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Early fitness consequences and hormonal correlates of parental behaviour in the social rodent, *Octodon degus*

Luis A. Ebensperger [a,*], Natalia Ramírez-Otarola [a], Cecilia León [a], María E. Ortiz [b], Horacio B. Croxatto [c]

[a] *Centro de Estudios Avanzados en Ecología & Biodiversidad, and Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Chile*
[b] *Instituto Chileno de Medicina Reproductiva (ICMER), Chile*
[c] *Departamento de Biología, Facultad de Química y Biología, Universidad de Santiago de Chile, Chile*

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ABSTRACT

Males are expected to assist their mates whenever this behaviour raises survival of offspring with little expense in terms of mating opportunities. At a more proximate level, cortisol and testosterone hormones seem involved in the expression of parental care in mammals. We examined the consequences to postnatal offspring development and survival of the males' presence in the social rodent, *Octodon degus*. Offspring quality and quantity, and maternal condition of females were contrasted among females rearing their litters in the presence of the sire, females breeding in the presence of a non-breeding female, and females breeding solitarily. We related these differences to variation in parental behaviour and plasma levels of testosterone and cortisol. Twenty two females and their litters were studied under constant conditions of adult density, nest availability, food availability, and breeding experience. Males huddled over and groomed offspring. However, neither the number nor the mass of pups from dams that nested with the sire differed from those recorded to breeding females that nested with a non-breeding female and females that nested solitarily. Body weight loss and associated levels of plasma cortisol in dams nesting with the sire were similar to those of solitary females, but higher than mothers nesting with a non-breeding female. Thus, male care had no consequences to offspring, and seemed detrimental to breeding females. Circulating levels of cortisol and total testosterone were either poor (mothers) or no (fathers, non-breeding females) predictors of parental care.

1. Introduction

The scattered distribution of parental behaviour across vertebrates indicates that this trait has evolved multiple times [1]. In mammals most species exhibit uniparental care where the females typically become the parental sex [2,3]. While paternal care is generally rare across mammals, it occurs more often in species of carnivores, primates and perissodactyls, in which biparental care is the rule [3]. A greater frequency of female uniparental care is expected given that mammalian females are more associated with offspring than males through pregnancy and lactation, two processes that are energetically costly [4].

Males are expected to assist their mates whenever the young that survive under biparental care exceeds survival under uniparental care times the mating success of a nonparental male [3]. Unsurprisingly, experimental studies that examine the consequences of a male's presence on quantity and quality of offspring in mammals have relied on rodent models amenable to experimentation. These studies support that the importance of a father's presence is contingent upon animals facing environmentally challenging conditions. Thus, the sire's presence enhances infant survivorship under cold (i.e., energetically stressful) but not under warm ambient conditions in the California mouse, *Peromyscus californicus* [5], and Djungarian hamsters, *Phodopus campbelli* [6]. Low temperatures also seem linked with male-increased offspring development in the striped mouse, *Rhabdomys pumilio* [7]. Challenging conditions related to a need to forage for food were recorded to interact with a male's presence to increase pup survival (but not pup growth) in *P. californicus* [8] and in the house mouse (*Mus musculus*) [9]. The presence of sires in Mongolian gerbils (*Meriones unguiculatus*), prairie voles (*Microtus ochrogaster*), and red-backed voles (*Clethrionomys gapperi*) has no direct effect on offspring growth and survival under less challenging rearing conditions [10–12].

A male might be expected to provide brood care under conditions where its presence has marginal consequences to offspring survival and growth provided that expectations for additional breeding attempts are relatively low [3]. Factors that may decrease probability of multiple mating in males include a spatially over dispersed distribution of females and high synchrony of female oestrus [13–16]. Expectations for

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* Corresponding author. Centro de Estudios Avanzados en Ecología & Biodiversidad, and Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile.
E-mail address: lebensperger@bio.puc.cl (L.A. Ebensperger).

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subsequent breeding could be further reduced in males of species that breed annually and in which annual mortality of adults is high.

To a more proximate level of causation, evidence is generally consistent with the hypothesis that hormones are implied in the expression of maternal and paternal behaviours in mammals [17,18]. Regarding paternal behaviour, the role played by different hormones is variable across species. Thus, while paternal behaviour takes place in association with relatively high levels of prolactin in male rodents and primates [but see Ref. [19]] with biparental care [20–23], this hormone seems unimportant to the expression of care in male rodents and carnivores of more polygynous species [24–26]. In some of these species, male parental and alloparental care is instead more associated with high circulating levels of cortisol [19,25] or corticosterone [27], a pattern that contrasts with other rodents and primates in which cortisol decreases upon delivery of offspring [17]. Likewise, variation across species characterizes the role of other hormones such as testosterone. Thus, a reduction in testosterone seems necessary at the onset of paternal and alloparental care in males of polygynous Mongolian gerbils, socially monogamous prairie voles, and black tufted-ear marmosets, *Callithrix kuhlii* [11,28–30]. In contrast, testosterone seems critical to the expression of male care in other biparental species [31,32], but see Ref. [20]. Taken together, a hormonal influence for paternal care in mammals remains indisputable. However, variation linked to roles played by different hormones across species indicates that underlying mechanisms cannot be assumed to be homologous [1,18]. Thus, studies on other, phylogenetically unrelated species may serve the double purpose of contributing to these patterns of variation and providing additional independent replicates to subsequent comparative analyses.

