Ethology Ecology & Evolution 9: 169-173, 1997

Infanticide among golden marmots (*Marmota caudata aurea*)

DANIEL T. BLUMSTEIN [1]

Animal Behavior Group, University of California, Davis, CA, USA
and
Fachbereich Biologie–Zoologie, Philipps Universität, Marburg, Germany

Received 27 February 1996, accepted 7 October 1996

Fifty-percent (36/72) of golden marmot (*Marmota caudata aurea*) pups that emerged above ground their first summer in Dhee Sar, Khunjerab National Park, Pakistan, died before their first hibernation. At least 22% (8/36) of this mortality was attributed to infanticide by new adult male group members. Carcasses were not cannibalized, thus infanticide probably was not a form of resource exploitation. Adult females who lost their entire litters to presumed infanticide were not more likely to breed in subsequent years; an observation inconsistent with infanticide being a form of sexual selection. Results are consistent with the hypothesis that males may kill unrelated pups to avoid providing care to unrelated young even though killed pups include potential future mates.

KEY WORDS: *Marmota caudata aurea*, juvenile mortality, infanticide.

INTRODUCTION

Although once considered dysfunctional and aberrant, there are now a variety of functional explanations of infanticide, the killing of young by older conspecifics (reviewed in HAUSFATER & HRDY 1984). Infanticide has been well documented in many species of sciurid rodents (SHERMAN 1981, 1982 and references therein; MCLEAN 1983, BRODY & MELCHER 1985, HOOGLAND 1985, TRULIO et al. 1986, TRULIO 1987, DOBSON 1990, VESTAL 1991, PERRIN et al. 1994, COULON et al. 1995, but see MICHENER 1982 for a discussion on why infanticide may not be so common). Functional hypotheses to explain infanticide in sciurid rodents include: resource-exploitation — the young are eaten (e.g., SHERMAN 1981, HOOGLAND 1985, TRULIO et

---

[1] Present address and address for correspondence: Department of Systematics and Ecology, University of Kansas, Lawrence, KS 66045, USA. (E-mail: marmota@falcon.cc.ukans.edu).

al. 1986, VESTAL 1991); sexual selection — adult males kill unrelated young to increase their reproductive success in future breeding attempts (HOOGLAND 1985); minimization of "investment" into unrelated young (MCLEAN 1983); or most commonly, the reduction of competition for limiting resources such as nest sites and/or food for either the perpetrator or for the perpetrator's descendants (SHERMAN 1981, BRODY & MELCHER 1985, HOOGLAND 1985, TRULIO et al. 1986). Infanticide has previously been reported only in one Old World sciurid (PERRIN et al. 1994, COULON et al. 1995). In this paper I describe evidence for, and discuss the function of, infanticide in another Old World sciurid, the highly social golden marmot (*Marmota caudata aurea*).

MATERIALS AND METHODS

The general social behavior of golden marmots was studied from 1988 to 1993 in Khunjerab National Park, Pakistan (details and results in D.T. BLUMSTEIN & W. ARNOLD unpublished data). Briefly, golden marmots were generally found in monogamous associations but lived in groups containing up to 7 adults which tended to be male-biased. In Khunjerab, marmots had a 4-5 month active season between late April and late September during which adults could potentially breed once. Breeding did not occur every year: only 17% of 89 social-group-years (a social group studied for a year) had young emerge above ground. From 1990 to 1993, causes of mortality of pups during their first summer was studied in detail. Marmot litters were completely live-trapped and marked as soon as they emerged above ground. Over 2400 hr of direct and regular observations on social groups were made during 465 days of field work; additional, and unquantified, observations were associated with regular livetrapping of marmots. A full census of each social group was attempted at least once each week. Because marmots did not disperse before their third summer (D.T. BLUMSTEIN & W. ARNOLD unpublished data), pup disappearance was always equated with mortality, and we attempted to determine the cause of each disappearance. Necropsies were performed on all pup carcasses recovered.

RESULTS

Pups emerged above ground in 11 different social groups; some marmot social groups produced pups in more than 1 year. We trapped all pups in 16 litters (n = 72 pups, median/modal litter size at emergence from the natal burrow = 4, range = 2-9). Of these pups, 50% (36/72) died at some point during their first summer.

Predation on pups was strongly inferred from sign (footprints and fresh scats) from predator kills (n = 5), finding predated remains of a pup (n = 1), or from seeing a healthy pup alive 1 day that suddenly disappeared after a Tibetan red fox (*Vulpes vulpes montana*) was spotted hunting around that social group (n = 2). I estimate predation was responsible for at least 22% (8/36) of these pup deaths.

