Physiology & Behavior 104 (2011) 948–954

Contents lists available at ScienceDirect

Physiology & Behavior

journal homepage: www.elsevier.com/locate/phb

Social stress and reproductive success in the female Syrian hamster: Endocrine and behavioral correlates

Marie Odile Monier Chelini [a,*], Rupert Palme [b], Emma Otta [a]

[a] Department of Experimental Psychology, Institute of Psychology, Av. Prof. Mello Moraes, 1721, University of São Paulo, São Paulo, Brazil
[b] Department of Biomedical Sciences/Biochemistry, University of Veterinary Medicine, Veterinärplatz 1, 1210, Vienna, Austria

ARTICLE INFO

Article history:
Received 22 September 2010
Received in revised form 27 May 2011
Accepted 10 June 2011

Keywords:
Hamster
Social stress
Reproductive success
Sociobiology
Cortisol
Estrogens
Progesterone
Fecal metabolites
Non-invasive monitoring
Endocrinology

ABSTRACT

In many mammal species, reproduction is not shared equally among the members of a social unit. Even though reproductive skew seems unlikely in females of solitary species, this phenomenon could result from environmental factors. Although solitary in the wild, captive Syrian hamsters (*Mesocricetus auratus*) are generally housed in groups. We investigated whether social stress produces some degree of reproductive skew in this solitary species and whether female reproductive success varies as a function of social rank. To assess the physiological relationship between social stress and fertility, we monitored reproductive hormones and glucocorticoids of solitary and pair-housed females during pregnancy by means of recently established non-invasive methods for measuring hormone metabolites in the feces. The patterns of fecal progesterone, estrogen and glucocorticoid metabolites were similar to those found in blood and reported in the literature for pregnant hamsters. As expected, dominant females had higher breeding success than subordinate females. However the rate of reproductive failure was also very high among the singly housed females of our control group. The number of pups per litter, the average sex-ratio in each group, and the mean weight of pups did not differ significantly among groups. Glucocorticoid concentrations were unaffected by housing and social rank and the few differences between the endocrine profiles of singly- and pair-housed females are not sufficient to explain the observed difference in breeding success. It is likely that social isolation impairs reproduction in the same manner as subordination. Our findings suggest that social isolation of animals accustomed to group living was equally as disturbing as cohabitation with an unknown conspecific.

1. Introduction

In many mammal species, reproduction is not shared equally among the members of a social unit. Known as reproductive skew, this phenomenon is ubiquitous among social, cooperatively breeding animals. Typically, a dominant individual monopolizes most (e.g. common marmosets [1]), if not all (e.g. naked mole-rats, *Heterocephalus glaber* [2]) of the group's reproductive output.

While high reproductive skew is relatively common among females of cooperatively breeding species, only low skew, if any, occurs in females that do not breed cooperatively [3]. A fortiori, reproductive skew seems unlikely in females of solitary species, and to the best of our knowledge, has only been reported in one such species. In a study of group-housed wolverines (*Gulo gulo*), a solitary species in the wild, Dalerum et al. [4] observed reproductive failures probably related to social rank, although no single female monopolized reproduction.

Social organization is affected by environmental factors such as density or resource distribution, and intraspecies variation in social systems related to environmental variability has been observed in a number of species. For example, studies conducted on populations of Bamboo rats (*Kannabateomys amblyonyx*) in southeastern Brazil found traits corresponding to either polygyny or monogamy depending on the region [5]. Similarly, African striped mice (*Rhabdomys pumilio)* live in groups in a semi-desert region but are solitary in the moist grasslands of South Africa [6]. Moreover, Sachser [7] showed that individual guinea-pigs interact in ways affected by previous social experiences. Finally, in the Dalerum et al. [4] study, group housed wolverines displayed social interactions similar to those of many obligate group-living species. If ecological factors affect sociability, we might expect that many behavioral and physiological mechanisms responsible for reproductive suppression are present as latent traits, even in species usually considered as solitary.

In several models for the social suppression of reproduction which have been described and used to study the evolution of social group formation [8] both behavioral and physiological mechanisms may account for the observed suppression. Lower reproductive success of subordinate females has been considered conventionally as an effect of subordination stress and related high levels of glucocorticoids.

---

* Corresponding author at: Departamento de Psicologia Experimental, Instituto de Psicologia, Av. Prof. Mello Moraes, 1721, CEP 05508-030, Cidade Universitária, São Paulo, Brazil. Tel.: +55 11 95742871.
E-mail address: marodile@usp.br (M.O.M. Chelini).

0031-9384/$ – see front matter © 2011 Elsevier Inc. All rights reserved.
doi:10.1016/j.physbeh.2011.06.006

However, in many species, dominant individuals show higher glucocorticoid levels than subordinates [3], and sexual behavior as well as reproductive hormone levels seems modulated by still unclear non-glucocorticoid-mediated mechanisms.

Although solitary in the wild [9]; captive Syrian hamsters (*Mesocricetus auratus*) are generally housed in groups. Grouping of adult hamsters forcing social interaction has been shown to produce symptoms of stress [10]. For this reason, the Syrian hamster has been considered as an ideal model for studying effects of social stress on reproduction [11]. Several authors reported the establishment of a stable social hierarchy in group-housed hamsters as well as some degree of reproduction suppression, including reduction in litter size and the percentage of male pups born from subordinate females [11–13].

On the other hand, more recent studies suggested that the exposure to social stress causes no long-lasting effects on the agonistic behavior of the female hamster [14,15]. Specifically, the group-housing-induced dominance hierarchy – stable in males – is unstable among females [16].

