Effects of parental status on male body mass in the monogamous, biparental California mouse

W. Saltzman[1,2], B. N. Harris[1,2]*, T. R. de Jong[1]†, P. P. Nguyen[1], J. T. Cho[1], M. Hernandez[1] & J. P. Perea-Rodriguez[1,2]

1 Department of Biology, University of California, Riverside, CA, USA
2 Evolution, Ecology, and Organismal Biology Graduate Program, University of California, Riverside, CA, USA

Correspondence

Wendy Saltzman, Department of Biology, University of California, 900 University Ave., Riverside, CA 92521, USA.
Tel: 951 827 6356; Fax: 951 827 4286
Email: saltzman@ucr.edu

Current addresses: *Department of Biological Sciences, Texas Tech University, 2901 Main Street, Lubbock, TX 79409, USA. †Department of Behavioral and Molecular Neurobiology, University of Regensburg, 93053 Regensburg, Germany.

Abstract

Studies of biparental mammals demonstrate that males may undergo systematic changes in body mass as a consequence of changes in reproductive status; however, these studies typically have not teased apart the effects of specific social and reproductive factors, such as cohabitation with a female *per se*, cohabitation with a breeding female specifically, and engagement in paternal care. We aimed to determine whether California mouse *Peromyscus californicus* fathers undergo systematic changes in body mass and if so, which specific social/reproductive factor(s) might contribute to these changes. We compared mean weekly body masses over a 5-week period in (1) males housed with another male versus males housed with a non-reproductive (tubally ligated) female; (2) males housed with a tubally ligated female versus males housed with a female that was undergoing her first pregnancy; (3) experienced fathers housed with versus without pups during their mate's subsequent pregnancy. Body mass did not differ between males housed with another male and those housed with a non-reproductive female; however, males housed with a non-reproductive female were significantly heavier than those housed with a primigravid female. Among experienced fathers, those housed with pups from their previous litter underwent significant increases in body mass across their mates' pregnancy, whereas fathers housed without pups did not. These results suggest that male body mass is reduced by cohabitation with a breeding (pregnant) female, but not by cohabitation with a non-reproductive female, and that increases in body mass across the mate's pregnancy are associated with concurrent care of offspring rather than cohabitation with a pregnant female. Additional work is needed to determine the mechanisms and functional significance, if any, of these changes in male body mass with reproductive condition.

Introduction

Females in all mammalian species provide care to their offspring, including both maternal behavior and lactation. Engaging in maternal care can be costly to females, as evidenced by decreased longevity and reductions in such processes as thermogenesis, physical activity and immune function (Speakman, 2008; Jasienska, 2009). These costs are likely to reflect the high energetic and nutritional demands of parenting (reviewed in Picciano, 2003; Speakman, 2008) and can play a key role in shaping life-history strategies (Roff, 1992; Stearns, 1992).

In approximately 5–10% of mammalian species, males also invest heavily in caring for their offspring (Kleiman & Malcolm, 1981; Woodroffe & Vincent, 1994). Depending on the species, paternal care can involve such behaviors as transporting, defending, playing with, socializing, grooming and warming offspring, and providing them with food, shelter or other resources (Kleiman & Malcolm, 1981). Some components of paternal care may have considerable energetic demands (Campbell *et al.*, 2009); however, the costs of paternal care have rarely been studied in mammals.

In those species in which males do provide extensive care for their offspring (i.e. biparental species), indirect evidence suggests that its costs can be substantial. Mammalian fathers that care for their young exhibit systematic changes in circulating or excreted concentrations of a number of hormones (e.g. prolactin, androgens, glucocorticoids, leptin) as a function of reproductive status (Wynne-Edwards & Timonin, 2007; Saltzman & Ziegler, 2014), and several of these hormones can have substantial effects on food intake, metabolism, energetics and body composition. For example, leptin suppresses food intake, increases energy expenditure, and reduces fat and body mass (Hamann & Matthaei, 1996; Klok, Jakobsdottir & Drent, 2007), whereas androgens can stimulate food intake but decrease fat and body mass (Asarian & Geary, 2006; Kelly & Jones, 2013). Accordingly, males in biparental species may undergo systematic changes in body

