics that are phenotypically plastic may change under laboratory conditions (Millar, 1989). Thus, laboratory conditions can provide misleading estimates of phenotypically plastic life-history characteristics of the wild source population. Recent work on life history strategies has emphasized the importance of phenotypic plasticity in characteristics such as litter size and frequency of reproduction, and suggests that some of the variation observed among populations may be better interpreted as phenotypic plasticity rather than as genetic differentiation (Boyce, 1988; Dobson, 1988). Second, although *Peromyscus* is one of the few rodent genera whose distribution extends from near the Arctic Circle to the tropics, comparatively few data have been obtained from tropical populations of this genus (Lackey, 1976, 1978; Olivera et al., 1986; Rickart, 1977), or from tropical mammals in general (Bronson, 1989).

Our major objective was to test the hy-

pothesis that there is no phenotypic plasticity in several life-history characteristics that could be estimated for a population of *Peromyscus nudipes* both in the laboratory and in the field. Because many studies use laboratory-raised mice to determine life-history characteristics, a second objective was to compare the reproductive performance of wild-caught females with laboratory-born females. We combine these results with additional observations on the growth, development, and reproduction of *P. nudipes* in the laboratory to develop a better description of the reproductive strategy of these mice. Of particular interest is a comparison of the reproductive potential of these animals in the laboratory, where food and energy are not limited, with their realized reproduction in the wild.

Our data were obtained from a population of the cloud forest mouse, *P. nudipes*, from Monteverde, Costa Rica. This population is of interest for two reasons. First, it is located at 10° N latitude, near the southern limit of the broad geographic range of this genus. Second, a dissertation by Anderson (1982), provides a considerable amount of information on reproductive characteristics of this population in the wild, which has been supplemented by Heideman and Bronson (1992).

Methods

Peromyscus nudipes was captured using Sherman live traps in primary forest in the transition zone between montane and cloud forest at 1,300–1,450 m near Monteverde, Puntarenas Province, Costa Rica. About 90% of the mice used in this study were captured in lightly disturbed primary forest on the property of J. Stuckey (10°17′52″N, 84°48′42″W) in the area of two of the three study grids used by Anderson (1982); in March, 1989, when sampling was most intensive, this was supplemented with animals from the property of R. and M. LaVal, 2 km to the northwest (10°18′38″N, 84°48′54″W). Habitats of this region were described by Buskirk and Buskirk (1976), Koptur et al. (1988), and Lawton and Dryer (1980). In general, rainfall at Monteverde is seasonal, with the dry season typically extending from December through early April (Heideman and Bronson, 1992). Plant and insect production varies with rainfall; moderate peaks in fruiting (Dinerstein, 1986) and insect abundance (Buskirk and Buskirk, 1976) occur in the wet season. Koptur et al. (1988) described a flowering peak during the dry season for subcanopy trees and shrubs, although they did not observe any peaks in fruiting.

Four collections of mice, each of 8 adult males and 13–16 adult females, were autopsied immediately after trapping in the late dry season (13–18 March 1989), early wet season (26 April–19 May 1989), mid wet season (22 August–25 September 1989), and early dry season (10–13 January 1990). All females were weighed, assigned to an age class (juvenile, subadult, or adult) according to pelage characteristics described by Heideman and Bronson (1992), and checked for lactational status and teat size. In those that were autopsied, reproductive organs were examined in the field and then preserved in formalin or Bouin's fixative for histology. Ovaries and uteri for histologic examination were embedded in paraplast, serially sectioned at 5–10 μm, and stained with hematoxylin and PAS (Humason, 1972). Voucher specimens collected during this study are deposited at the Instituto Nacional de Biodiversidad in Costa Rica and at the Museum of Natural History of The University of Kansas. We follow Timm et al. (1989) in considering *P. nudipes* as a distinct species, but this taxon may be a subspecies of *P. mexicanus* (Carleton, 1989).

