

Evolution of Monogamy, Paternal Investment, and Female Life History in *Peromyscus*

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The timing of reproductive development and associated trade-offs in quantity versus quality of offspring produced across the life span are well documented in a wide range of species. The relation of these aspects of maternal life history to monogamy and paternal investment in offspring is not well studied in mammals, due in part to the rarity of the latter. By using five large, captive-bred populations of *Peromyscus* species that range from promiscuous mating with little paternal investment (*P. maniculatus bairdii*) to social and genetic monogamy with substantial paternal investment (*P. californicus insignis*), we modeled the interaction between monogamy and female life history. Monogamy and high paternal investment were associated with smaller litter size, delayed maternal reproduction that extended over a longer reproductive life span, and larger, higher quality offspring. The results suggest monogamy and paternal investment can alter the evolution of female life-history trajectories in mammals.

Keywords: reproduction, maternal age, monogamy, paternal investment, *Peromyscus*

Life history refers to the pace of development and the distribution of reproductive effort over the life span (Clutton-Brock, 1984, 1989; Stearns, 1989) and includes at least two distinct components that are independent of species size (Bielby et al., 2007; Gaillard et al., 1989). Bielby and colleagues' large-scale analysis identified reproductive timing (measured by age of weaning) and trade-offs in the quantity and quality of offspring (measured by neonatal birth

weight), as core features of mammalian life history. The social ecological conditions that influence the evolution of these traits are not fully understood, but likely include age-related mortality risks. High risk due to predation and other ecological factors favor early reproduction and production of a larger number of lower quality offspring (Clutton-Brock, 1991; Reznick & Endler, 1982; Steiner, Tuljapurkar, & Orzack, 2010). Low juvenile mortality risks appear to be critical for the evolution of a life-history pattern characterized by delayed reproductive timing and production of fewer, higher quality offspring, and parental investment can substantially influence these risks (Charnov, 1993; Promislow & Harvey, 1990). At the same time, even within the same species, as exemplified in kittiwake (*Rissa tridactyla*) sea birds, ecological pressures and constraints, including nutrient availability, can lead to different populations displaying distinct life-history patterns (Steiner et al., 2010).

Mammalian species with extensive parental investment generally show delayed reproductive timing and produce fewer, higher quality offspring in comparison to related species with less intensive investment (Gaillard et al., 1989). For the vast majority of these species, parenting is provided largely or exclusively by mothers (Clutton-Brock, 1989). To the extent that maternal behaviors contribute to life-history evolution, perhaps through reducing offspring mortality (Charnov, 1993), the pattern should be pronounced in mammalian species with high levels of biparental investment (Geary & Flinn, 2001). It has been shown in birds that females from species with biparental care primarily increase the number of eggs when paired with attractive males, but females from species that exhibit only maternal care produce larger, but not more eggs when mated with comparable males (Horváthová, Nakagawa, & Uller, 2012).

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In contrast to the situation in birds (Burley & Johnson, 2002), the prediction is difficult to test in mammals, as paternal care is found in less than 5% of mammalian species (Clutton-Brock, 1989; Kleiman, 1977). Monogamy and paternal care do not always coincide in mammals (Komers & Brotherton, 1997), but when these traits do, the associated life-history pattern differs from that of related, polygynous species (Clutton-Brock, 1984; Stearns, 1989). When paternal investment is found in mammals, the life-history correlates are in keeping with the hypothesis that this investment can influence the evolution of female life history, specifically enabling the delay of reproduction and the production of fewer, higher quality offspring, relative to related species without such patterns of behavior (Clutton-Brock, 1991).

We tested this hypothesis with a large number of out-bred animals representing five species of *Peromyscus* that differ significantly in level of monogamy, paternal investment, and maternal life-history development. The use of captive bred animals predictably resulted in much lower mortality than occurs in their wild counterparts, which are subject to intense predation, starvation, and other risks (Errington, 1946). However, these analyses permit the assessment of life-history patterns as they unfold across multiple breeding cycles, for a comparable length of time (~2 years) spanning species within the *Peromyscus* genus (see Figure 1), and permit inferences to be drawn on whether long-term rearing under laboratory conditions significantly alters life-history patterns (Drickamer & Vestal, 1973). By using multivariate methods that enabled the modeling of female life-history trade-offs across these species and controlling for phylogeny, we assessed two main predictions: (a) Females of polygynous species with low paternal investment begin reproduction at an earlier age and produce larger litters of lower quality offspring, and (b) paternal investment is correlated with delayed female reproduction and production of smaller litters of higher quality offspring. Our data also allowed for estimation of the relation between monogamy, paternal investment, and the dynamics of female reproduction across maternal age: specifically, changes in litter size and attrition.

The genus *Peromyscus* serves as a particularly valuable group for studying the evolution of life-history trade-offs, as it includes closely related species that inhabit a wide range of ecologies from desert areas to urban dwellings, and displays the full range of

mammalian mating systems (see Figure 1; Bradley et al., 2007; Drickamer & Vestal, 1973; King, 1968; Kirkland & Layne, 1989). *Peromyscus maniculatus* includes more than 60 widely dispersed subspecies that vary in life-history development and paternal behavior, although many of these differences have yet to be fully characterized (Birdsall & Nash, 1973; Dewsbury, 1985; Millar, 1989). Our focus herein is on *Peromyscus maniculatus bairdii* (hereafter termed deer mouse), which mates promiscuously with males that provide comparatively little to no parental care (Dewsbury, 1981, 1984). This species likely represents the ancestral state of the *Peromyscus* breeding system, as illustrated by the phylogenetic tree suggested by Kalcounis-Rüppell and Ribble (2007; see Figure 1). The white-footed mouse (*Peromyscus leucopus*) exhibits a similar social structure and mating system to deer mice. However, paternal care may be facultatively expressed depending on social and ecological conditions. The oldfield mouse (*P. polionotus subgriseus*) is a close relative to the deer mouse, but is one of three putatively monogamous *Peromyscus* species with stable mating pairs and biparental cooperation in offspring rearing (Wolff, 1989). The California mouse (*P. californicus insignis*) is considered exclusively monogamous, maintaining permanent and stable mating pairs, and exhibiting high levels of obligate biparental investment (Dudley, 1974; Gubernick & Teferi, 2000; Ribble & Salvioni, 1990), which likely represents an evolutionarily more recent breeding system. The cactus mouse (*P. eremicus*) is a phylogenetically close relative of the California mouse (see Figure 1), but less is known about the extent of paternal behavior in this species. What is known suggests that cactus mouse males exhibit facultative monogamy and paternal care (Kalcounis-Rüppell & Ribble, 2007; Wolff, 1989).

