Infanticide in the Alpine marmot (*Marmota marmota*)

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We report the first case of directly observed infanticide in the Alpine marmot (*Marmota marmota*). Moreover, previous and present observations suggest that 12 young could have been killed by infanticide in the population under study. The bodies of five of them were found with similar neck injuries. In all cases, infanticidal animals were adult males entering a territory in the absence of the resident or having taken over the territory. As in the Arctic ground squirrel, *Spermophilus parryii*, infanticide could have evolved in Alpine marmots as a part of the reproductive strategy of new resident males. According to Arnold (1990), young increase the energetic cost for related animals hibernating with them. Thus, while a rapid return to oestrus is not a realistic outcome, because it occurs only in early spring, infanticide could reduce hibernation costs for the female and increase her reproductive potential in the following year. A sexual selection hypothesis would explain infanticide in Alpine marmot.

KEY WORDS: sciurids, Alpine marmot, infanticide.

The adaptive significance of infanticide still remains controversial (Hrdy & Hausfater 1984, Labov et al. 1985). The many explanations offered for the evolution of infanticide include cannibalism, sexual selection, parental manipulation, competition for limited resources, social pathology and also (Elwood & Ostertag 1984, Pierotti 1991) intergenerational conflict. In sciurids, infanticide is widespread and has been reported in many species: *Marmota flaviventris* (Armitage et al. 1979, Brody & Melcher 1985), *Spermophilus beldingi* (Sherman 1982), *Spermophilus columbianus* (Michener 1982, Balfour 1983), *Spermophilus parryii* (MacLean 1983), *Cynomys ludovicianus* (Hoogland 1985). In a recent paper, Perrin et al. (1994) reported observations of the intrusion of adult males into the home range of some familial groups of the Alpine marmot. In two groups, three and four young respectively were present when the intrusion occurred. In one case, the intruding male was driven out by the resident male but one of the young was not seen thereafter. In the second case, the intruder evicted the resident and all the four young disappeared during the following days. The authors found the body of only one young which presented neck injuries. They considered infanticide by the intruding males as a possible explanation for the sudden disappearance of the young. However, killing of the young was not directly observed.
Here we report two new cases of infanticide, one of which was directly seen and filmed. To our knowledge it is the first case of directly observed infanticide in the Alpine marmot.

In our study site (Réserve de la Grande Sassière, 2400 m above sea level, French Alps), several groups have been studied since 1990 and 212 resident marmots have been trapped and individually ear-tagged. When present in a group, young were also marked and observed by focal animal sampling (Altman 1974).

In 1993, group B was composed of an adult pair and three yearlings (one male and two females). On 14 July, six young (three males and three females) emerged from their birth burrow. From mid-July, the resident adult male was no longer seen. The cause of his disappearance is not known. On the following days, several successive intrusions of one 3-year-old male (RLE) from neighbouring group C were observed and on 24 July, RLE reached the main burrow system of group B. No agonistic interaction occurred and resident yearlings behaved in a friendly manner (nosing and greeting, allogrooming) towards the newcomer. On the contrary, the young seemed to avoid him. On 26 July, a 2-year-old male (WLE) also from group C joined RLE in the burrow system of group B. The two males were seen visiting and marking all the burrow entrances. WLE frequently chased the resident young and on 27 July, WLE attacked a young female and killed her. Post mortem examination showed that the occipital bone was broken and the cervical vertebrae were crushed by the bite. Four days later, a young male was found dead showing a similar wound. In 1994, RLE, WLE and the three yearlings present in 1993 were still resident in group B. Reproduction took place and five young emerged on 3 July.

On 15 July 1994, the resident male of group J died. A few days later, the five young of the group disappeared and we found the bodies of two of them presenting similar injuries.

These observations and those reported by Perrin et al. (1994) for the same population, lead to some comments.

(1) An intruding male can kill young in the Alpine marmot. Due to its swiftness and to the unpredictability of the time of its occurrence, infanticide is difficult to observe. Because all of the dead young we found had similar wounds, we suspect infanticide occurred in all of these cases.

(2) In most cases, intruders are dispersers in search of a home range. We observed and trapped RLE male in several different areas from May.

(3) The absence of a resident adult male seems to be quickly detected by the individuals of neighbouring groups. In all the reported observations, the resident male was temporarily out of sight, missing or dead when intrusions occurred.

(4) Taking over a home range can be achieved almost simultaneously by several males migrating from the same group and recruitment can follow.

(5) Infanticide can lead the resident female to move with her young. In group B, the adult female and the four remaining young were no longer observed. In August, an ear-tagged adult with four young — two of which had coloured ear-tags corresponding to tags of presumably surviving young of group B — was seen on the peripheral area of group B. In fact, we have now ascertain that at least two young survived. They were caught as yearlings in May 1994 on the group C home range and identified by their ear tags. We do not know if their mother was still alive.

(6) Agonistic interactions do not necessarily occur between intruders and the resident adult female or yearlings (Perrin et al. 1993, this paper). They are much more frequent when 2-year-old resident males are present (Perrin et al. 1993).
In the Alpine marmot parental manipulation can be discarded because males did not kill their own offspring. Cannibalism seems not to be involved because the killer male did not attempt to eat the young he had just killed and in all the other cases, the bodies of the killed young were found intact except for the bites on their neck.

As in the Arctic ground squirrel (Spermophilus parryii, MacLean 1983), infanticidal individuals were males and infanticides occurred in definite circumstances, i.e. just after the infanticidal males had taken control of the group or had tried to do so (Perrin et al. 1994, this work). Therefore, we discard the social pathology hypothesis. We then suggest that infanticide in Alpine marmots has evolved as a part of the reproductive strategy of males replacing a resident male in a group as shown in Arctic ground squirrel (MacLean 1983), primates (Hausfater et al. 1982, Hausfater 1984), and lions (Packer & Pusey 1983).

Resource competition is not easy to discard and our data do not allow an evaluation of this possibility.

According to the intergenerational conflict hypothesis (Pierotti 1991) adults could engage in infanticide to avoid the costs associated with the adoption of unrelated offspring. However in Alpine marmots infanticidal behaviour is not performed by females and seems not to be initiated by soliciting young. Moreover, the new resident male would not bear the cost of the unrelated hibernating young (Arnold 1990).

According to the sexual selection hypothesis, infanticide may secure mating opportunities for the intruding male. While short term oestrus induction is not a possible explanation in Alpine marmots because oestrus is annual and occurs in early spring, the male could benefit from preventing further maternal investment and preserving the future reproductive potential of its new partner. Arnold (1990) has shown that the presence of young induces an increased energetic cost for the related animals hibernating with them. Therefore, infanticide could reduce the cost of social thermoregulation borne by the female during winter.

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