

Energetic costs of biparental care behavior in the Siberian dwarf hamster *Phodopus sungorus*

Costos energéticos de la conducta de cuidado biparental en el hamster Siberiano
Phodopus sungorus

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ABSTRACT

In the laboratory and under semi-natural conditions, both male and female Siberian dwarf hamsters (*Phodopus sungorus*) contribute to the care of their young. This study focuses on the energetic costs of parental care in both male and female Siberian dwarf hamsters. In general, parent males and females had higher resting metabolic rate in the presence of pups than parents alone in comparison to control unmated males and females. No significant differences were detected between parent males alone and control unmated males. Parent females had a higher resting metabolic rate in the presence of pups and when they were alone, as compared with control unmated females. This suggests that there was an increased energy expenditure associated to behavioral changes observed in the presence of pups in both males and females. The high metabolic rate female parents without their offspring is likely due to the physiological costs of lactation. The consequences of this behavior in terms of survival value and reproductive success are discussed.

Key words: Biparental care, energy cost, Siberian hamster.

RESUMEN

En condiciones seminaturales y de laboratorio, las hembras y machos de hamsters siberianos (*Phodopus sungorus*) contribuyen al cuidado de sus crías. En este trabajo estudiamos el costo energético del cuidado parental en machos y hembras de esta especie. En general, los padres (hembras y machos) presentan una alta tasa metabólica de reposo en presencia de sus crías en comparación a padres solos y a animales control. No se detectaron diferencias significativas entre padres machos solos y machos controles. Las hembras muestran una tasa metabólica de reposo mayor en presencia de sus crías que cuando se encuentran solas; estas últimas también mostraron una mayor tasa metabólica que hembras controles. La elevada tasa metabólica en reposo en presencia de las crías parece ser consecuencia de cambios conductuales asociados al cuidado parental tanto en hembras como en machos. La elevada tasa metabólica de madres sin sus crías parece reflejar el costo de lactación. Se discuten las consecuencias de esta conducta de cuidado biparental en términos de valor de sobrevivencia y éxito reproductivo.

Palabras claves: Cuidado biparental, costo energético, hamster siberiano

INTRODUCTION

Biparental care involves both parental benefits and costs, and appears to be caused by hormonal mechanisms during reproduction (Matt *et al.* 1990). Parental care has implications in ecological and evolutionary patterns, including life-history strategies (Orians 1969, Trivers 1974, Kleiman 1977, Begon 1985, Clutton-Brock 1991). Using mammalian carnivores as a model and a correlative approach, Gittleman & Oftedal (1987) pointed out that there is a consistent

association between biparental care and high growth rates in canids. In contrast, animals with strictly maternal care have reduced growth rates in pups (e.g., felids and viverrids). Ecological factors such as cold and food availability increase parental care and enhance survival of pups. In fact, Wolf *et al.* (1983) documented that in passerines, when the male parent was removed, a decrease in offspring survival was observed mostly at lower temperatures.

Biparental care is not widespread among rodents (Kleiman 1977). The Siberian dwarf

hamster, *Phodopus sungorus* (Cricetidae), which inhabits the steppes of continental Asia (Siberia), evolved under harsh seasonal environmental conditions, including scarce sheltering vegetation and wide seasonal changes in ambient temperatures, coupled with strong seasonal variation in food abundance, photoperiod and humidity (Weiner 1987). Because individuals of this species live in such a severe environment, their breeding is restricted to only a few months of the year. Therefore, it is essential that pups grow quickly in a short period of time to allow for the maximum number of litters. Thus, biparental investment might be essential to ensure reproductive success under these environmental and time constraints.

The extent to which *P. sungorus* exhibit biparental care is controversial. Wynne-Edwards (1987) found that in Siberian dwarf hamsters held under standard laboratory conditions, the presence or absence of the male had no effect on pup survival. However, Foster *et al.* (1990)¹ documented that in the laboratory both females and males of this species frequently showed parental care behaviors such as scent marking and grooming of pups, nest building, and nesting with pups. In addition, endocrine studies of Matt *et al.* (1990) point out that males of *P. sungorus* paired with pregnant females, demonstrate a gradual increase in plasma levels of prolactin (PRL) toward later stages of pregnancy. Matt *et al.* (1990) postulated that the elevated PRL levels act to: a) facilitate behaviors towards the pups such as nest building, nesting, and grooming, and b) stimulate aggressive behaviors in defense of the pups against an intruder. In view of the naturally harsh environment of *P. sungorus*, one would predict that biparental care would be even more extensive in the field. In fact, we recently observed biparental care in individuals of this species maintained in a large outdoor enclosure under semi-natural conditions.