Method

Subjects

Data from 60 mating pairs were chosen at random from each of five *Peromyscus* species (total $n = 300$) acquired from the *Peromyscus* Genetic Stock Center (PGSC; University of South Carolina, Columbia, SC). Each strain was descended from wild-caught ancestors that were bred in the laboratory for 21 to 63 years

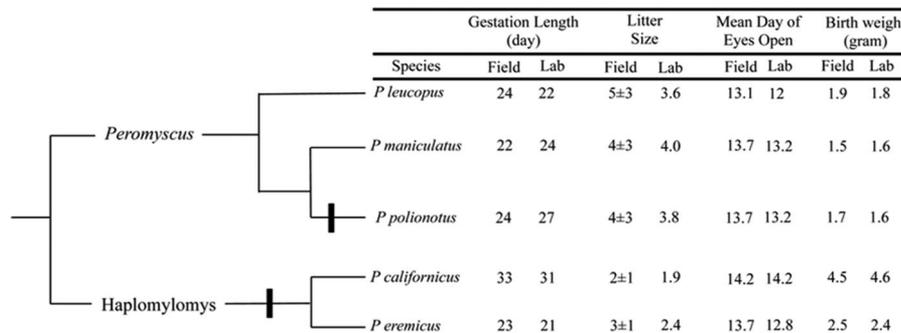


Figure 1. Influences of phylogeny and mating system in *Peromyscus*. Monogamy appears to have evolved multiple times in *Peromyscus*, perhaps once in the *Haplomylomys* subgenus (*P. californicus* and *P. eremicus*) and after the divergence of *P. maniculatus* and *P. polionotus*. Black bars indicate evolution of a monogamous mating system. Associated life history traits are from reviews of field studies (Layne, 1968; Millar, 1989), and empirical studies of laboratory colonies (Dawson, 1965, 1966; Gubernick, 1988; Joyner et al., 1998).

(captured in Washtenaw County, MI in 1948; Ocala National Forest, FL in 1952; Burke County, NC in 1982; Santa Monica Mountains, CA in 1987, and Tucson, AZ in 1993 for deer, oldfield, white-footed, California, and cactus mice, respectively) in a standardized and uniform environment, as discussed further below, across species, over time, and maintained as out-bred populations. This facility strictly adheres to the United States Department of Health and Human Services, National Institutes of Health (NIH) guidelines for the care and use of laboratory animals. Mating pairs were selected at random with the caveat that one cohort of mating pairs was collected from the originating colony (Wave 1; e.g., mating pairs within 5–15 years of colony inception) and another cohort was collected from the current colony (Wave 2; e.g., mating pairs from 2000–2008). Captivity lessens selective pressures, such as starvation and predation, which can result in differences across wild and captive populations (McPhee, 2004); litter size and attrition rates were compared across Wave 1 and Wave 2. Together, the dataset includes 538, 457, 552, 722, and 632 litters and 2420, 1811, 1310, 1789, 2357 offspring for white-footed, deer, California, cactus, and oldfield mice, respectively.

Animal Husbandry

The *Peromyscus* colonies are maintained at the PGSC by using standard laboratory methods (Joyner, Myrick, Crossland, & Dawson, 1998). Mice were housed in 18 by 25 cm polypropylene cages, with ad libitum access to food and water, maintained in a 16:8-hour light/dark cycle, with a temperature range of 22–25 °C and humidity of 50 ± 5%. Average age at first estrus for laboratory white-footed, deer, California, cactus, and oldfield mice is 46, 49, 80, 39, and 30 days of age, respectively (Dawson, 1965, 1966; Gubernick, 1988), and in each case is within the range found in wild populations (Layne, 1968). Females are presumed spontaneous ovulators with a five day estrous cycle (Joyner et al., 1998). Animals were paired for breeding (one female to one male for all species) without deliberate selection except to avoid sib-sib and parent-offspring mating. Once the pair bond was formed, addition of foreign male animals was avoided to ensure that litter outcomes were not confounded by pregnancy block.

Peromyscus females enter postpartum estrus approximately 12 hours after delivery and rebreed with the resident male soon thereafter. Mating pairs were checked daily for newborn or overt gestating females. Copulatory plugs are inconspicuous in some *Peromyscus* species, and are thus not a reliable indicator of successful mating in these species (Joyner et al., 1998). This assessment was therefore not performed. When a new litter was discovered, the date of birth (postnatal day one) and number of pups were recorded. Length of gestation for nonlactating females varied across species: 23, 23, 31, 21, and 23 days for white-footed, deer, California, cactus, and oldfield mice, respectively (Dawson, 1965, 1966; Gubernick, 1988; Joyner et al., 1998). The smaller species were weaned between 25 and 31 days (i.e., white-footed, deer, cactus, and oldfield) and the larger California mouse between 30 and 36 days (King, 1968). Sex determination was done by comparing anogenital distance and presence of external male or female genitalia. Upon reaching sexual maturity, breeding males and females were placed in individual cages and males remained with females until either the partner died or the pair failed to produce a litter within three months. It should be noted that a genetic bot-

tleneck in the breeding program of *P. polionotus* in 1978–1980 reduced the founders of the current stock to 13 individuals. As a result, the *P. polionotus* colony currently has a relatively high inbreeding coefficient (~.30). Thus, interpretations of female *P. polionotus* life-history parameters are made herein with this cautionary note.