mass and body fat levels during their mate's gestational and lactational periods. For example, in two biparental primates, the common marmoset *Callithrix jacchus* and the cotton-top tamarin *Saguinus oedipus*, expectant fathers undergo significant weight gain during their mate's pregnancy, especially in the final month, followed by weight loss in the early lactational period (Sánchez *et al.*, 1999; Achenbach & Snowdon, 2002; Ziegler *et al.*, 2006, 2009). Biparental prairie vole *Microtus ochrogaster* fathers also lose weight, as well as subcutaneous fat, while caring for pups (Campbell *et al.*, 2009; Kenkel, Suboc & Carter, 2014).

The specific social and reproductive factors influencing body-mass changes in fathers have often been difficult to identify. For example, in many studies of biparental mammals – most of which are socially and/or genetically monogamous – fatherhood was confounded with cohabitation with a female, which could potentially influence male body mass independently of parental status. Moreover, because females in the species that have been studied undergo post-partum ovulation (McNeilly *et al.*, 1981; Gubernick, 1988; Carter *et al.*, 1989; Ziegler *et al.*, 1990), these studies often have not distinguished between potential effects of the mate's pregnancy and of caring for dependent offspring from the previous litter (but see Sánchez Rodríguez *et al.*, 2008).

Similar to the common marmoset, cotton-top tamarin and prairie vole, a study of the genetically monogamous and biparental California mouse *Peromyscus californicus* (Gubernick & Alberts, 1987; Ribble & Salvioni, 1990; Ribble, 1991) found that body mass of experienced fathers increased significantly toward the end of their mate's pregnancy and decreased during the early post-partum period; however, this study was not designed to identify specific reproductive and social determinants of these changes (Harris, Perea-Rodriguez & Saltzman, 2011). In the present study, we further investigated changes in male body mass as a function of social and reproductive status in laboratory-housed California mice. Females produce litters of 1–4 pups at ~35-day intervals and are almost continuously pregnant due to post-partum estrus (Gubernick, 1988; unpubl. data). Pups are weaned at approximately 30–40 days of age and disperse from the natal nest at about 80 days (Ribble, 1992; Gubernick & Teferi, 2000). Fathers invest heavily in their offspring, engaging in all the same post-partum parental behaviors as mothers (except nursing), and to a similar extent (Gubernick & Alberts, 1987).

We addressed the following questions: (1) Does cohabitation with a non-reproductive female affect male body mass compared to cohabitation with a male? (2) Does cohabitation with a pregnant female affect male body mass compared to cohabitation with a non-reproductive female? (3) In experienced fathers, are changes in body mass across the mate's pregnancy affected by the presence of pups from the previous litter? To answer these questions, we compared body mass over a period of 5 weeks among adult male California mice in five conditions: males housed with another male, males housed with a non-reproductive (tubally ligated) female, males whose mates were pregnant for the first time, and experienced fathers whose mates were pregnant and who either did or did not live with pups from their previous litter.

We predicted that (1) males housed with non-reproductive females would have body mass similar to those housed in same-sex pairs, as neither group faced the energetic demands of fatherhood; (2) expectant fathers would gain body mass across their mate's pregnancy, in preparation for the birth of pups, whereas males housed with non-reproductive females would not show a systematic change in body mass during a comparable period of time; (3) among experienced breeders, this body-mass gain would be more pronounced in expectant fathers that were not simultaneously caring for their previous litter (i.e. experienced breeders whose previous litter had died) compared to expectant fathers that were also caring for their previous litter, as mass gain in the latter group would be offset to some extent by the energetic demands of pup care.

Materials and methods

Animals

We used California mice that were born and reared in our breeding colony at the University of California, Riverside (UCR) and that were descended from mice purchased from the Peromyscus Genetic Stock Center (University of South Carolina, Columbia, SC, USA). Mice were housed in standard, shoebox-style, polycarbonate cages ($44 \times 24 \times 20$ cm) containing aspen shavings for bedding and cotton wool for nesting material, with *ad libitum* access to food (Purina Rodent Chow 5001, PMI Nutrition International, St Louis, MO, USA) and water. Lights were on a 14:10 light : dark cycle, with lights on from 05:00 to 19:00 h. Ambient temperature was approximately 23°C, and humidity was approximately 65% (Harris *et al.*, 2011). Cages were checked daily and changed weekly.