These data suggest that males might be involved in parental care (Foster *et al.* 1990, Matt *et al.* 1990). Male parental care has also been observed in other rodents, such as *Peromyscus californicus* (Dudley 1974 a,b, Gubernick & Nelson 1989) and the presence of this behavior is also correlated with elevation in plasma levels of PRL in this species. According to Clutton-Brock (1991), the main benefit of parental care to the care-giver lies in its effects on growth, survival and breeding success of its offspring. In addition, male parental care could affect many components of subsequent reproductive success of a female parent. However, the energy costs of this behavior in time and energy (parental expenditure or cost of parental care), remain poorly understood.

Male parental care may be a trait selected for in individuals inhabiting harsh physical and biotic environment (e.g., high predation risk for young, low ambient temperatures, short time for reproduction). However, even though biparental care might have an evolutionary benefit, it may also involve additional energy costs for parents, that is, maintenance of an energy budget sufficient to satisfy the present needs of the parents plus energy and time allocation in care of pups (see Begon 1985, Clutton-Brock 1991).

In this study we examined the energetic costs of biparental care in *P. sungorus*, with emphasis in male parental expenditure. We determined and compared the energetic costs of parental care in parent males and females of this species both in the presence and absence of their young.

MATERIAL AND METHODS

Animals and treatments

All animals of the same age were obtained from the colony at Arizona State University and transferred to the Powdermill Biological Station (which belongs to The Carnegie Museum of Natural History), located within the physiographic division referred to as the Allegheny Mountains Section of the Appalachian Plateau

¹FOSTER CF, GM CREVER & KS MATT (1990) Role of prolactin in parental care in male Siberian dwarf hamsters. *American Zoologist* 30: 25A.

Province, Pennsylvania, U.S.A. (40°10'N, 79°60'W). Six breeding pairs, and six of each unmated male and female controls were placed in individual plexiglass cages (28 by 17.5 by 13 cm). The cages were provided with loosely packed wood shaving for bedding. Food (Purina Laboratory Chow 5001) and water were provided ad lib. Animals were maintained in an outdoor laboratory with natural photoperiod and ambient temperature.

All experiments were conducted during June 1991, and studies began when the pups were one week old. We used families (parents and pups) whose pups ranged in individual body mass (m_b) from approximately 4 to 12 g. Parental care and energy expenditure were stimulated by changing the animals to a new environment (metabolic chamber). A total of six families (male and female parents and pups), and control unmated males and females were studied. We measured oxygen consumption in parent males and females with their pups, in parent males and females maintained during 1.5 h without their pups, and in control unmated males and females.

entering the oxygen analyzer. Animals were tested in an horizontal 380 ml glass jar with food and wood shavings, and equipped with air inlet and outlet (rate of air flow = 1000 ml/min). RMR was measured within thermoneutrality (30 °C), and computed according to the method of Depocas & Hart (1957) and Hill (1972), expressed as the minimum value of oxygen consumption per gram per hour ($mlO_2/g\ h$), and corrected for standard temperature and pressure conditions. Measurements were conducted during 1.5 h and in the resting phase of the animals activity cycle (0800 to 1700 h).

Families (parent male, lactating female and pups) were placed in the metabolic chamber and RMR measurements were conducted, then the parent male was removed and the parent female and pups were immediately measured. The difference between family and parent female plus pups was computed as male parental expenditure or male parental cost. The same protocol was followed for estimation of female parental expenditure. Parent males and females, and control (unmated) males and females were measured alone.

Oxygen consumption

Resting metabolic rate (RMR) as an estimation of energy costs, was measured in the laboratory using a positive pressure «push-through» assembly with a Beckman 755 paramagnetic oxygen analyzer. Air was flowed through columns of soda lime and Drierite to remove CO_2 and H_2O before

Statistical analysis

The significance of treatments on RMR was assessed by a Kruskal-Wallis test. To determine significances of differences between the variables after the Kruskal-Wallis, we used the non parametric a posteriori #C test for multiple comparisons (Steel & Torrie 1985). Differences between

TABLE 1

Resting metabolic rate (mean \pm SE) of males and females of *Phodopus sungorus* under different treatments. Similar letters indicate non statistically significant differences between treatments.

Tasa metabólica de reposo (media \pm EE) de machos y hembras de *Phodopus sungorus* bajo diferentes tratamientos. Las letras similares indican diferencias estadísticamente no significativas entre grupos experimentales.

Treatments	n	Resting Metabolic Rate ($mlO_2/g\ h$)	
		Males	Females
Parent with Pups	6	2.494 \pm 0.326a	3.061 \pm 0.551c
Parent without Pups	6	0.958 \pm 0.098b	1.562 \pm 0.246c
Control	6	0.900 \pm 0.048b	0.874 \pm 0.072d

any two independent means were assessed by the Mann-Whitney U-test. Significance level was 0.05, means are reported with one standard error.

RESULTS

There were no significant differences in body mass between unmated controls and parents (parent males $mb = 32.90 \pm 1.65$ g, control unmated males $mb = 35.61 \pm 2.26$ g, parent females $mb = 30.27 \pm 1.29$ g, control unmated females $mb = 32.47 \pm 1.72$ g, mean \pm SE). Mann-Whitney U-test, $P > 0.168$ for parent males versus control males, and $P > 0.236$ for parent females versus control females.