Data Coding

Information on maternal age at reproduction (date of litter birth – date of maternal birth) and number of offspring born (litter size) and weaned was obtained from PGSC records. Preliminary data analyses indicated no significant sex ratio effects for litter size or sex differences in attrition and thus data were collapsed across sex. Attrition was considered the difference between number of offspring born and weaned. The various species were classified according to Dewsbury's (Dewsbury, 1981) monogamy index. The index was carefully constructed based on life-history traits and behaviors that vary across monogamous to polygynous reproductive strategies and are summarized in Table 1. Available data were used to classify species on each of these traits and then summed to create an overall index, as shown in Table 2, with positive scores suggesting a monogamous reproductive strategy and negative scores a polygynous strategy; California mouse (10), cactus mouse (6), oldfield mouse (5), white-footed mouse (1), deer mouse (–5). Of the 12 *Peromyscus* species classified by Dewsbury, California and cactus mice were considered the two most extreme monogamous species and deer mice were at the other end of the spectrum and considered the most extreme polygynous/promiscuous (hereafter termed promiscuous) species.

Analyses

Two sets of multilevel models were used to assess species differences in the relation between maternal age and number of offspring born and offspring attrition (i.e., number born – number weaned). The first set provided species-specific contrasts with the white-footed mouse as the reference group, as it occupies a position (i.e., 1) on Dewsbury's (1981) scale between the highly monogamous and highly promiscuous species. Species effects, linear and quadratic maternal age (age²) effects, and interactions between species and age effects were first entered into a full model, which allowed species to differ on all effects. The full model was then compared to restricted models that forced species to be the same by dropping the linear or quadratic interactions. The difference in the corresponding log likelihoods, the likelihood ratio test, was assessed by χ^2 , with significance indicating species differences. In all cases, the interactions were significant (i.e., linear and quadratic age effects by species). The Akaike (1974) information criterion values and corresponding χ^2 tests are listed in the Appendix. In models predicting attrition, the same procedure was followed, except linear and quadratic litter sizes were also entered as predictors, in addition to maternal age.

In the second set of analyses, species contrasts were replaced by corresponding codes from Dewsbury's (1981) index; specifically, number of offspring was predicted by the monogamy index, linear and quadratic maternal age variables, and the interactions. In contrast, offspring attrition was predicted by monogamy index, litter size (i.e., number of pups born), linear and quadratic maternal age variables, and the interactions. To account for phylogenetic differences (see Fig-

Table 1
Correlates of Monogamous and Promiscuous Mating Systems Used in Monogamy Scale

Proposed correlate	Prediction	Score range
Sexual dimorphism	Exaggerated in promiscuous mating systems and reduced in monogamous species.	+2 to -2
Latency to initiate copulation	Longer in monogamous species.	+2 to -2
Allogrooming	Monogamous species engage in more allogrooming than promiscuous species.	+2 to -2
Number of ejaculations	Multiple ejaculations per copulatory session are more common in promiscuous species and related to sperm competition.	+2 to -2
The Coolidge effect	Renewed, post-copulatory sexual interest in novel female is greater in promiscuous males.	+2 to -2
Presence of a plug	Presence of a copulatory plug more common in promiscuous species.	+1 to -1
Reproductive potential (litter size)	Low reproductive potential, e.g., smaller litter sizes, favors pair bond formation and is typical in monogamous species.	+2 to -2
Paternal behavior	Male participates in the rearing of young in many monogamous but not promiscuous species.	+2 to -2
Rate of physical maturation (age of eye opening)	Species occupying stable territories and exhibiting monogamy have slower maturation rates relative to promiscuous species.	+2 to -2
Rate of sexual maturation	Rate of sexual maturation is delayed in monogamous species.	+2 to -2
Presence of a scrotum	Concealed testes common in solitary, monogamous males, but not promiscuous males.	Data not presented

Note. Adapted from "An exercise in the prediction of monogamy in the field from laboratory data on 42 species of muroid rodents" by D. A. Dewsbury, 1981, *The Biologist*, 63, pp. 138–162. Copyright 1981. For each proposed correlate, species data was divided into five groups and assigned to scores ranging to -2 to +2, where -2 indicates a score where monogamy is not predicted and +2 indicates a score where monogamy is predicted.

ure 1), species were nested within phylogenetic branches, with the California and cactus mice in one branch (*Haplomylomys*) and the white-footed, oldfield, and deer mice in the other (*Peromyscus*). These analyses allowed for estimation of how timing of female reproduction, number of offspring born, and offspring attrition varied across the continuum of breeding systems found in *Peromyscus*.

The linear and nonlinear mixed effects program in R (Pinheiro, Bates, DebRoy, Sarkar, & R Development Core Team, 2010) was used for both sets of analyses, with litters nested within mothers, mothers nested within species, and species nested within phylogenetic branches (for the monogamy index analyses). Contour maps of the relations among monogamy index and maternal age, litter size, and pup attrition were simulated based on the equations in the second set of analyses using R (Sarkar, 2008).

Results

The focus herein is on the relations between degree of monogamy and female life history, and these results are presented in the third Results section. The species-specific effects may also be of interest to scientists who study one or several of these species, and thus, we also present these results with the potential caveat, as addressed below, that captivity might be an influencing factor.

Captivity Effects

There were no differences in litter size across Wave 1 and Wave 2 for any species. Moreover, no across-wave differences in attrition were evident for the white-field, cactus, or oldfield mice. Attrition decreased (25% vs. 16% for Waves 1 and 2, respectively) for the California mouse, $t(52) = -2.06$, $p = .04$, and increased (11% vs. 22%) for the deer mouse, $t(399) = 3.10$, $p = .002$. Follow-up multilevel models revealed that wave did not interact with maternal age or litter size in predicting attrition for California or deer mice ($ps > .10$), and thus, wave differences did not substantially affect the estimates reported in the following sections.