At 27–32 days, prior to the birth of the next litter of siblings, pups were permanently removed from their natal cage and housed in same-sex groups containing four age-matched, related and/or unrelated animals. When mice reached early adulthood ($\geq$90 days of age), they were either placed into breeding pairs (one male and one female), placed into non-reproductive pairs (one male and one tubally ligated female; see below) or housed in virgin-male pairs with another male from their original same-sex group (Table 1). Typically, opposite-sexed pairmates were no more closely related to each other than first cousins.

Male and female mice were weighed to the nearest milligram twice weekly, at 3- to 4-day intervals, for at least 5 weeks. For breeding pairs, this included the 5 weeks prior to the birth of the first litter (new breeders, NB; $n = 116$) or a subsequent litter (experienced breeders, EB; $n = 30$). Experienced breeding pairs had produced one to four litters prior to the beginning of data collection (1.52 ± 0.15, mean $\pm$ SEM). For non-reproductive opposite-sex pairs (males pair-housed with a tubally ligated female, TL; $n = 28$) and males housed in same-sex pairs (virgin males, VM; $n = 31$), the period of data collection was matched to that of new breeders undergoing data collection at the same time. Hereafter, we refer to the date of parturition in new and experienced breeding pairs, and the corresponding date in virgin-male pairs and pairs with tubally ligated females, as the index date. Each male was used in only

Table 1 Housing/reproductive condition, sample size and mean ± SE age for each group of male California mice *Peromyscus californicus*

Condition	n	Age (days) at index date	Sex of cagemate	Mate pregnant?	Pups present?	Analyses[a]
Virgin males (VM)	31	150.90 ± 3.98	M	No	No	1
Males with tubally ligated (TL) females	28	162.71 ± 3.43	F	No	No	1,2
New breeders (NB) housed with first-time pregnant females	116	160.76 ± 2.37	F	Yes	No	2
Experienced breeders without pups (EB-no pups)	8	224.38 ± 6.78	F	Yes	No	3
Experienced breeders with pups (EB-pups)	22	234.95 ± 5.16	F	Yes	Yes	3

[a]Analysis 1: effect of cagemate's sex; analysis 2: effect of reproductive versus non-reproductive female cagemate; analysis 3: effect of housing with versus without pups in experienced breeders.

one housing condition and contributed only a single, 5-week set of body-mass data to the final dataset.

Body mass was determined between 09:00 and 17:00 h. In a preliminary study of 10 adult males (none of which were used in the full study) weighed at both 09:00 and 17:00 h on a single day, body mass showed a slight but significant decline across the course of the day (09:00 h: 44.2 ± 2.3 g; 17:00 h: 43.7 ± 2.3 g, mean + SE; $t = 3.61$, $P = 0.006$). Because the change across time in this preliminary study was minimal (mean = −0.5 g), and because time of day at weighing in the main study did not differ systemically across weeks or among groups undergoing data collection within a specific 5-week period, time-of-day effects on body mass are unlikely to have affected our results in a biased manner.

Tubal ligations

Females to be housed in non-reproductive pairs underwent bilateral tubal ligation 6–8 days before being paired with a male. Surgeries were performed as previously described (Harris & Saltzman, 2013). Between surgery and pair formation, females were housed individually to facilitate recovery.

Analysis

For each male mouse, we calculated weekly mean body mass (typically the average of two measurements) for 5 consecutive weeks. For new and experienced breeders, an animal's mean mass for week −1 was calculated from all body-mass data collected from that animal 1–7 days before the index date (day of parturition), the mean for week −2 was calculated from all body-mass data collected 8–14 days before the index date, etc. For males in the VM and TL conditions, we used this same procedure to calculate weekly mean body masses for the 5 weeks prior to the index date.