In March 1989, an additional 24 males and 24 females were trapped, examined externally, and transported to Texas to establish a breeding colony. During the first 5 weeks after transport to Texas, mice were housed in pairs in polyethylene cages measuring 36 by 32 by 16 cm within a Duo Flo negative-airflow portable quarantine chamber (BioClean Lab Products Inc., 255 West Spring Valley Avenue, Maywood, NJ) on a light cycle of 11.5L:12.5D at 28 ± 1°C. Mice were provided with a diet of Wayne Breeder Blox (Allied Mills, Inc., Chicago, IL) and acidified tap water ad lib. Two males died within 2 months and two females were killed for pathologic analysis, leaving a total of 22 pairs. After quarantine, the temperature was reduced to 23 ± 1°C. As part of a study on the effects of photoperiod on reproduction, mice were exposed to a variety of light cycles (Heideman and Bronson, 1992). Data from animals in light cycles from 8L:16D to 16L:8D are included here because there were no significant effects of photoperiod. Breeding pairs were housed in polyethylene cages measuring 46 by 26 by 20 cm. At 25 days of age, young mice were weaned and isolated in polyethylene cages measuring 29 by 18 by 12 cm. Purina Formulab 5008 chow (Ralston-Purina Co., St Louis, MO) and acidified tap water were given ad lib.

Information on growth rate and maturation was obtained from 0 to 120 days. Young were weighed at 2-day intervals until 24 days of age. The day of appearance of hair and the day of eye opening was recorded. At 30, 40, 50, 60, 70, and 120 ± 1 days of age, males were lightly anesthetized with methoxyflurane (Metophane, Pitman-Moore Inc, Mundelein, IL), their scrotum was moistened, and the length and width of the right testis were measured externally with dial calipers. At 50 ± 1 days of age, females were deeply anesthetized with methoxyflurane and their ovaries and uteri were examined through a small abdominal incision. Reproductive development was assessed on a scale of 1 (tiny ovary lacking large follicles or corpora lutea, and uterus <0.5 mm diameter) to 5 (large ovary with corpora lutea or large preovulatory follicles, and uterus ≥1 mm). At 70 ± 1 days of age, 23 males and 19 females were autopsied. Paired testes and paired seminal vesicles stripped of fluid were weighed. Ovaries and uteri were scored as noted previously. Females were assumed to have achieved puberty when their uteri were enlarged and their ovaries contained corpora lutea or large preovulatory follicles. Sixteen males aged 55–70 days were paired with females 60 days or older, and ages at fertilization were determined by backdating 28 days (the duration of gestation in nonlactating females) from the birth date of the first litter.

Dates of insemination and fertilization were determined by microscopic examination of daily vaginal lavages. Duration of gestation was calculated as the interval from the night of insemination to the day young were first observed.

Interbirth intervals of lactating females were calculated as the interval between successive litters. Interbirth intervals >50 days were excluded because an intervening litter could have been cannibalized soon after birth, and thereby not recorded. A mean interbirth interval was calculated for each female with six or more interbirth intervals.

The weaning period was determined with young 15–30 days old by estimating the proportions (0, 5, 20, 40, 60, 80, 95, or 100%) of milk and rodent chow in their stomachs. The state of development of cheekteeth of these mice was recorded.

Analysis of variance or Student *t*-tests were used in comparisons involving continuous variables. *G*-tests were used in comparisons of categorical variables. Means are presented with standard errors. Comparisons of litter size between or among wild, wild-caught, and laboratory-born females were made using Mann-Whitney *U* (*U* statistic or Kruskal-Wallis (*H* statistic) tests. Some categories of litter-sizes were grouped (size one with two and size four with five) in tests for a relationship between litter size and other reproductive parameters because there were few litters of size one or five. Because there were significant differences among individuals for both average interbirth interval and average litter size for wild-caught and for laboratory-raised females, these variables were recalculated and presented as grand means treating each female as a single point and using her mean interbirth interval or litter size in the calculation.