Species Differences

Maternal age and litter size. Species differed in litter size, $\chi^2(4) = 210.71$, $p < 0.0001$, and in litter size dynamics across maternal age; the interaction between maternal age squared (age^2) and species was significant $\chi^2(4) = 73.57$, $p < 0.0001$, as was the linear interaction, $\chi^2(4) = 54.16$, $p < 0.0001$. The intercept in Table 3 is the estimated mean litter size for the white-footed mouse, holding age constant, and the significant age and age^2 effects indicate that litter

Table 2
Monogamy Scale Values for the Five *Peromyscus* Species

Species	Dimorphism	Intromission latency	Allogrooming	No. ejaculations	Coolidge effect	Presence plug	Litter size	Paternal behavior	Eyes open	Sum	No. of measures
<i>P. californicus</i>	—	+2	+2	+2	—	—	+2	+1	+1	+10	6
<i>P. eremicus</i>	+2	+2	+1	+2	—	-1	0	+1	-1	+6	8
<i>P. maniculatus</i>	-2	+1	-1	0	-2	-1	-1	-1	0	-5	9
<i>P. leucopus</i>	-2	+1	+2	+1	—	-1	-1	+1	0	+1	8
<i>P. polionotus</i>	+2	+2	—	+2	+2	-1	0	+1	0	+5	8

Note. Adapted from Dewsbury's (1981) Table 6 and Table 7.

Table 3
Maximum Likelihood Estimates for Prediction of Litter Size Across Species and Maternal Age

	Estimate	Standard error	t-value	p-value
(Intercept)	4.900	0.168	29.20	0.00005
Age	-0.518	0.174	-2.97	0.003
Deer	-1.207	0.306	-3.95	0.0001
California	-3.086	0.334	-9.23	0.00005
Cactus	-2.637	0.293	-9.00	0.00005
Oldfield	-2.279	0.314	-7.27	0.00005
Age ²	0.026	0.009	2.97	0.003
Deer*age	1.619	0.499	3.25	0.0012
California*age	1.320	0.453	2.91	0.0036
Cactus*age	0.898	0.389	2.31	0.021
Oldfield*age	3.063	0.458	6.69	0.00005
Deer*age ²	-0.780	0.193	-4.03	0.0001
California*age ²	-0.279	0.142	-1.97	0.0489
Cactus*age ²	-0.197	0.118	-1.67	0.0956
Oldfield*age ²	-1.199	0.158	-7.60	0.00005

Note. *df* = 2590 for all estimates; Age = maternal age at time of birth (years); White-footed mouse served as the reference group.

size varied nonlinearly across maternal age for this species. The corresponding pattern is shown in Figure 2. The effects for the four remaining species are contrasted against the white-footed mouse. For example, holding age constant, the mean litter size for the California mouse was 1.81 (4.9 - 3.086), and this value differs significantly from that of the white-footed mouse (i.e., 4.9, *p* < .0005). The

significant interactions between species, age, and age² indicate that the pattern of change in litter size across maternal age differs from that of the white-footed mouse for each of the four other species.

Based on the pattern in Figure 2, we contrasted cactus and California mice by reanalyzing the multilevel model and by using the latter species as the reference group. The corresponding model

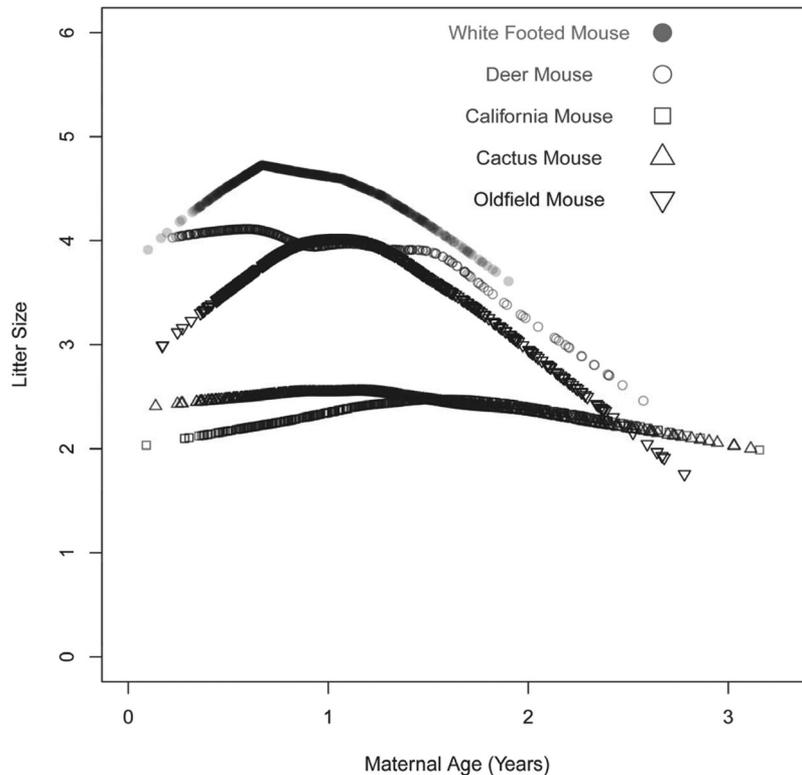


Figure 2. Variation in litter size across maternal age and species. The dots represent Lowess curves (Cleveland, 1981), which estimate nonlinear relations by using local regression, and thus allow for a more precise examination of nonlinear relationships than linear regression models with quadratic terms.

revealed no significant differences in mean litter size ($p = .23$) or change in litter size across maternal age (i.e., the age and age² effects, $ps > .43$). A contrast of deer and oldfield mice revealed a larger litter size for deer mice at the youngest maternal ages (estimated from the intercept, $p = .004$), a significant difference in the interaction between litter size and maternal age ($p = .02$), and a trend for the relation between litter size and maternal age² ($p = .09$). In essence, the pattern of change in litter size across maternal age shown in Figure 2 differed significantly for deer and oldfield mice.

Maternal age and offspring attrition. Attrition occurred in 37% of all litters, and 20% of all pups died before weaning. Mean attrition was white-footed (0.26), deer (0.18), California (0.19), cactus (0.18), and oldfield (0.25) mice. Species differed in attrition, $\chi^2(4) = 11.72$, $p = 0.02$, and in change of attrition across maternal age. The interaction between maternal age² and species was significant, $\chi^2(4) = 34.15$, $p < 0.0001$, as was the linear interaction, $\chi^2(4) = 34.38$, $p < 0.0001$. Species also differed in attrition across litter size, with the interaction between litter size squared (litter size²) and species being significant, $\chi^2(4) = 17.57$, $p = 0.0015$, as was the linear interaction, $\chi^2(4) = 15.27$, $p = 0.004$. As shown in Figure 3, attrition rate did not vary across maternal age for the white-footed mouse (as indicated by nonsignificant age and age² effects, Table 4) but differed across litter size. The contrasts in Table 4 indicate that the correlation between maternal age and attrition for California and oldfield mice was similar to that of white-footed mice. In contrast, attrition in deer mice compared with white-footed mice first increased with increasing maternal age, and then decreased. The exact opposite pattern of decreasing and then increasing attrition across maternal age was observed for cactus mice.