Datasets for body mass, age and index date were inspected visually and checked for normality using Shapiro–Wilks tests. All body-mass values and age data were log$_{10}$-transformed to reduce skewness and kurtosis. We performed separate repeated-measures analyses of covariance (ANCOVAs) comparing pairs of reproductive conditions in order to address each of our *a priori* questions – that is, to determine the effects on male body mass of (1) sex of the cagemate (VM vs. TL); (2) reproductive condition of a female pairmate (TL vs. NB); (3) concurrent housing with dependent pups in experienced

breeding males (EB with vs. EB without pups) (Table 1). Prior to each ANCOVA, we compared age at index date between the two groups using independent-samples t-tests. We also compared age-adjusted week −5 body mass via ANCOVA to determine whether initial body mass differed between the two groups at the beginning of data collection.

For analyses of experienced fathers with ($n = 22$) and without ($n = 8$) pups present, we also used inter-birth interval (IBI; days elapsed from the birth of the previous litter to the birth of the litter at the end of data collection) as a covariate. IBI data were log$_{10}$-transformed to improve normality.

None of the ANCOVAs passed Mauchly's test of sphericity (all P-values < 0.001); therefore, the Huynh–Feldt (1976) adjustment was used for within-subject effects {adjusted results mirrored sphericity-assumed results in all but one instance [week × IBI in EB with and without pups analysis, $P = 0.019$ (sphericity-assumed) vs. 0.055 (adjusted)]}. All data passed Levene's test for equality of error variances (all $Ps > 0.079$). Sidak-adjusted comparisons (Abdi, 2007; Ruxton & Beauchamp, 2008) were used for all post-hoc analyses. All analyses were performed using SPSS v. 20 (IBM, Armonk, NY, USA). All tests were two-tailed, and P-values < 0.05 were considered statistically significant.

## Results

Effect of sex of cagemate

We compared body mass across weeks in males housed with another male (VM) and those housed with a tubally ligated female using age as a covariate. Male body mass was not affected by sex of the cagemate ($F_{1,56} = 3.26$, $P = 0.076$), week ($F_{1.71,95.96} = 1.34$, $P = 0.266$) or the interaction between week and cagemate's sex ($F_{1.71,95.96} = 1.05$, $P = 0.346$; Fig. 1). We found no interaction between week and age ($F_{1.71,95.96} = 1.45$, $P = 0.240$), but body mass increased with increasing age ($F_{1,56} = 8.15$, $P = 0.006$). Tubally ligated males were significantly older at index date than were VM ($t_{57} = 2.35$, $P = 0.020$). VM and TL did not differ in body mass at week −5 ($F_{1,56} = 2.32$, $P = 0.133$).

