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Paternal Care in Collared Lemmings (*Dicrostonyx richardsoni*): Artifact or Adaptation?

ANNA MARIA (TUCHSCHERER) GAJDA[1] and RONALD J. BROOKS[1]

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ABSTRACT. Experiments conducted in large enclosures using 13 pairs of collared lemmings (*Dicrostonyx richardsoni*) and their pups examined the effects of three different treatments on paternal care. Treatments tested whether males altered their attentiveness to the pups when certainty of paternity was in question (through presence of a strange male), when alternative activities were available (through access to a running wheel), and when both factors were present simultaneously. Males covered and groomed pups equally among treatments. During the first five days of observation, males with access to a running wheel paid significantly less attention to strange males relative to males without access to a running wheel. Continuous exposure to the strange male may have been responsible for this short-term effect. Since covering and grooming of pups were unaffected by the presence of a strange male, the fathers' perceptions of their certainty of paternity were probably unaffected. Maintenance of paternal care under diffferent conditions and in large enclosures provides further evidence that paternal care is not an artifact of laboratory conditions. Paternal care in collared lemmings may have evolved to maximize fitness of both sexes during winter.

Key words: collared lemming, paternal care, winter breeding, fitness

RÉSUMÉ. Des expériences menées dans de grands enclos, et mettant en jeu 13 couples de lemmings à collerette (*Dicrostonyx richardsonii*) et leurs petits, évaluaient les effets de 3 traitements différents sur les soins paternels. Ces traitements vérifiaient si les mâles modifiaient l'attention qu'ils portaient à leurs petits lorsque leur paternité était mise en doute (par la présence d'un mâle étranger), lorsque d'autres activités étaient disponibles (par l'accès à une roue d'exercice), et lorsque ces 2 facteurs étaient présents en même temps. Les mâles protégeaient leurs petits et les nettoyaient de la même façon lors des différents traitements. Au cours des 5 premiers jours d'observation, les mâles qui avaient accès à une roue d'exercice prêtaient nettement moins attention aux mâles étrangers, comparativement aux mâles qui n'avaient pas accès à une roue. L'exposition continue au mâle étranger peut expliquer cet effet à court terme. Vu que les soins visant à protéger et à nettoyer les petits n'étaient pas affectés par la présence d'un mâle étranger, la perception qu'avaient les pères quant à la certitude de leur paternité n'était probablement pas affectée. Le maintien des soins paternels dans différentes conditions et à l'intérieur de grands enclos offre une preuve supplémentaire à l'appui que ces soins ne sont pas créés par les conditions de laboratoire. Les soins paternels chez le lemming à collerette ont peut-être évolué afin de maximiser la santé physique des 2 sexes en période hivernale.

Mots clés : lemming à collerette, soins paternels, reproduction hivernale, santé physique

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INTRODUCTION

Most small rodents provide at least some paternal care when confined to small cages, but there is only anecdotal or indirect evidence of this behaviour in the wild (Manning, 1954; Tuchscherer, 1990). Therefore, some researchers (e.g., Daly and Wilson, 1978; Hartung and Dewsbury, 1979; Xia and Millar, 1988) have argued that many examples of paternal care are artifacts of the close confinement of laboratory cages. Male collared lemmings (*Dicrostonyx richardsoni*) provide extensive paternal care in small cages (Shilton and Brooks, 1989) but generally do not appear to do so in the wild (Tuchscherer, 1990). Summer research on collared lemmings suggests that the mating system is polygamous (R.J. Brooks, 1993).

In this study, we test the hypothesis that paternal care is not a behaviour only performed under close confinement and in very simple environments. We examined the effects of increased space and the presence of alternative activities on paternal care in collared lemmings under laboratory conditions. Three predictions were made: 1) Male collared lemmings would continue to provide paternal care when in larger enclosures. 2) Relative to a control, males would maintain equal levels of paternal care when they had access to a running wheel. 3) Relative to a control, males would decrease their attendance to the pups when a strange male was present due to the uncertainty of paternity. If paternal care persisted when the male was provided with a large enclosure and outlets for alternative activities, then the hypothesis that male collared lemmings provide paternal care in the wild would be supported.

METHODS

A metal rack held four 73 cm × 137 cm × 30 cm varnished plywood enclosures, each enclosure having glass on one 137 cm side (Fig. 1). A wire-mesh barrier was fixed 16 cm behind the glass front. The area enclosed by the barrier and the glass formed a compartment in which strange males were housed. The remainder of each enclosure housed the pairs with litters. Physical separation prevented the pair from attacking and potentially killing the strange male. In the pair's portion of each enclosure, a doorway allowed passage to a running wheel 30 cm in diameter. A running wheel was placed on an extension of the metal rack behind each enclosure. Access to the running wheel was provided by a plastic tube. A dark plastic door allowed control of access to the running wheel. The mated pair's portion of the enclosure was partially divided by a wooden wall perpendicular to the barrier, providing an area in which the male could be separated visually from the female and the litter. Food and water were provided *ad libitum*. Enclosures were bedded with Grit-O-Cob and shredded paper.