A comparison of the data of RMR (Table 1) reveals a significant difference between parent males with their pups (parental expenditure or cost of male parental care), and parent males alone; and between parent males with their pups and control unmated males (Kruskal-Wallis, $H = 11.415$, $P < 0.031$; a posteriori, $P < 0.005$ between groups). However, no significant differences were detected between parent males alone and control unmated males (a posteriori test, $P > 0.52$). RMR of male parents with their pups was approximately 2.7 times the RMR values of male parents alone and of control unmated males (Table 1).

Similarly, parent females with pups showed a significantly higher RMR compared with control unmated females (Kruskal-Wallis, $H = 12.363$, $P < 0.0207$). We detected nonsignificant differences between females alone compared with females with pups (a posteriori test, $P > 0.355$). RMR of females with pups was nearly 2 times higher than females alone, —but not significantly different (a posteriori test, $P > 0.452$), and 3.5 times higher than control unmated females (Table 1).

DISCUSSION

Our results strongly suggest that male *P. sungorus* involved in parental care incur an increased metabolic expenditure. This increased expenditure is evident in parental

males only in the presence of their pups (Table 1). This suggests that increased metabolic rate in these males is associated with their displays of parental behavior. This goes contrary to the data for females, in which resting metabolic rate was elevated both in females with their pups and in parent females alone as compared with control unmated females. This may reflect the fact that increases in energy expenditure in females are the result of both behavioral and physiological (lactation) changes.

Matt *et al.* (1990), postulated that elevated levels of PRL act to facilitate behaviors that benefit the pups, such as nest building, nesting, and grooming. Perhaps these changes in PRL are important for inducing both behavioral and metabolic changes that occur with parental care. Our unpublished observations of biparental care in a large outdoor enclosure also support these suggestions. In addition, during our measurements of oxygen consumption we observed the same behaviors of parents towards the pups, which is reflected in a high rate of metabolism (Table 1).

Thus, these behavioral displays and the previously documented hormonal profiles (Schoech & Matt 1989², Foster *et al.* 1990¹, Matt *et al.* 1990, Murphy 1991) are now correlated with the high rate of energy expenditure in both parent males and females with pups (i.e., parental care and expenditure). These physiological, behavioral and energetic features appear to be triggered by the presence of pups.

The metabolic response of the parent female is similar to that of the parent male, but its magnitude increases depending on the presence or absence of the pups. Females with pups showed a higher energy expenditure than parent females alone and control unmated females. However, in contrast to males, parent females alone had a higher metabolic rate than control unmated females. These results may be best explained by the physiological cost of

²SCHOECH SJ & KS MATT (1989) Plasma testosterone levels in male hamsters housed with females vary in response to female reproductive cycle *American Zoologist* 29:98A.

lactation. In fact, the energy expenditure of lactation in mammals lies between 2 and 5 times that for non-reproductive females, and the average caloric intake could be up to 200% (Randolph *et al.* 1977, Thompson & Nicoll 1986, McClure 1987). In *P. sungorus* the metabolizable energy intakes of females during lactation exceed the maintenance energetic requirements by 45% in small and 90% in large litters (see Weiner 1987). Also, Schierwater & Klingel (1986) documented a 24 to 37% increase in the energy costs of production and nursing one litter in this species. Thus, the higher parent expenditure in females as compared to males, could be explained by the behavioral cost of parental care plus the cost of lactation.

According to Weiner (1987), the body mass of females of *P. sungorus* increases during pregnancy and decreases during lactation. However, even though body mass of parent females was slightly lower than unmated controls, we did not observe significant differences between both groups. The absence of a decrease in body weight with lactation may be explained by the fact that these animals have postpartum estrus and many of the females were therefore pregnant during the lactational period.

The disadvantage of this short term increase in energetic costs may be outweighed by the long term fitness benefits. According to Clutton-Brock (1991), the energy expended in reproduction and related processes (i.e., parental care) is not necessarily correlated with an adverse effect on the animal's survival and subsequent breeding success. We postulate that biparental care in *P. sungorus* might be a genetically based trait that is essential to increase the chance of offspring's survival (Gittleman 1985). In addition, male parental care may also be a behavior with indirect consequences on parent females. That is, male parental care may allow an energy saving in females and affect other components of females' subsequent reproductive traits, including their post-partum fecundity, and the survival of the second offspring. This parental behavior may be required to compensate for the high winter

mortality (*sensu* Weiner 1987) that would be predicted for individuals living in a such harsh environments.

Thus, given that time and energy constraints may play a principal role in determining reproductive success in *P. sungorus*, the previously documented hormonal changes in PRL (e.g., Foster *et al.* 1990¹, Matt *et al.* 1990) influencing biparental care and associated cost, might be a selected trait among individuals of this species to achieve high survivorship and reproductive success during a short time of environmentally favorable conditions.

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