Infanticide may also have been responsible for another 22% (8/36) of first summer mortality. I never observed an adult marmot killing a pup, but strongly infer infanticide from the following observations. Two unconsumed pup carcasses, and one "scavenged" carcass were found possessing small puncture and/or bite wounds to the head and/or feet, tail, and back. While two weasel species (*Mustela erminea* and *M. altaica*) are found at the study site (BLUMSTEIN 1995), I do not think the bites were caused by weasels; weasels were not commonly seen around marmots, the carcasses were not consumed, and bite wounds were not restricted to the neck. The bite wounds could have been produced by other, larger, marmots and their location and pattern is consistent with wounds inflicted on a fleeing marmot. Adult males were much larger than pups: adults generally weighed between 3-5 kg, while pups were weaned at about 0.4 kg, and reached about 1.3 kg by late August (D.T. BLUMSTEIN & W. ARNOLD unpublished data). Additionally, two injured and limping pups were observed in two different social groups. Examination of these pups revealed what appeared to be small bite wounds on their back and legs; both pups later died.

Groups where pups were inferred to be killed by infanticidal marmots had one unique feature; a new adult male marmot joined the social group after the pups emerged above ground. Three social groups had new males move in, 12 groups had no new members, and one group had a new adult female. The presence of a new male significantly reduced juvenile survivorship. Only 24% (5/21) of pups survived the first summer in groups with a new adult male while 31/51 survived when no new male was present ($\chi^2 = 6.7$, $P = 0.01$). There was no evidence of differential pup survival in the group with a new adult female; 3/4 survived their first summer with a new female, 33/68 survived when there was no new female (Fisher exact $P = 0.36$).

Pups observed limping seemed to avoid areas where the new male was, even if this meant not interacting with other group members. Pups in groups without new males seemed fully integrated into the social group as evidenced by play, greeting, and the sharing of sleeping burrows. Pups in groups with new adult males were not obviously "protected" by other residents, including putative parents and older siblings. However, there was a tendency for groups with pups to be more likely to "resist" the immigration of new males; 4/6 immigrations into groups with pups were associated with aggression towards the immigrant male, while only 6/26 immigrations into groups without pups were associated with aggression towards the immigrant male (Fisher exact $P = 0.06$).

Females in groups where a new male was inferred to be infanticidal the previous season weaned young at similar frequencies as females who did not lose young to infanticidal males in the previous season; 1 of 3 females weaned young following infanticide the year before, whereas 2 of 10 females weaned young who suffered no infanticide the year before (Fisher exact $P = 1$).

DISCUSSION

I assume male intergroup movement caused infanticide as previously reported in the closely related alpine marmot (*Marmota marmota*; PERRIN et al. 1994, COULON et al. 1995). As with these two previous reports, my sample sizes of inferred infanticide are small. Infanticide in other sciurids often occurs before pups are weaned and emerge from their natal burrows (HOOGLAND 1995). Both male and female golden marmots changed social groups throughout the active season (D.T. BLUMSTEIN & W. ARNOLD unpublished data). It is possible that by focusing on post-emergence infanticide, I underestimate the actual frequency of infanticide and miss potential additional functions of infanticide. For instance, there are different functions of male and female black-tailed prairie dog (*Cynomys ludovicianus*) infanticide (HOOGLAND 1995). While golden marmot reproduction was rare, and thus there were a small number of potential infanticidal events, 22% of golden marmot pups appeared to be killed by infanticidal males. Such high frequencies, with the exception of black-tailed prairie dogs, are rare among sciurids (HOOGLAND 1995: 125). Why are male golden marmots infanticidal?

Infanticide may simply be the non-adaptive consequence of male aggression. New males may attempt to become dominant to all residents and pups may neither be able to flee nor to fight back successfully. However, because there may be a cost to killing female pups who might become future potential mates (HOOGLAND 1995), there should be some fitness benefit to maintain infanticidal behavior.

Because the two recovered carcasses attributed to infanticide did not appear to be consumed, and because casual examination of marmot scats did not reveal clumps of marmot hair, infanticide appeared not to be a resource-exploitation strategy.

Although the pattern of infanticide is consistent with the sexual-selection hypothesis — only males were thought to be infanticidal — there was no direct evidence that infanticide increased the probability of weaning young the next year in this relatively small data set. It is likely that maternal care has some energetic/physiological costs (e.g., thermoregulation of young during hibernation [ARNOLD 1993]) and that infanticide reduces these costs making it more likely that females will breed with infanticidal males in subsequent years (COULON et al. 1995). Arguing against the sexual-selection hypothesis for golden marmots are the observations that sexually-selected infanticide has generally been assumed to work on a shorter relative time scale (e.g., PACKER & PUSEY 1984), and that the infrequency of female breeding makes it less likely that infanticidal males will be present when a female can/does breed.

Burrow systems could be viewed as somewhat limiting resources since marmots colonized no new areas (D.T. BLUMSTEIN & W. ARNOLD unpublished data). If so, both sexes would benefit from infanticide to reduce competition for these potentially limiting resources. That infanticide was only observed associated with intergroup movement by males but not females may be an artifact of small sample sizes. However, male infanticide may reflect the true pattern for golden and other Old World marmots (PERRIN et al. 1994, COULON et al. 1995).