[1]Department of Zoology, University of Guelph, Guelph, Ontario, Canada N1G 2W1

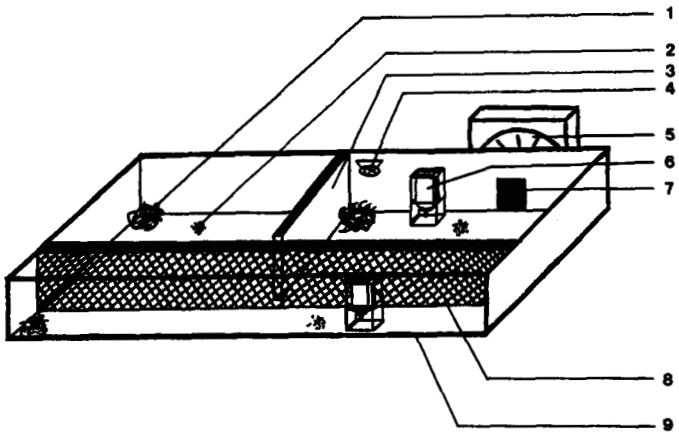

FIG. 1. One of four identical enclosures used in the collared lemming paternal care experiment. During the observations, enclosures were placed vertically on a metal rack. Refer to the text for a complete description. Diagram is not to scale. Label explanations are: 1) shredded paper used as nesting material; 2) food; 3) partial partition in mated pair's portion of enclosure; 4) mirror placed above nest; 5) exercise wheel; 6) water bottle and stand; 7) entrance to exercise wheel; 8) wire mesh barrier separating strange male's portion of enclosure (front) from that of mated pair's (rear); 9) glass front.

Although the size of the enclosures was not sufficient to remove a potential cage effect, these enclosures did allow greater freedom of movement of the pair and pups and also provided alternative activities not available in small mouse cages.

Four treatments were run simultaneously. They were 1) control (pair and pups alone), 2) strange male (pair and pups with strange male on opposite side of a wire-mesh barrier), 3) running wheel (pair and pups with free access to a running wheel) and 4) strange male and running wheel (second and third treatments combined). Laboratory-raised pairs of collared lemmings with no previous parenting experience were placed into one of four treatments on the day their pups were born. Assignment to treatment was sequential: the first pair into the first treatment, the second pair into the second treatment, etc. Pairs were placed in enclosures only after parturition to avoid pregnancy disruptions (Mallory and Brooks, 1980). Thirteen pairs were assigned to treatments: four pairs to the control, and three pairs to each of the three remaining treatments.

Observations on specific pairs began the day after placement in enclosures. When relevant, strange males were placed into compartments at the same time as the mated pair and pups. Mirrors were positioned above nests to ensure a clear view of all nest activities. A single observer recorded observations at 2 min intervals for 1 h periods at 0800, 1300 and 1900 daily. For every hour of observation, therefore, 30 data points were recorded per pair. Observations were conducted until pups were 20 days old. There were 12 behaviour classes recorded during the experiment, as follows: 1) Observes or makes movement towards strange male on opposite side of wire-mesh barrier. 2) Covers one or more pups on or off the nest; male must actively huddle over pups, not just lie on or beside them. 3) Digs in bedding. 4) Eats or drinks. 5) Grooms female or attempts to copulate with her. 6) Grooms pups on or off the nest. 7) Inactive off the nest. 8) Nest builds: takes nesting material to nest or rearranges nest. 9) Autogrooms on or off nest. 10) Retrieves a pup. 11) Sleeps in nest with or without pups; no attempt to cover pups is made. 12) Runs on exercise wheel.

These behaviours were segregated by the location of the female (on nest or off nest); thus a total of 24 unique classes existed. One behaviour was recorded per instantaneous observation.

Pup ages were divided into four groups to reflect the developmental changes that occurred in the 20-day period: day 1–day 5 — the pups rarely moved out of the nest; day 6–day 10 — the pups began to stray from the nest; day 11–day 15 — the pups' eyes opened, facilitating increased exploration of the enclosures; day 16–day 20 — the pups were essentially independent.

Four behaviour patterns (attention paid to strange male, covering pups, retrieving pups and grooming pups) were used as indices of paternal care. Relative proportions of each of these behaviours to all behaviours were used in the statistical analyses.