The significant litter-size and litter-size² effects in Table 4 indicate that for the white-footed mouse, attrition decreased with

increasing litter size, reaching a minimum at litters of four to five pups, and then increased for larger litters. All four species demonstrated a different pattern of attrition across litter size than white-footed mice. For all four species, attrition first decreased with larger litter sizes, and then increased with expanding litter sizes. The coefficients in Table 4 for litter size² indicate that attrition increased more rapidly after the initial decline for California and cactus mice than for deer and oldfield mice. In short, species differences in overall attrition were comparatively smaller than species differences in the pattern of attrition across maternal age and especially across litter size.

Monogamy Scale

Litter size. The model shown in Table 5 estimates age related change in litter size across the monogamy continuum. As reproductive strategy becomes increasingly biased toward monogamy, the interaction between litter size and maternal age was altered, as indicated by the significant linear ($p = .0002$) and quadratic ($p = .0117$) interactions between monogamy and maternal age. Because monogamy and maternal age are continuous, not categorical variables, a contour map was generated to better depict how litter size varied across these continua (Figure 4; litter size is represented by the contour lines within the figure). At all ages, litter size decreased as monogamy index increased, and rate of decline in litter size occurred more rapidly across maternal age as monogamy index decreased. The latter effect is illustrated in the second panel for two points on the monogamy index. For species with a promiscuous mating system (i.e., I. a monogamy value of -3), females produced larger litters and their reproductive potential peaked early and declined quickly with age. On the other hand, in highly monogamous species (i.e., II. a monogamy value of 8), females produced smaller litters and demonstrated less variation in litter size across their reproductive life span.

Attrition. The model estimating how offspring attrition varied with maternal age (ranging from 0.25 to 2.25 years) and litter size (born) across the monogamy continuum is shown in Table 6. Figure 5 represents the corresponding contour map for litters containing one to five pups. The contour lines indicate attrition rate and are symmetrical across the first and second halves of the plot, and thus estimated rates for older animals must be interpreted with caution. For each litter size, lighter areas represent regions of relatively low attrition and darker areas illustrate regions of relatively high attrition. Attrition was consistently higher for singletons relative to larger litters, and ranged between 30% and 60% across maternal age and monogamy index, albeit comparatively lower for monogamous species. For monogamous species, the lowest attrition ($<15\%$) occurred for litters of three and between the ages of roughly 0.75 to 1.5 years. Comparable attrition was found for promiscuous species with litters comprised of four or five, and dams less than 1 year old. Consequently, the optimal litter size in terms of offspring survival was three for monogamous species and five for promiscuous ones, with the former having a longer reproductive span at a later maternal age within which this optimum occurred.

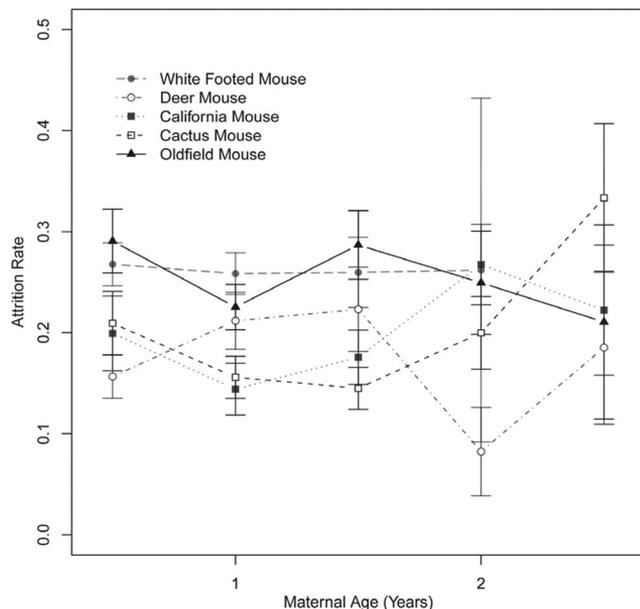


Figure 3. Mean (standard error) attrition rate by maternal age and species.

Discussion

The species of *Peromyscus* assessed in this study span the gamut of mammalian reproductive strategies, ranging from the common

Table 4
Maximum Likelihood Estimates for Prediction of Attrition Rate Across Species, Maternal Age, and Litter Size

	Estimate	Standard error	t-value	p-value
(Intercept)	0.567	0.111	5.13	0.000
Age	-0.015	0.047	-0.32	0.7518
Deer	0.168	0.154	1.09	0.2758
California	0.064	0.163	0.39	0.695
Cactus	0.240	0.150	1.60	0.1092
Oldfield	0.146	0.145	1.01	0.312
Age ²	0.000	0.002	0.12	0.9048
Litter size	-0.139	0.047	-2.93	0.0034
Litter size ²	0.015	0.005	2.80	0.0052
Deer*age	0.327	0.136	2.40	0.0163
California*age	-0.166	0.124	-1.34	0.1797
Cactus*age	-0.234	0.106	-2.21	0.0269
Oldfield*age	0.052	0.127	0.41	0.6848
Deer*age ²	-0.125	0.053	-2.35	0.0187
California*age ²	0.076	0.039	1.95	0.0508
Cactus*age ²	0.098	0.032	3.07	0.0022
Oldfield*age ²	-0.024	0.044	-0.55	0.5848
Deer*litter size	-0.183	0.065	-2.84	0.0045
California*litter size	-0.206	0.091	-2.25	0.0243
Cactus*litter size	-0.237	0.080	-2.96	0.0031
Oldfield*litter size	-0.102	0.060	-1.72	0.0858
Deer*litter size ²	0.017	0.008	2.27	0.0232
California*litter size ²	0.057	0.017	3.39	0.0007
Cactus*litter size ²	0.048	0.014	3.43	0.0006
Oldfield*litter size ²	0.011	0.007	1.61	0.1065