Results

Fertility.—Nineteen of 22 wild-caught females produced at least one litter during the 22-month span of the study. Five females gave birth during the 2-month period of quarantine and adjustment. During the next 12 months, the 19 breeding females produced an average of 7.4 ± 0.8 litters. Two females each produced 11 litters during this period, and another five females produced 9–10 litters. Litter production declined during the next 6 months of the study. The decline was due in part to mortality (three females), in part to pairs that stopped bearing litters (three pairs), and in part to pairs that produced litters at longer intervals. Average litter size, at birth, of wild-caught females was 2.9 ± 0.1 (range, 1–5 young for 193 litters of 19 females). This litter size did not differ significantly from the average

number of implanted embryos in pregnant females in the wild (2.8 ± 0.1; range, 1–4; $n = 26$; $z = 0.48$; $P > 0.10$). The average interbirth interval for wild-caught, lactating females was 33.3 ± 0.6 days (range, 26–48 days for 140 interbirth intervals of 18 females). Individual wild-caught females varied significantly in both average interbirth interval (from 30.8 ± 0.5 to 39.1 ± 2.1 days; $F = 4.74$; $P < 0.001$; $n = 13$ females with six or more intervals) and litter size (from 1.7 ± 0.2 to 3.7 ± 0.3; $F = 6.28$; $P < 0.001$; n = the same 13 females, each with nine or more litters). Litter size did not vary significantly in relation to lactational status ($t = 1.34$; $P > 0.10$) or parity (litter sizes of 2.7 ± 0.1, 2.5 ± 0.2, 3.1 ± 0.2, 3.1 ± 0.2, 3.1 ± 0.4, 2.9 ± 0.3, 3.4 ± 0.5, 2.3 ± 0.3 for litter number 1–8, respectively, with $n = 31$, 18, 15, 12, 11, 7, 7, and 7, respectively; $P > 0.10$ by ANOVA with post hoc contrast comparisons of the first litter with all other litters and the first two litters with all others). Survival of young was high. Of litters produced by wild-caught females, at least one young survived until weaning in 94% of 172 litters in which young were not removed.

Laboratory-born females produced and weaned fewer litters per unit time than did wild-caught females. Of 55 laboratory born females, 76% produced litters, as compared to the 86% of wild-caught females ($G = 1.02$; $P > 0.10$). However, the 42 breeding-laboratory born females produced an average of only 4.8 ± 0.5 litters/year. Survival in these litters was poor. All young in 47% of 42 first litters and 35% of 146 subsequent litters were killed or abandoned by their parents. Only 17 of the 42 laboratory born breeding pairs were successful in weaning at least one young from at least 80% of their litters, as compared to 17 of 19 wild-caught breeding pairs ($G = 14.28$; $P < 0.001$). Average litter size of laboratory born females, 2.9 ± 0.1, was not significantly different from that of wild-caught or wild females ($H = 0.39$; $P > 0.10$; $n = 31$ laboratory born females).

Wild-caught individuals in the laboratory weighed ca. 50% more than the early pregnant, nonlactating adults caught and autopsied in the field during the wet season. The latter, in turn, weighed more than the adult females caught during the dry season (wild-caught females in the laboratory: 63.8 ± 2.1 g, $n = 23$; wet season, 44.5 ± 1.1 g, $n = 20$; dry season, 41.1 ± 0.7 g, $n = 50$; $P < 0.05$).

Ovulation and early embryonic development.—Ovulation occurs spontaneously in *P. nudipes*. Nineteen virgin females 70 days of age had corpora lutea. The reproductive tracts of two additional females with corpora lutea were examined histologically; both contained recently ovulated ova in their oviducts.

Surprisingly, many (20 of 46) embryos in stages ranging from one-cell to uterine blastocyst lacked a zona pellucida, and in nine others the zona pellucida was apparent only as fragments associated with embryos. This occurred in mice both from the field and from the laboratory. Early loss of the zona pellucida also is characteristic of *P. polionotus* (Laffoday, 1957; Layne, 1968; Smith, 1939). It is possible that the early loss of the zona pellucida is related to reproductive failure in *P. nudipes*. Development up to late morula and early blastocyst stages occurred within the oviduct. One female held three early blastocysts (32–64 cells) just above the junction of the oviducts with the uterus. No other blastocysts occurred within oviducts, and all embryos within uteri were at or beyond the blastocyst stage.