Based on the above, our study had two major objectives. First, we examined the consequences of the males' presence on maternal condition and early offspring growth and survival in the social rodent, *Octodon degus*. We chose degus because several aspects of the reproductive biology and demography of these rodents indicate that a cost in terms of mating opportunities to male degus is probably nil. Degus typically breed once per year [33]: mating at the time of litter delivery (i.e., 3 months after the main mating episode) as a result of postpartum oestrous is rare (L.A. Ebensperger unpublished observations). In addition, most adults (and males in particular) die before two years of age [34–36], suggesting that success during first breeding event has a major impact on lifetime fitness. We predicted these conditions would favour males of this species providing paternal care to some extent. Degus live in social groups where a variable number of females (1–4) share an underground burrow system and a foraging area with one or two males [37,38]. While communal nesting by lactating females under semi-natural and natural conditions has been well demonstrated [37,39], the role played by males remains unknown. During lactation, males also share underground burrows with the females.

A second major objective of our study was to examine hormonal correlates of parental behaviour in these rodents. Most endocrinological evidence on parental care in rodents comes from murid species (mice, rats) where prolactin, cortisol, and testosterone seem to play roles. In contrast, proximate correlates of paternal care among hystricognath species lag behind despite the prevalence of reports of paternal behaviour in these rodents [40]. While no endocrinological studies have examined the parental behaviour of degus, glucocorticoids (mainly cortisol) and androgens (testosterone) mirror major breeding events in wild populations [41–43], implying that these hormones may play roles.

2. Methods

2.1. Study subjects, animal housing and experimental setting

The study subjects were one year old, laboratory raised *O. degus* (Pontificia Universidad Católica de Chile), representing a first generation of wild pregnant female descendants captured in Rinconada de Maipú (33°23′ S, 70°31′ W; 30 km west of Santiago), central Chile. Upon weaning (ca. 30 days of age), degu subjects were kept in same sex-sibling pairs inside 45 by 23 by 21 cm clear polycarbonate rat cages with a bedding of hardwood chips, and water and food (rabbit commercial pellet) provided ad lib. Animals were kept in a ventilated room exposed to a 12:12 h light:dark cycle with temperatures controlled between ca. 15–25 °C. Available data for 2003 through 2008 recorded at the Pudahuel weather station (Dirección Meteorológica de Chile), distant 15 km from Rinconada de Maipú, indicated that minimum air temperature averages 5.5 and 7.4 °C during September and October (time during which lactation and offspring weaning takes place), respectively. Maximum air temperature during September and October averages 19.2 and 22.5 °C.

When 3 months of age, female siblings were marked with an ear tag and transferred to a cage with either a full sister (related) or a completely unrelated female. Pairs of related ($n=15$) and unrelated ($n=18$) female pairs were then allowed to mate with a same age, unrelated male when 10 months of age. Upon 60 days of the introduction of males, time at which pregnant females were easy to recognize, animals were assigned to one of three conditions and transferred to experimental cages and housed in a different room.

Three experimental conditions were compared. Two of these consisted of (1) a female raising her litter in the presence of the sire ($n=7$ female–male pairs), and (2) a female raising her litter in the presence of a non-breeding female (i.e., the former female cage mate that did not became pregnant during the previous stage) ($n=7$ female–female pairs). Thus, sires and non-breeding females were socially familiar to the breeding female, a realistic condition for degus. Breeding females were randomly assigned to nest with a full sib or an unrelated non-breeding female. Previously, we demonstrated that kinship between a breeding female that nested with a non-breeding female does not influence offspring development, survival and body condition of dams [44]. These two social conditions allowed us to separate the potential effect of maleness care from that due to the presence of an additional adult. With the aim of comparing our results to previous studies, we also included (3) a condition in which a female raised her offspring solitarily ($n=8$ females). All three experimental conditions to which female subjects were assigned (solitary, breeding with male, breeding with female) were established from previous trios in which only one of the two females became pregnant. It has been argued that pregnancy of dams that mate during postpartum estrus may potentially overshadow the effects due to the presence of fathers on female behaviour [10]. While postpartum estrus has been suggested in degus [45], its occurrence is rare [46]. Most critical to this study, none of the experimental females that nested with the male through lactation became pregnant.

Approximately 7–15 days before estimated delivery, breeding females and their cage mates (experimental conditions 1 and 2) were transferred into squared-shaped (61.5 by 62.0 by 40.5 cm) clear acrylic aquaria, and housed in a different (experimental) room. The rear section of these cages was provided with two clear nest boxes to facilitate observation (18 by 29 by 15 cm) lined next to each other. Solitary nesting females were housed into rectangular-shaped (61.5 by 31.5 by 40.5 cm) clear acrylic aquaria. The rear section of these aquaria housed a single clear nest box made of clear glass (18 by 29 by 15 cm). These cage dimensions allowed us to keep adult density constant through the experiments. Cage size (and the resulting space per animal) may influence food intake and metabolic expenditure in captive rodents [47]. While in these cages, degu subjects were supplied with a 1–2 cm layer of saw dust as bedding material, and water ad lib. Food consisted of rabbit commercial pellet and was provided in such a way that females obtained no more than their empirically determined energy requirements for adult lactating and non-lactating females [48]. Photoperiod of room housing the animals inside the experimental room was controlled and set according to conditions of temperature and photoperiod of a natural population of