Note. *df* = 2580 for all estimates; Age = Maternal age at time of birth (years); white-footed mouse served as the reference group.

pattern of high levels of polygyny or promiscuous matings to the least common involving high levels of monogamy and biparental care (Clutton-Brock, 1989). However, not all species that engage in biparental care are monogamous. For instance, in some *Calitrichid* monkeys, such as the Saddle-back tamarin (*Saguinus fuscicollis*), females mate with several males and all prospective fathers assist in parental care (Goldizen, 2003). The species studied herein did not capture all of the variation of mating system but nevertheless provided a unique opportunity to examine the covariation of mating system and female life history among a group of related mammals. Moreover, the use of multilevel models with large numbers of females, litters, and pups across the five *Peromyscus* species allowed for estimates of the relation between maternal life history and mating system within the limits of the

reproductive life spans of these species (see also Drickamer & Vestal, 1973). Their life spans and livelihoods were not reduced by ecological risks (e.g., food availability and predation risk) suffered by their wild counterparts (Layne, 1968; Millar, 1989). These ecological perils can influence juvenile mortality and reproductive pattern in adulthood and thus introduce a potential confound that was avoided with analyses on these animals bred in captivity (Reznick & Endler, 1982; Steiner et al., 2010). While these data only demonstrate strong correlation, they still provide useful insights into how degree of monogamy and male reproductive effort, as reflected in Dewsbury's (1981) index may influence the evolution of female life history.

Maternal age at maximum litter size and distribution of reproduction across the life span varied systematically with Dewsbury's

Table 5
Maximum Likelihood Estimates for Prediction of Litter Size Based on Degree of Monogamy and Maternal Age

	Estimate	Standard error	<i>df</i>	t-value	p-value
(Intercept)	3.816	0.533	2594	7.16	0.00005
Age	-0.568	0.088	2594	-6.45	0.00005
Monogamy	-0.110	0.044	2	-2.49	0.1304
Age ²	0.051	0.012	2594	4.21	0.00005
Age*monogamy	0.123	0.033	2594	3.74	0.0002
Monogamy*Age ²	-0.029	0.011	2594	-2.52	0.0117

Note. Age = maternal age at time of birth (years); Monogamy is based on Dewsbury (1981), coded 10, 6, 5, 1, and -5, respectively for the California, cactus, oldfield, white-footed, and deer mouse.

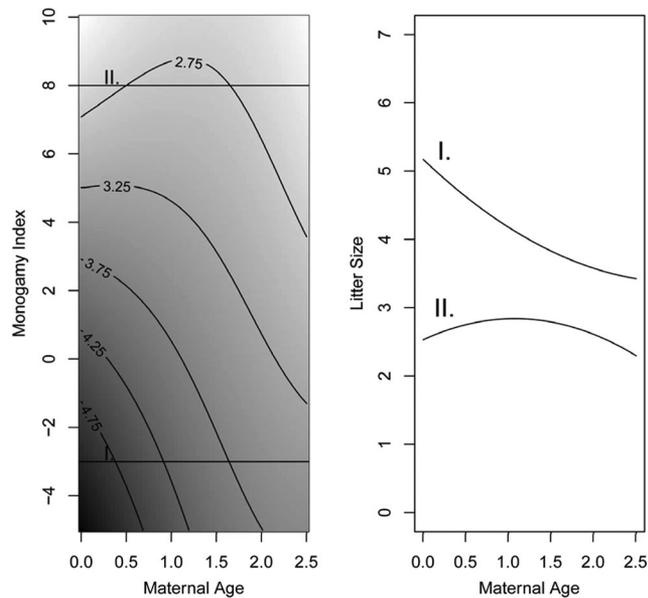


Figure 4. The first panel depicts a contour map derived from the Table 5 equation. The contour lines are litter size. The placement and sharp negative slope for larger litters (e.g., for 4.75) indicate that promiscuous species produce larger litters than monogamous ones and show a rapid decline in litter size with maternal age. Monogamous species produce smaller litters and continued to maintain or increase litter size with maternal age, before reproductive decline. The second panel illustrates these shifts for species with monogamy index values of 8 (II.) and -3 (I.).

(1981) monogamy index. Deer mice were rated at the extreme of polygyny for *Peromyscus* species, and these females showed a life-history pattern consistent with that found in other species employing this breeding system (Clutton-Brock, 1984; Gaillard et al., 1989; Harvey & Clutton-Brock, 1985; Promislow & Harvey, 1990; Stearns, 1989). Compared to the highly monogamous California and cactus mice, female deer mice produced larger litters of lower-quality (i.e., smaller) offspring, demonstrated a peak reproductive potential at an earlier age, and a sharper decline in litter size with aging (Millar, 1989). Drickamer and Vestal (1973)

reported a similar pattern with a large-scale study of laboratory colonies of these same species. The two monogamous *Peromyscus* species were highly similar on these traits and exhibited a similar life-history pattern commonly found with monogamous species and high levels of biparental care (Clutton-Brock, 1991; Dewsbury, 1981; Gaillard et al., 1989). Moreover, these reproductive strategies differed from those of deer mice and the other more promiscuous species in terms of timing and distribution of reproduction and quantity and quality of offspring (Bielby et al., 2007).