Effect of reproductive status of female cagemate

Comparison of body mass across weeks in males paired with a tubally ligated female and males housed with a female
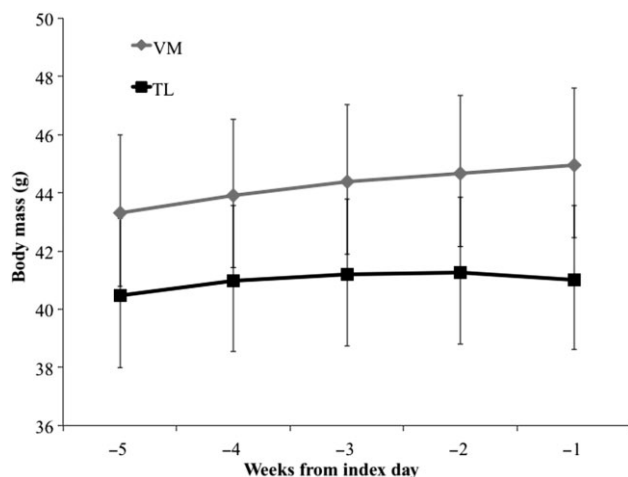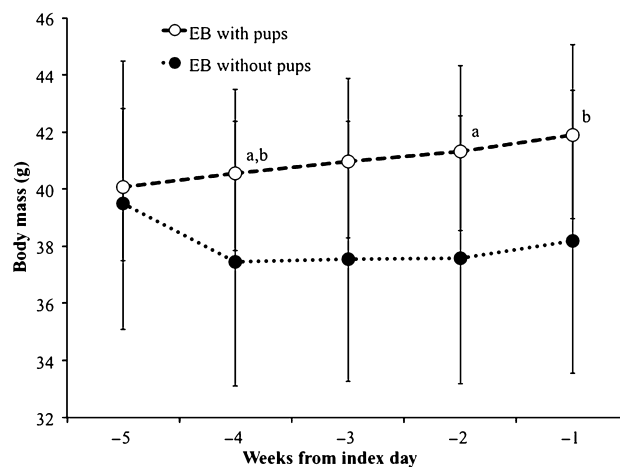
Figure 1 Body mass across weeks in virgin males (VM) housed with another male and in males paired with tubally ligated (TL) females. Data presented are back-transformed means ± 95% confidence intervals at a back-transformed age of 155.99 days. Body mass was not affected by housing condition, week or a week × condition interaction.
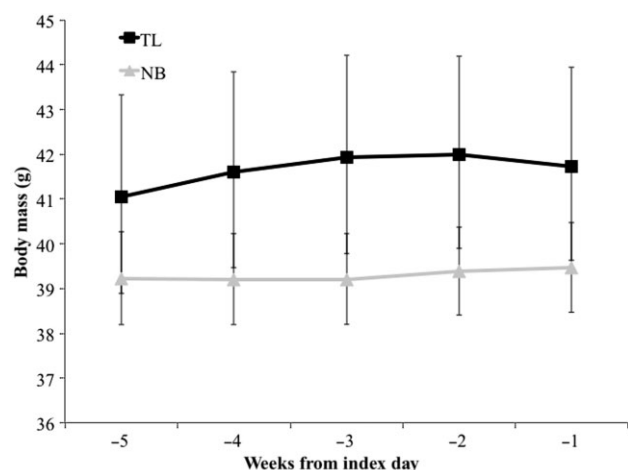
Figure 2 Body mass across weeks in males paired with tubally ligated (TL) females and in newly breeding (NB) males pair-housed with primigravid females. Data presented are back-transformed means ± 95% confidence intervals at a back-transformed age of 159.51 days. Overall, TLs were significantly heavier than NB males (main effect of reproductive condition, *P* < 0.05).

pregnant with her first litter (NB) revealed that TL males weighed more than NBs overall ($F_{1,141} = 4.07$, $P = 0.046$; Fig. 2). Body mass also increased with age ($F_{1,141} = 5.43$, $P = 0.021$), but no other significant effects were found (week: $F_{1.95,275.24} = 1.34$, $P = 0.552$; week × reproductive condition interaction: $F_{1.95,275.24} = 1.70$, $P = 0.185$; week × age interaction: $F_{1.95,275.24} = 0.62$, $P = 0.536$). NB and TL did not differ in age at index date ($t_{142} = 0.557$) or body mass at week −5 ($F_{1,141} = 2.23$, $P = 0.138$).

Figure 3 Body mass across weeks in experienced breeding (EB) males with and without surviving pups from the previous litter. Data presented are back-transformed means ± 95% confidence intervals at a back-transformed age of 231.05 days and back-transformed inter-birth interval of 40.70 days. Statistics correspond to Sidak-adjusted post-hoc tests following a significant week × condition interaction ($P = 0.009$). Only EB males with pups experienced significant changes in body mass across weeks. Within this condition, time points with the same superscript differ significantly from one another ($Ps < 0.05$).

Effect of cohabitation with pups in experienced fathers

We compared body mass in experienced fathers whose previous litter had died naturally (i.e. as a result of stillbirth, congenital or health problems in the pups, and/or infanticide; on postnatal day 0–4) and those whose pups had survived. EBs with surviving pups had significantly shorter IBIs than those without surviving pups ($t_{28} = 2.88$, $P = 0.007$), and IBI was included as a covariate.