Gestation, parturition, decline of the corpora lutea, and post-partum estrus.—The average duration of gestation for nonlactating females was 27.8 ± 0.2 days (range, 26–28 days; $n = 8$ laboratory born females). Parturition was followed closely by post-partum estrus, as indicated by frequent interbirth intervals of 26–30 days. Additionally, vaginal lavages from two females on the day after parturition contained abundant spermatozoa, whereas lavages from the same females on the day of birth and on the 2nd day following did not. One female examined 1.5 days post-partum had ova just beyond the infundibular region of her oviducts, whereas two females examined 3 days post-partum had two-cell embryos located in the ampullar region of the oviducts.

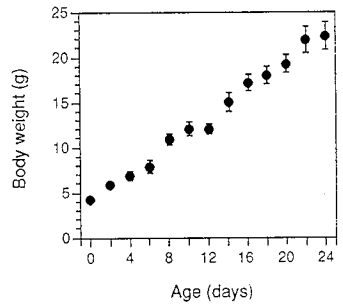

FIG. 1.—Mean (±*SE*) body weight of individuals in litters of laboratory born young *Peromyscus nudipes* from 0 to 24 days (those symbols without bars conceal their standard errors; n = 9–14 litters except for day 0, $n = 29$ litters, and day 20, $n = 6$ litters).

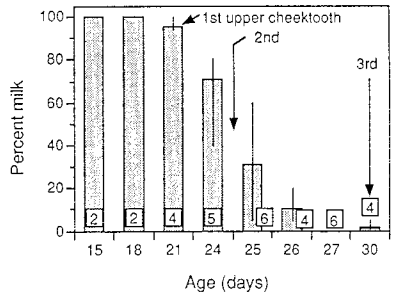

FIG. 2.—Approximate proportion of the stomach contents composed of milk in *Peromyscus nudipes* aged 15–30 days (bars indicate the mean, vertical lines the range; sample sizes are enclosed in squares in each column). Arrows indicate the median age of eruption of upper cheekteeth; lower cheekteeth erupted slightly earlier.

By the 2nd or 3rd day following parturition the old corpora lutea (now corpora albicantia) were regressing, with many fibroblasts and few large luteal cells ($n = 3$). Many females with one- to four-cell ova or embryos still held corpora albicantia as well as the corpora lutea of the new pregnancy (11 of 20). Fifteen females with more advanced embryos either held inconspicuous corpora albicantia (two females with unimplanted blastocysts) or lacked corpora albicantia (13 females with embryos that ranged from eight-cell morulae to near term).

Lactation and weaning.—The average mass of individual young on the day of birth was 4.3 ± 0.1 g ($n = 29$ litters). There was a slight, but nonsignificant, tendency for young from larger litters to be lower in body mass ($F = 2.31$; $P > 0.10$; $n = 29$ litters). Maternal body mass of laboratory born females did not differ from those of wild-caught females (63.0 ± 2.8 and 64.7 ± 3.4, respectively; $t = 0.39$; $P > 0.10$). Body mass of neonates of laboratory born females did not differ from that of neonates of wild-caught females (4.2 ± 0.1 and 4.6 ± 0.3, respectively; $t = 1.42$; $P > 0.10$). Young of laboratory born pairs were slightly lighter than those of wild-caught pairs at all but one age from 0 to 18 days, but the differences were small (<1.5 g) and statistically significant only on days 2, 16, and 18; small samples prevented statistical comparison on days 20–24. Growth was steady from birth to weaning (Fig. 1).

The age of eye opening averaged 15.2 ± 0.7 days ($n = 14$ young). Under laboratory conditions, with only hard-pellet food available, young began eating solid food at ca. 21 days of age, just as the first upper cheekteeth were erupting (Fig. 2). Milk was infrequent in their stomachs after day 26, shortly after the second upper cheekteeth had erupted.