The initial conditions that underpinned the evolution of monogamy and paternal investment in these species are not fully characterized (Komers & Brotherton, 1997). Yet, one mechanism through which this investment influences female life history and likely evolved entails reduced offspring mortality. Male California mice exhibit pronounced levels of paternal care in the laboratory (Gubernick & Ablerts, 1987) and in field studies (Ribble, 1992a, 1992b). Ribble found that 94% of California mice pups born survived through weaning, as contrasted with a median of 30% and 39% in two comparable field sites for deer mice (Kalcounis-Rueppell, Millar, & Herdman, 2002). This finding does not imply that paternal investment initiated the evolution of monogamy in *Peromyscus*, but rather paternal care and female life history presumably coevolved. Those breeding pairs that exhibited these traits were more likely to pass their genes onto future generations compared with polygynous pairings, where only maternal care was provided. Ribble's finding that male California mice that remained monogamous had higher reproductive success than polygynous males suggests that the costs of mate switching and breeding with multiple female partners may have been an important early evolutionary step (Kvarnemo, Moore, Jones, Nelson, & Avise, 2000). With the high associated cost of polygynous relationships, there was an opportunity for the evolution of male parenting to the extent that this effort reduced offspring mortality or increased later reproductive competitiveness (e.g., as related to size) of offspring (Charnov, 1993; Clutton-Brock, 1991; Gubernick & Teferi, 2000), as appears to occur in California mice.

Maternal age and pup attrition also varied in consistent ways across the monogamy index and litter size. Whether attrition resulted from infanticide, parental neglect, or poor offspring quality cannot be determined from our data, but the pattern is consis-

Table 6
Maximum Likelihood Estimates for Prediction of Attrition Rate Across Maternal Age, Litter Size, and Level of Monogamy

	Estimate	Standard error	df	t-value	p-value
(Intercept)	0.683	0.064	2590	10.68	0.00005
Age	0.033	0.024	2590	1.39	0.1645
Monogamy	-0.014	0.009	2	-1.52	0.2688
Age ²	-0.013	0.003	2590	-3.84	0.0001
Born	-0.250	0.023	2590	-10.95	0.00005
Born ²	0.027	0.003	2590	9.55	0.00005
Monogamy*age	-0.030	0.009	2590	-3.38	0.0007
Monogamy*age ²	0.012	0.003	2590	3.90	0.0001
Monogamy*born	0.012	0.004	2590	3.20	0.0014
Monogamy*born ²	-0.001	0.001	2590	-1.45	0.1476

Note. Age = Maternal age at time of birth (years); Born = number born in litter; Monogamy is based on Dewsbury (1981), coded 10, 6, 5, 1, and -5 , respectively for the California, cactus, oldfield, white-footed, and deer mouse.

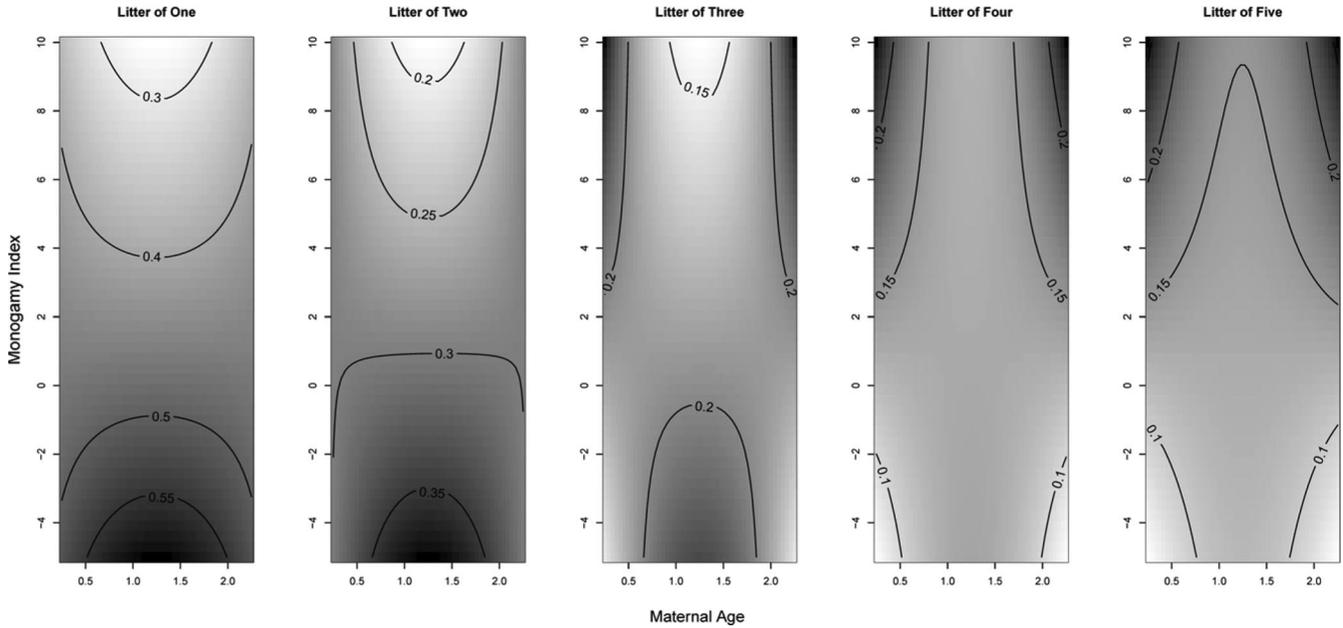


Figure 5. The panels show contour maps derived from Table 6 for litter sizes of one to five offspring across maternal age and monogamy index. Contour lines are attrition rates with lighter regions indicating low attrition and darker ones representing high attrition.

tent with life-history trade-offs (Morris, 1986; Trivers, 1974). The highest attrition rates were found for litter sizes smaller than those typically found in the wild (for example, 1 or 2 pups for deer mice and 1 pup for California or cactus mice; Havelka & Millar, 2004; Millar, 1994), and the lowest for litter sizes mirroring those found in the wild. Singletons in particular experienced relatively high attrition in all species, implying that the reproductive costs of rearing a healthy singleton, such as lactation and delayed remating, may be higher than the cost of terminating investment. Littermates of a singleton may have been resorbed postimplantation, or the birth of a singleton may signal poor offspring or maternal reproductive quality (Gosling, 1986).¹

The finding that deer-mice attrition remained low for litters of up to six pups is in keeping with Myers and Master's (1983) data, that larger female deer mice tend to produce a greater number of offspring, rather than larger sized individuals. Deer mice that could, in theory, produce larger competitive offspring do not. Rather, these animals invest in producing more lower quality offspring, in essence an increased quantity but inferior quality reproductive strategy. These results are consistent with quantity-quality trade-offs being a key component of life-history evolution (Bielby et al., 2007). The implication is directional selection for larger litters in this species, as expected for a species with high juvenile mortality (Kalcounis-Rueppell et al., 2002). The more important finding is that the most highly monogamous species, California and cactus mice, rarely produced litters of more than four pups, and when they did so, there was a tendency for attrition to increase relative to litter sizes of two or three pups. Even in the absence of predation and ad libitum access to food and water, the results suggest optimal litter size is about half the size as those of deer mice, as well as white-footed and oldfield mice, as expected with a higher quality, lower quantity reproductive strategy, and

comparatively low juvenile mortality. In a field study, Chew and Chew (1970) found that 64% of cactus mice born survived to weaning.