Male body mass across weeks of the mate's subsequent pregnancy differed between fathers living with pups and those whose previous litter had died (week × condition interaction: $F_{1.98,51.47} = 5.15$, $P = 0.009$). EB housed with surviving pups showed significant changes in body mass over weeks (see below), whereas EB whose pups had died did not (all *P*-values > 0.191; Fig. 3). Specifically, EBs with pups tended to gain mass in the second half of their mate's pregnancy: they were heavier at week −2 than at week −4 ($t = 4.00$, $P = 0.017$) and heavier at week −1 than at week −4 ($t = 3.50$, $P = 0.006$); they also tended to be heavier at week −1 compared to week −5 ($t = 3.17$, $P = 0.056$). EB with and without pups present did not differ significantly from one another in any individual week (all *Ps* > 0.205).

No other significant effects were found (week: $F_{1.98,51.47} = 0.650$, $P = 0.526$; age: $F_{1,26} = 0.32$, $P = 0.579$; IBI: $F_{1,26} = 1.26$, $P = 0.271$; presence of pups: $F_{1,26} = 1.07$, $P = 0.310$; week × IBI interaction: $F_{1.98,51.47} = 3.08$, $P = 0.055$; week × age interaction: $F_{1.98,51.47} = 0.19$, $P = 0.827$). EB with and without surviving pups did not differ in age at index date ($t_{28} = 1.11$, $P = 0.278$).

Discussion

In this study, we sought to expand upon previous findings that fathers in biparental mammalian species undergo changes in body mass before and during periods of infant care, by identifying the specific social and reproductive factors contributing to these changes. We found that body mass did not differ between virgins housed with an age-matched male and males housed with a tubally ligated female. On the other hand, males whose mates were pregnant with their first litter weighed significantly less than males housed with tubally ligated females. These results suggest that sex *per se* of the cagemate might not influence body mass in males, but that cohabitation with a reproductive (pregnant) female may reduce male body mass or attenuate increases in body mass over time, as compared to cohabitation with a non-reproductive female.

In the biparental rodents (California mouse, prairie vole) and monkeys (common marmoset, cotton-top tamarin) in which body-mass changes in fathers have been characterized, females typically undergo post-partum ovulation, at least in captivity; thus, the lactational and gestational periods often coincide. Consequently, body-mass changes in experienced fathers cannot be attributed readily to effects of infant care versus effects of the mate's pregnancy. To distinguish between these possibilities, we compared body mass across the mate's pregnancy between experienced breeders that were and were not housed with pups from their previous litter (i.e. fathers whose pups had survived or died, respectively). These analyses revealed that fathers housed with pups underwent significant, progressive increases in body mass during their mate's subsequent pregnancy, whereas fathers housed without pups did not. These results must be interpreted cautiously, however, as body mass of fathers housed with and without pups did not differ significantly at any time point. The body-mass changes seen in experienced fathers housed with pups are similar to results of a previous study, in which male California mice housed with their first litter of pups during their mates' second pregnancy showed a marked rise in body mass shortly before their mates gave birth, followed by a drop in mass within the first few days after parturition (Harris *et al.*, 2011). Similarly, in both common marmosets and cotton-top tamarins, expectant fathers gain body mass primarily toward the end of their mate's pregnancy (Ziegler *et al.*, 2006).

If increases in body mass across the mate's pregnancy function to prepare expectant fathers for the energetic challenges of paternal care, as has been proposed (Ziegler *et al.*, 2006; Sánchez Rodríguez *et al.*, 2008), these increases might be expected to occur in all males housed with pregnant females; however, they might be less pronounced in fathers caring for a litter due to the concurrent energetic demands of paternal care. In contrast, our findings suggest that changes in fathers' body mass across their mates' pregnancy may be driven largely by interactions with pups (i.e. paternal care) rather than by the mate's pregnancy *per se.* This could also account for the absence of body-mass changes across the mate's first pregnancy in new breeders.

Importantly, the correspondence between cohabitation with pups (i.e. engagement in paternal care) and body-mass changes in experienced breeders in this study might not reflect a causal relationship between the two; instead, a common factor might have influenced both survival of the previous litter and subsequent mass gain in fathers. For example, both loss of infants and absence of body-mass changes during the mate's subsequent pregnancy could have resulted from atypical hormonal responses to fatherhood in these males (see, e.g., Good, Harris & Ihunnah, 2005).