Assuming that females were receptive on the night following parturition, lactation extended gestation by an average of 4.5 days. The duration of this extension was weakly related to the size of the litter being suckled. The extension of gestation was 3.6 ± 0.6 days for small litters (1–2), 4.5 ± 0.6 for litters of three, and 6.2 ± 0.7 for large litters (4–5; $n = 51$, 63, and 25 interbirth intervals, respectively; $F = 3.12$; $P < 0.05$). In contrast, the duration of the extension was strongly related to individual differences

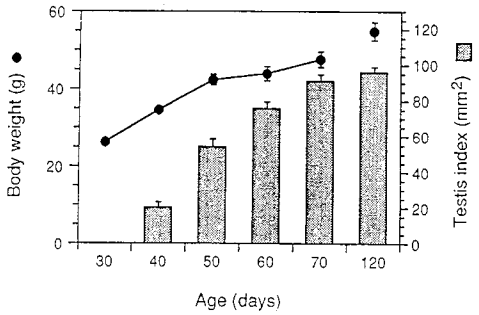

FIG. 3.—Post-weaning body weight and testis size (length times width) of laboratory born male *Peromyscus nudipes* (mean ± standard error; n = 36 for age 30–70 days, n = 8 for age 120).

among females ($F = 4.74$; $P < 0.001$; n = 13 wild-caught females with six or more interbirth intervals during lactation). For these 13 females, the average duration of the extension ranged from 1.8 ± 0.5 to 10.1 ± 2.1 days.

Post-natal growth and reproductive development.—The sexes did not differ significantly in body mass at 24, 50, 70, or 120 days of age, and they did not differ significantly in growth rate (t-tests; $P > 0.05$ for all comparisons). Growth was rapid during suckling (0.75 g/day) and 24–50 days (0.73 g/day), slower at 50–70 days (0.35 g/day), and slow at 70–120 days (0.13 g/day; Figs. 1 and 3). By 50 days of age, most young mice in the laboratory had reached body masses typical of adults in the wild.

At 30 days of age, no females had attained puberty (zero of eight), as indicated by autopsy. By 40 days of age, 56% of 9 females had undergone their pubertal ovulation, by 50 days of age 86% of 37 had done so, and by 70 days of age 100% of 19 had done so. Growth of the testes was most rapid at 40–60 days of age, and by 70 days these organs approached the size of those in breeding adults (Fig. 3). The three youngest males paired with females were 55 days old, and two of these three males inseminated females at 62 and 63 days of age, respectively. Fertility rates for 70–80-day-old males (seven conceptions from 13 pairs) were comparable to those of males >100 days old.

Discussion

We measured four parameters in the laboratory that are relevant to understanding the reproductive strategy of *P. nudipes* in the wild; litter size, rates of growth and development, age of fertility onset, and frequency of litter production. The average litter size at birth in the laboratory, about three individuals, was almost identical to that seen in late-pregnant females trapped and autopsied in the wild. Thus, there is little evidence of phenotypic plasticity in this trait in this stock of animals. Individual females varied widely in both average litter size and interbirth interval, despite being housed under identical conditions in the laboratory. This suggests that there is considerable individual variation, potentially genetically-based, in these traits in the Monteverde population. We saw no evidence that litter size influenced neonatal body weight, and litter size was not affected by parity. Both of these relationships have been reported in other studies of *Peromyscus* (e.g., Myers and Master, 1983).

Maturation and growth were rapid in our laboratory colony. Young of both sexes achieved body masses typical of adults in the wild at ca. 7 weeks of age. Most females had gone through their pubertal ovulation by 6–8 weeks of age. The testes of young males reached adult size in ca. 10 weeks, and some males became fertile by 9 weeks of age. Age at eye opening and age at weaning to solid food were comparable to those of other species of *Peromyscus* (Millar, 1989). We collected no data on growth and reproductive development in the wild for comparison, but Anderson (1982), reported on the basis of 2.4 years of mark-recapture data that <10% of female *P. nudipes* at Monteverde reproduced in the wet season of their birth or in the following dry season. Thus, development to reproductive maturity may be much slower in the wild than in the laboratory, and age at first reproduction is greater in the wild.