As Dewsbury (Dewsbury, 1981) noted, care should be taken when comparing and interpreting monogamy index ratings of contrasting species within the same genus. We assumed, for instance, a linear interaction between monogamy index score and female life-history traits, but such is not necessarily the case. Nevertheless, the correlation between monogamy index score and patterns reported herein for the large number of females and litters in our sample are generally consistent with Dewsbury's classification of *P. maniculatus* (at least *P. m. bairdii*) as highly polygynous and *P. eremicus* and *P. californicus insignis* as highly monogamous, and *P. polionotus* and *P. leucopus* exhibit facultative monogamy. Our results also suggest *P. polionotus* (oldfield mouse) may tend more toward promiscuous mating than indicated by Dewsbury's index, and the white-footed mouse (classified as neither highly monogamous nor highly promiscuous) may be more similar to that of the promiscuous deer mouse than the monogamous California mouse, suggesting promiscuous mating may be a more common reproductive strategy than facultative monogamy and biparental care (Xia & Miller, 1991).

Similarly, the oldfield mouse has been classified as tending toward a monogamous reproductive strategy (Dewsbury, 1981),

¹ We assessed whether the singleton effects were elevated in primiparous females by comparing litter size across first and second litters; white-footed (3.3% and 4.9% of litters were singletons for first and second litters, respectively), deer (7.1, 1.9), California (11.3, 24.5), cactus (14.0, 17.5), and oldfield (12.5, 3.6). None of the effects were significant ($ps > .10$).

but their maternal life history reflected mixed promiscuous and monogamous characteristics. As found with promiscuous species, oldfield mice produced relatively large litters but their reproductive peak was somewhat later than that of deer and white-footed mice. These animals also showed a consistently high attrition rate across maternal age that reached its maximum at the age their litter size peaked, suggesting selective culling may be a feature of their reproductive strategy. One possibility is that because monogamy has evolved more recently in this species than in the California and cactus mice (Kalcounis-Rüppell & Ribble, 2007), infanticide may be a mechanism for quality selection of offspring. In other words, evolution has not had sufficient time to select for smaller litter sizes in oldfield mice, but the females in this species may have evolved a behavioral strategy to focus investment on fewer and presumably larger, high-quality offspring. We do not have information on whether infanticide was more likely with smaller than larger pups in this species, but this possibility is a testable hypothesis for follow-up studies.

Conclusion

Our results with captive-bred peromyscine species supports the notion that Dewsbury's (1981) index or others of this nature may facilitate modeling of female life history across species that span the range of mammalian breeding systems.² Of note, our findings provide a useful estimate of trade-offs that appear to coevolve for species that move from an ancestral state of polygyny or promiscuous mating with little paternal investment, as observed in deer mice, to monogamy (or lower levels of polygyny), with increasing levels of paternal investment (Clutton-Brock, 1989; Gaillard et al., 1989; Kalcounis-Rueppell & Ribble, 2007; Kleiman, 1977). Of course, diverse mammals with delayed reproductive onset and production of few quality offspring do not exhibit paternal investment, but they exhibit high levels of maternal investment and in some cases alloparenting by maternal kin (such as in lions; Packer et al., 1988), both of which reduce offspring mortality risks and increase reproductive payoffs to production of fewer higher quality and more socially competitive offspring (Harvey & Clutton-Brock, 1985; Stearns, 1989). Nevertheless, when it occurs in mammals, paternal investment must be considered as a potential factor on maternal reproductive life-history evolution, including that of humans (Geary & Flinn, 2001).

² Dewsbury (1981) also provided monogamy index information for eight species of *Microtus* and Innes and Millar (1994) provided an extensive review of female life-history traits for each of them (*M. californicus*, *M. canicaudus*, *M. montanus*, *M. ochrogaster*, *M. oeconomus*, *M. pennsylvanicus*, *M. pinetorum*, *M. xanthognathus*). We did not of course have the extensive database reported here for *Peromyscus*, and thus correlations between mean life-history values across these species and monogamy index values are of low power and need to be interpreted with caution, but nonetheless, these data reveal patterns that support Dewsbury's procedure. Specifically, higher monogamy scores were correlated with smaller litter sizes ($r(6) = -.43, p = .29$), longer gestation times ($r(6) = .68, p = .06$), higher neonatal weight ($r(6) = .23, p = .59$), and later weaning ($r(6) = .40, p = .33$). Follow up studies of *Microtus* life history that employ databases and procedures similar to ours would be highly informative.

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(Appendix follows)

Appendix

Akaike Information Criterion (AIC) and Likelihood Ratio Tests for Nested Species-Specific Contrasts

Model	AIC	χ^2	<i>p</i>
Litter Size and Maternal Age			
Full	9281	—	
Age invariant	9327	53.36	.0001
Age ² invariant	9353	79.32	.0001
Attrition, Maternal Age and Litter Size			
Full	1766	—	
Age invariant	1773	14.81	.005
Age ² invariant	1778	19.25	.0001
Litter size invariant	1772	13.30	.01
Litter size ² invariant	1780	21.66	.0002

Note. Lower AIC values indicate better model fit (Akaike, 1974). The χ^2 , with 4 *df* (i.e., the difference in number of parameters comparing nested models) for all tests, is for the negative log likelihood differences comparing the full model in which all species are allowed to differ from one another to restricted models in which age or litter-size effects are forced to be equal for all species.

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