In contrast to our results, findings in other biparental mammals indicate that fathers lose body mass during periods of infant care. In cotton-top tamarins, fathers have been reported to gain mass across their mates' pregnancy and to lose mass while caring for infants; however, whether the females in these studies conceived post-partum, and therefore whether males were providing infant care during their mate's pregnancy, is not clear (Sánchez *et al.*, 1999, 2005; Achenbach & Snowdon, 2002; Ziegler *et al.*, 2006; Sánchez Rodríguez *et al.*, 2008). In a longitudinal study of prairie voles, fathers underwent significant reductions in body mass shortly before the birth of their second litter, but not before the birth of their first litter, compared to their own values prior to and shortly following pair formation (Campbell *et al.*, 2009). In this species, therefore, paternal care, rather than cohabitation with a pregnant female, appears to drive loss of body mass in breeding males. The hypothesis that providing infant care leads to loss of body mass in (non-reproductive) males (as well as in non-reproductive females) is supported by findings from free-living, cooperatively breeding meerkats *Suricata suricatta* and banded mongooses *Mungos mungo*, in which the amount of infant care performed by individual non-reproductive alloparents was correlated with the extent of body-mass loss (Clutton-Brock *et al.*, 1998; Hodge, 2007).

The physiological and/or behavioral mechanisms underlying changes in male body mass across reproductive conditions are not known. One possibility is that males housed with breeding females have higher energy utilization (due, e.g., to increased physical activity and/or elevated basal metabolic rate) compared to non-fathers. Other potential mechanisms, which are not mutually exclusive, include changes in food intake and in assimilation efficiency. Notably, whether California mice rely primarily on fat stores to meet the energetic demands of parenting (i.e., capital breeders) or instead use increased food intake (i.e., income breeders; Jönsson, 1997) is not known; however, studies of *Peromyscus leucopus* suggest that females of this species are primarily income breeders (Millar, 1975).

The functional significance, if any, of body-mass changes in California mouse fathers, or in fathers in other biparental mammalian species, is also not known. Several authors (Sánchez *et al.*, 1999; Achenbach & Snowdon, 2002; Campbell *et al.*, 2009) have suggested that reductions in body mass with fatherhood are not beneficial *per se* but, on the contrary, are inherent costs associated with the energetic demands of paternal care. Others (Ziegler *et al.*, 2006; Sánchez Rodríguez *et al.*, 2008) have focused on body-mass gain in fathers across their mates' pregnancy, suggesting that these increases prepare fathers for the energetic challenges of caring for infants. Our findings both that males housed with pregnant females had

lower body mass than males housed with non-reproductive females, and that fathers housed with pups – but not fathers housed without pups – showed increases in mass across the period of paternal care, suggest both that breeding is energetically expensive overall and that dynamic changes in fathers' body mass are driven by paternal care rather than by preparation for the upcoming demands of fatherhood, at least in the California mouse. Alternatively, changes in male body mass with housing condition and breeding experience might simply be byproducts of changes in such hormones as prolactin, testosterone, or progesterone (Saltzman & Ziegler, 2014), all of which have been found to vary with reproductive condition in male California mice (Gubernick & Nelson, 1989; Trainor *et al.*, 2003). Whether loss of body mass in fathers, or attenuation of increases in body mass, do in fact represent costs and have any effects on Darwinian fitness under natural conditions is not known. The functional significance, if any, of these changes could be illuminated by comparative studies of biparental and uniparental congeners.

It is especially noteworthy that significant between-group differences and within-group changes in male body mass, in California mice as well as other biparental mammals, have been found in laboratory-housed animals, which do not face such energetic demands as searching for food, defending territories, mate-guarding, thermoregulating under harsh ambient temperature conditions, or detecting and avoiding predators. Studies of fathers in biparental species living under natural conditions are likely to reveal even more pronounced effects of reproductive status on body mass (e.g. Sánchez *et al.*, 2005) and would provide new insights into the biology of paternal care.

Acknowledgments

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