Wild-caught pairs in our laboratory colony had the potential to produce as many as 11 litters/year for at least 20 months. Laboratory-born pairs produced litters that were similar in numbers and body weight to those of wild-caught pairs, but the laboratory born pairs produced fewer litters per unit of time, growth rates of their young were slightly lower, and they were more likely to abandon or kill their offspring. The fewer litters recorded for the laboratory born animals reflected in part a tendency to cannibalize young at birth before a litter could be observed and recorded. Thus, the deficits induced by laboratory rearing in *P. nudipes* seem to be primarily, and possibly exclusively, traceable to abnormalities in their parental behavior. Similar, although generally milder, deficits due to laboratory rearing have been reported for other species of *Peromyscus* (Millar and Threadgill, 1987; Price, 1967; Williams et al., 1965). This result re-emphasizes the need for caution in applying laboratory data on reproductive rates to populations in the field.

Females in the wild at Monteverde produced litters at a much lower rate than in the laboratory. Few females were pregnant with one litter while nursing another (only seven of 27 adults), and four of these had 1- to 16-cell embryos in their oviducts, stages that are extremely likely to fail under conditions of energetic stress (Heideman and Bronson, 1992). This suggests that most wild females wean one litter before becoming pregnant with the next. Thus, interbirth intervals may be on the order of 2 months or more in duration, even during the wet season. Overall, then, this suggests a maximum production of four, or perhaps five, litters during the 7–8 months of each wet season. Anderson (1982) concluded on the basis of 2 years of mark-recapture data that adult females in the population at Monteverde produced, on average, only two litters per year, and that few or no females in this population produced more than three litters in 1 year. Regardless of whether our maximum or Anderson's mean value is closer to the long-term average for this population, the realized reproduction of these animals in the wild is obviously far below their potential reproduction, as revealed in the laboratory.

A large part of the discrepancy between the potential and realized reproduction of these animals can be traced to repeated reproductive failures by wild females during the 4–5-month dry season. As previously described by Heideman and Bronson (1992), females in this population continued to ovulate and mate during the dry season, but implantation seldom occurred in this season and, when it did, the fetuses were lost prior to mid-pregnancy; only during the wet season was reproduction successful. However, these mice apparently did not achieve their full reproductive potential even during the 7–8-month wet season.

Two kinds of evidence suggest that low realized reproduction at Monteverde may be a result of food insufficiency, mildly so during the wet season and more severely during the dry season. First, we previously have shown that mild food-restriction yields the same degree and kind of reproductive failure seen in the wild during the dry season (Heideman and Bronson, 1992). Second, the high rate of reproduction seen in our laboratory colony was among wild-caught individuals weighing ca. 50% more than the early pregnant, nonlactating adults caught and autopsied in the field during the wet season. The latter, in turn, weighed more than the adult females caught during the dry season. Adult males also weighed less during the dry season than during the wet season (Heideman and Bronson, 1992), suggesting that the seasonal difference in females is not due to weight gain consequent to early pregnancy.

The combination of the field and laboratory data allow us a better understanding of the life-history of *P. nudipes*. In the wild,

the Monteverde population exhibits a reproductive pattern that seems, on the surface, to be relatively K-selected compared to that of most other *Peromyscus*. That is, they exhibit a relatively large body size both neonatally and during adulthood, an annual period of reproductive quiescence, a low reproductive rate during the breeding season, and, probably, a delayed first reproduction. Our laboratory data show that this view is incomplete. As seen in the absence of energetic constraint in the laboratory, underlying this pattern is the potential to mature and reproduce with great rapidity. There is a high degree of phenotypic plasticity in age at first reproduction, frequency of litter production, and seasonality of litter production, although there was no evidence of phenotypic plasticity in litter size. Thus, these mice are reproductive opportunists in that they attempt to reproduce continually, sometimes failing during the wet season and always failing during the dry season. Different populations of this species might express life-history characters in quite different ways. In more favorable habitats or years, these mice might express their ability to mature rapidly and reproduce frequently and nonseasonally, while in others they would produce their small litters at long intervals, as they do at Monteverde.

As a final comment, it is clear that neither field nor laboratory studies alone would have given us a real appreciation of the reproductive tactics of the *P. nudipes* population at Monteverde. Our findings certainly support Millar's (1989) suggestion that we need a better understanding of the effects of captivity on reproduction in *Peromyscus*, as well as more direct comparisons between field and laboratory-derived data.

Acknowledgments

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