Using contrasts to minimize possible correlations in behaviour patterns between consecutive time periods, ANOVAs were calculated to test for changes in male behaviour among the four pup age periods and among treatments. The Student Newman-Keuls Test was subsequently used if the ANOVA showed significant ($P \leq 0.05$) effects in order to determine which treatments differed. If the ANOVA showed a significant effect but the Student Newman-Keuls did not, then the effect was taken to be not significant (Snedecor and Cochran, 1980).

RESULTS AND DISCUSSION

Three of the four behaviours chosen as paternal care indices were used in the analyses; retrieving pups occurred too infrequently to be included. Table 1 summarizes the relative level of each paternal activity for each treatment; values for each pup age period have been provided, in addition to an average value for 20 days.

Following Storey and Snow's (1987) methodology, we also have shown evidence of paternal care in collared lemmings. There was no significant difference in the amount of covering or grooming performed by fathers among the four treatments (Table 2). Males provided care for pups in small cages (Shilton and Brooks, 1989), but in that environment the males had no alternative areas in which to move, nor did they have alternative activities available. In this study, all males continued to provide paternal care in larger enclosures and at equal levels, regardless of whether or not alternative activities were possible. The maintenance of paternal care under diverse conditions in the laboratory suggests that paternal care is not simply an artifact of small cage confinement.

Attention paid to a strange male while the female was on the nest occurred more frequently in the treatment with only the strange male compared to the treatment with the strange male and a running wheel (Table 2). When examined across pup developmental stages, this difference occurred only until the pups were five days old (Table 3). These findings

TABLE 1. Proportions of paternal care behaviours expressed as a percentage of total observations (values for each pup age period ± standard deviation are provided, as well as an overall value)

Treatment	Behaviour	Time Period				
		Day 1-5	Day 6-10	Day 11-15	Day 16-20	Overall %
Control	covers — female on nest	3.61± 4.48	3.69±2.73	6.09±3.13	3.58± 0.22	4.26±2.92
	covers — female off nest	18.78± 8.29	23.05±5.87	15.12±7.37	14.48±10.01	18.66±1.20
	grooms — female on nest	1.29± 0.57	2.28±1.36	3.65±1.26	2.10± 1.06	2.24±1.45
	grooms — female off nest	4.33± 2.46	4.49±4.5	2.24±0.86	2.08± 1.37	0.30±0.21
Running wheel	covers — female on nest	1.86± 0.17	1.75±0.55	5.57±2.73	3.04± 1.27	2.79±0.48
	covers — female off nest	24.36±15.16	16.79±9.71	22.01±9.45	26.82±13.34	20.34±9.72
	grooms — female on nest	0.79± 0.58	1.27±1.01	1.71±1.17	0.66± 0.08	1.19±0.29
	grooms — female off nest	3.52± 2.87	2.7 ±0.91	3.42±2.33	2.88± 0.64	3.06±1.39
Strange male	covers — female on nest	5.46± 3.58	4.69±4.86	2.77±0.47	1.40± 0.72	4.71±3.84
	covers — female off nest	17.98±13.16	15.52±2.96	18.67±5.29	19.16± 2.45	16.79±4.06
	grooms — female on nest	1.94± 1.91	3.47±1.46	3.50±2.03	3.04± 1.78	2.85±0.48
	grooms — female off nest	4.39± 3.67	4.46±1.65	5.71±3.w	8.35± 6.74	5.44±3.38
	observes strange male — female on nest	5.38± 2.15	1.07±1.31	0.63±0.60	0.36± 0.51	2.w ±0.67
	observes strange male — female off nest	0.07± 0.13	0.12±0.21	0.23±0.41	0.22± 0.31	0.16±0.22
Strange male and running wheel	covers — female on nest	3.30± 2.98	2.17±0.2	2.19±0.79	1.96± 3.39	2.55±1.03
	covers — female off nest	35.62±10.48	23.32±5.58	16.93±4.2	17.65± 1.56	22.00±4.28
	grooms — female on nest	1.24± 1.64	2.04±1.53	2.39±1.65	0.57± 0.39	1.78±0.71
	grooms — female off nest	7.04± 6.53	6.77±2.76	5.20±2.90	7.02± 5.12	6.20±2.85
	observes strange male — female on nest	1.15± 1.02	0.46±0.24	0.30±0.34	0.19± 0.17	0.51±0.33
	observes strange male — female off nest	0.38± 0.42	0.22±0.38	0	0.17± 0.29	0.18±0.15

TABLE 2. Probability values from ANOVA of overall effect of treatment on paternal care

Behaviour	Probability of significance
Covers — female on nest	0.66
Covers — female off nest	0.68
Grooms — female on nest	0.06
Grooms — female off nest	0.52
Observes strange male — female on nest	0.01*
Observes strange male — female off nest	insufficient data

*The Student Newman-Keuls Test verified that there was a signficant difference between the strange male and strange male and running wheel treatments.