Potential endocrine influences on aggressive and submissive behavior have been examined with ambiguous results. Pratt and Lisk [12] reported a significant reduction in circulating progesterone concentrations in female hamsters exposed to social subordination early in pregnancy. Although they did not provide any physiological measure of the hypothalamic–pituitary–adrenal (HPA) axis activity, they suggested that the stress-related activation of HPA is responsible for this decrease. In contrast, Fritzsche et al. [16] found higher levels of progesterone in both dominant and subordinate group-housed cycling females when compared with those housed individually. Females treated with an estradiol or testosterone implant displayed less submissive behavior than females receiving progesterone or no hormone [17]. The exact role of adrenal glucocorticoids in the modulation of agonistic behavior and their potential effects on the reproductive success of female hamsters is still unclear.

The aim of our study was to examine the effects of social grouping on the female Syrian hamster, both before and at the beginning of gestation. We investigated whether social stress produces some degree of reproductive skew in this solitary species and whether female reproductive success varies as a function of social rank. In order to assess the physiological relationship between social stress and fertility, we monitored reproductive hormones and glucocorticoids of solitary and pair-housed females during pregnancy by means of recently established non-invasive methods [18,19] for measuring the respective hormone metabolites in the feces.

We hypothesized that: 1) the fertility of the dominant females would be similar to those in isolation; 2) reproductive skew would occur in pair-housed females; 3) there would be more reproductive failure among subordinate females than among dominant or isolated females; 4) subordinate females would deliver smaller litters than dominant or isolated females; 5) a female bias in the sex ratio would only occur in subordinate females, and finally; 6) endocrine profiles would differ between groups.

2. Material and methods

2.1. Animals and housing conditions

The subjects were 34 adult (12 weeks of age; mean body weight 170 ± 15 g) female Syrian hamsters (*Mesocricetus auratus*) kept in isosexual groups of four or five individuals from weaning. These hamsters were born and raised in the Laboratory Animal Facility of the Departamento de Patologia, Faculdade de Medicina Veterinária e Zootecnia, Universidade de São Paulo, Brazil, whose Ethics Committee approved the experimental design. The animals were housed in standard propylene cages in the same animal facility under conventional conditions (12:12-h light:dark, lights on at 03:00 h; room temperature: 22 ± 2 °C; 20 changes of air per hour; air pouch filters). Specific pelleted food (Nuvilab CR1, Nuvital, Curitiba, Brazil) and filtered bottled tap water were supplied ad libitum. The animals were free from any common pathogens according to the FELASA Health Monitoring Recommendations [20]. In order to facilitate feces collection for endocrine analysis, absorbent paper pads were used in place of wood-shaving bedding.

2.2. Procedure

At least two consecutive 4-day cycles per female were monitored before the beginning of the trial by detection of the characteristic post-ovulatory discharge in the morning following ovulation. One animal was discarded because it was not regularly cycling. Among the others we selected 11 pairs of non-relative females (PH = pair housed) with similar body weight (± 5 g). As the expression of aggressive behavior is estrus-cycle dependent, females in a pair had synchronized estrus cycles [16,21]. Each female was marked with a commercial hair dye in a recognizable pattern to facilitate behavioral recording. These animals remained housed in pairs for 10 days. The remaining 11 females, forming the control group (ISOL = isolated), were housed singly.

To determine the social rank of pair-kept females, the behavior of each pair was observed continuously during three 10-min sessions with 4-day intervals between sessions. Before these observations each pair was separated for 20 min during the routine cage exchange and then regrouped in a clean cage containing 7 food pellets scattered on the floor. Aggressive (upright/side offense, chase, bite, attack) and defensive (upright/side defense, flee, full submissive posture) behaviors regarded as specific markers or indices of social stress [22] were recorded, as well as how many food pellets each animal secured. Huck et al. [13] showed that dominant females successfully removed food from the subordinate females. In each encounter one point was given to the female which displayed more aggressive behavior and one point to the female that secured more food pellets. The female who had the higher score in at least two sessions was considered dominant (DOM) and the other one was subordinate (SUB). All sessions were completed during the first 2 h of the dark phase of the LD cycle under dim red light.

On the first estrus (D0) following the first behavioral observation, all females were mated with proven breeders. Each female was housed with a male for 24 h. Afterwards the former female pairs were regrouped until completing 10 days. All the females were then transferred to individual cages and stayed singly housed until parturition (D16). All cages were daily monitored and parturitions registered on the exact day when they occurred. However, to avoid cannibalism, common in hamsters when females are disturbed after delivery [23], it was only on Day 4 after parturition (D20) that pups were counted and sexed (by measurement of anogenital distance), and dams and litters were weighed.

2.3. Collection of fecal samples

To habituate the females to the sampling procedure, feces collection started 10 days before pair forming. It proceeded daily until the day before parturition to avoid cannibalism. Sample collection took place between 14:00 and 15:00 h at the end of the light period. As hamsters void frequently a small but quite variable number of fecal pellets, samples were easily obtained by transferring each animal into a separate cage until it defecated (approximately 15 to 20 min). After defecation, it was immediately returned to its home cage and fecal samples were collected directly from the cage floor.

2.4. Steroid analyses

Fecal steroids were extracted using the methanol-based procedure described by Palme [24]. Because hamster feces are very dry, lyophilization was not necessary. After the homogenization of each fecal sample, we shook an aliquot of 0.5 g (dry weight) or the whole sample for 20 min on a multivortex with 5 ml of 80% methanol for