Infanticidal males could have minimized their own investment into unrelated pups (PIEROTTI 1991). Such investment could have occurred during the summer (e.g., allogrooming, alarm calling, territorial defense) or during the first hibernation (e.g., social thermoregulation that may benefit young more than adults; ARNOLD 1993). However, none of these behaviors were obligatory, so a new resident could enter a group and not "invest in young". Nevertheless, if new male residents behaved aggressively towards subsequent intruders, they might "protect" the social group's young whether related or not. It seems odd that adult males killed unrelated female pups who could conceivably become future mates (see also PERRIN et al. 1994, COULON et al. 1995, HOOGLAND 1995). More detailed data on reproductive success are required to conclude that adult male golden marmots kill unrelated young to avoid providing care to unrelated young.

ACKNOWLEDGMENTS

I thank the government of Pakistan and the Khunjerab Village Organization for permission to work in Khunjerab and hospitality while in Pakistan. I thank Nisar Ullah Baig, Janice Daniel, Marc Foggin, Ali Ahmed Jain, Abdul Hasan, Steve Henderson, Emily Loomis, Jorge

Lopez, Diane Patterson, Mohammed Karim Shah, and three groups of University of California Research Expedition Program participants for field assistance. Funding was provided by generous support from: The National Geographic Society, the Fulbright-Hayes program, the University of California-Davis, The American Institute of Pakistan Studies, the NSF Research Training Grant in Animal Behavior to UC Davis, the World Wide Fund for Nature - Pakistan, the World Pheasant Association-Pakistan, the US National Park Service - International Division, Sigma Xi, The Explorers Club, and The American Society of Mammalogists. Commercial support was provided by Bushnell - A Division of Bausch and Lomb, Deckers Corporation (Teva), Delta Airlines, Hi-Tec Sports, Sterigenics, and The North Face. Data analysis and manuscript preparation were supported by a Deutscher Akademischer Austauschdienst postdoctoral fellowship and the Fachbereich Biologie - Zoologie, Philipps-Universität Marburg. Final manuscript preparation was supported by NIH NRSA #1 F32 MH10793-01/2. I am grateful to Ken Armitage, Walter Arnold, John Hoogland and anonymous reviewers whose comments have improved this paper.

REFERENCES

Arnold W. 1993. Social evolution in marmots and the adaptive value of joint hibernation. *Verhandlungen der Deutschen Zoologischen Gesellschaft* 86: 79-93.

Blumstein D.T. 1995. An ecotourist's guide to Khunjerab National Park. *Lahore: World Wide Fund for Nature-Pakistan.*

Brody A.K. & Melcher J. 1985. Infanticide in yellow-bellied marmots. *Animal Behaviour* 33: 673-674.

Coulon J., Graziani L., Allainé D., Bel M.C. & Pouderoux S. 1995. Infanticide in the Alpine marmot (*Marmota marmota*). *Ethology Ecology & Evolution* 7: 191-194.

Dobson F.S. 1990. Environmental influences on infanticide in Columbian ground squirrels. *Ethology* 84: 3-14.

Hausfater G. & Hrdy S. B. (Edits) 1984. Infanticide: comparative and evolutionary perspectives. *New York: Aldine Publishing Co.*

Hoogland J.L. 1985. Infanticide in prairie dogs: lactating females kill offspring of close kin. *Science* 230: 1037-1040.

Hoogland J.L. 1995. The black-tailed prairie dog: social life of a burrowing mammal. *Chicago: University of Chicago Press.*

McLean I.G. 1983. Paternal behaviour and killing of young in arctic ground squirrels. *Animal Behaviour* 31: 32-44.

Michener G.R. 1982. Infanticide in ground squirrels. *Animal Behaviour* 30: 936-938.

Packer C. & Pusey A.E. 1984. Infanticide in carnivores, pp. 31-42. In: Hausfater G. & Hrdy S.B., Edits. Infanticide: comparative and evolutionary perspectives. *New York: Aldine Publishing Co.*

Perrin C., Allainé D. & Le Berre M. 1994. Intrusion de males et possibilité d'infanticide chez la marmotte alpine. *Mammalia* 58: 150-153.

Pierotti R. 1991. Infanticide versus adoption: an intergenerational conflict. *American Naturalist* 138: 1140-1158.

Sherman P.W. 1981. Reproductive competition and infanticide in Belding's ground squirrels and other animals, pp. 311-331. In: Alexander R.D. & Tinkle D.W., Edits. Natural selection and social behavior: recent research and new theory. *New York: Chiron Press.*

Sherman P.W. 1982. Infanticide in ground squirrels. *Animal Behaviour* 30: 938-939.

Truilo L.A. 1987. Infanticide in a population of California ground squirrels: functional significance and comparative importance. *Ph.D. Dissertation, University of California, Davis.*

Truilo L.A., Loughry W.J., Hennessy D.F. & Owings D.H. 1986. Infanticide in California ground squirrels. *Animal Behaviour* 34: 291-294.

Vestal B.M. 1991. Infanticide and cannibalism by male thirteen-lined ground squirrels. *Animal Behaviour* 41: 1103-1104.