TABLE 3. Probability values from ANOVA of effect of age of pups on paternal care

Behaviour	Day 1-5	Day 6-10	Day 11-15	Day 16-20
Covers — female on nest	0.26	0.33	0.05	0.61
Covers — female off nest	0.40	0.30	0.38	0.89
Grooms — female on nest	0.94	0.85	0.89	0.99
Grooms — female off nest	0.73	0.81	0.22	0.87
Observes strange male — female on nest	0.05*	0.51	0.12	0.07
Observes strange male — female off nest	insufficient data			

*The Student Newman-Keuls Test verified that there was a significant difference between the strange male and strange male and running wheel treatments.

imply that each father in the strange male treatment eventually became habituated to the strange male's inability to approach the nest. Alternatively, paternal vigilance may have decreased as the pups developed and became less vulnerable to infanticide (Mallory and Brooks, 1978). Regardless, the differences suggest that males avoid confrontation with other males when possible, and that guarding against infanticide (Mallory and Brooks, 1978) may be performed mainly by the females. Females appear to be more aggressive than males both intrasexually and intersexually (Brooks, 1970; Brooks and Banks, 1973), further supporting this suggestion.

In our study, fathers exposed to strange males did not act differently toward their pups compared to fathers in the other two treatments. Originally, we predicted that males would decrease their attendance to the pups due to uncertainty of paternity, but an increase in attendance due to the proximity of a potentially infanticidal male (Mallory and Brooks, 1978) was also a possibility. However, neither effect was observed. There are plausible explanations for the null results. The fathers may not have considered strange males to be a threat to their certainty of paternity or to the survival of their pups. Each father may have used a timing mechanism (Perrigo *et al.*, 1990) to determine that the pups were his, and the lack of other males near him or his mate before the pups were born may have strengthened the father's paternal certainty. Regarding the possibility of infanticide, a father may have initially responded to the strange male as being a threat, but rather than this response being manifested in the form of increased direct paternal attendance, it was manifested in increased vigilance towards the strange male.

Why should paternal care occur in the wild — of what ultimate benefit could it be to the male? Collared lemmings can reproduce during the winter (Krebs, 1964) when ambient temperatures are often below −40°C and temperatures at the snow-ground interface, where nests are made, can drop to −35°C (MacLean *et al.*, 1974). Because lemmings do not hoard food in the nest or store large amounts of fat

(Chappell, 1980), the female must leave the nest and the pups to forage. However, lemming pups are unable to control their body temperature until they are about nine days old, when hair covers the entire body (Hansen, 1957), and thus they require adult body heat to maintain their body temperature until day 9. A 55 g lemming requires 63 g of forage per day for maintenance, with locomotory and reproductive costs adding enormously to the energetic requirements (Chappell, 1980). It is probable that a thermally stressed female must feed several times a day to produce sufficient milk to feed her pups. During this time, paternal care would be particularly advantageous. If a male were present when the pups are born, then he could protect and keep the pups warm whenever the female left the nest to feed. Males and females might also reduce their thermoregulatory costs by staying together in the nest and sharing each other's body heat; winter congregations of *Microtus pennsylvanicus* are thought to be important for energy conservation (Webster and Brooks, 1981).

In winter, lemmings mainly move in subnivean tunnels. This restriction in movement probably also restricts the number of females with which a male comes in contact. Therefore, male mating opportunities may be lower in winter than in summer. If a male cannot find more than one female, then it is to his benefit to help raise the pups with the single female; by so doing, he can increase the chances of his pups' survival and thereby increase his fitness. It is also possible that a male's certainty of paternity (Storey and Snow, 1987) is higher in the winter, when relatively few males would have access to his mate. If the male were more certain that his mate's offspring were also his, he would be more likely to provide care to the pups than if he were uncertain of the pups' paternity.

Obviously, extensive fieldwork is necessary to determine if, why and when paternal care occurs in natural situations. Experiments in large outdoor enclosures would be useful. Summer and winter observations could be made on enclosed populations, and the provision of nest boxes with one-way glass and video cameras would allow observations of lemmings under more natural conditions. Such experiments could indicate when paternal care is most prevalent and could suggest better methods for exploring paternal care in natural environments. Winter research on ecology, behaviour and thermoregulatory biology and physiology of all animals that breed under the snow is scarce but warrants effort, considering the knowledge that could be gained on adaptations to cold stress and restricted access to food.

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