

Male-caused failure of female reproduction and its adaptive value in alpine marmots (*Marmota marmota*)

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We studied reproductive performance of free-living alpine marmots (*Marmota marmota*) for 14 years in the National Park of Berchtesgaden, Germany. Female reproduction was influenced by body condition and social factors. Reproduction depleted fat reserves, and only females emerging from hibernation with sufficient body mass were able to reproduce successfully. Marmots lived in social groups in territories defended by a dominant male and female. Subordinate females never reproduced, regardless of body mass. Territory takeovers by males impaired reproduction of dominant females, but only if the takeover occurred after the mating period. Reproductive failures occurred despite clear signs of pregnancy such as enlarged nipples or late molt. Decreasing progesterone levels after the mating period and the lack of evidence for direct infanticide by new territorial males suggest a block of pregnancy as a likely explanation for reproductive failures in groups with male takeovers during gestation. Rendering female reproduction impossible increased future reproductive success of new territory owners. Nonparous females saved the energetic cost of maternal investment and thus emerged with higher body mass in the following spring. In line with this, females failing to wean young had higher reproductive success in the subsequent year. *Key words:* Bruce effect, females, infanticide, *Marmota marmota*, marmots, reproductive failure, reproductive suppression. [*Behav Ecol* 10:592–597 (1999)]

There is an ever growing number of reports on the occurrence of infanticide in mammals (Hausfater and Hrdy, 1984; Smuts and Smuts, 1993), especially in rodent species (Labov et al., 1985). Particularly among ground-dwelling sciurids, infanticide seems to be a common male behavior (Blumstein, 1997; Coulon et al., 1995; Dobson and Kjellgaard, 1985; Hoogland, 1985; McLean, 1983; Perrin et al., 1994; Sherman, 1982; Steiner, 1972; Vestal, 1991). Males taking over a territory or social group are especially likely to kill the present offspring. Apart from this classical type of direct infanticide, there is another possibility for males to manipulate female reproduction. Bruce (1959) first reported that the presence of an unfamiliar male can lead to a block of gestation in pregnant mice. This “Bruce effect” has been found to exist in several rodent species (Huck, 1984; Schwagmeyer, 1979), primates (e.g., Mori and Dunbar, 1985), and wild horses (Berger, 1983). Presumably male pheromones, for example, from urine, elicit the abortion or resorption of embryos (Hafer, 1990; Keverne, 1983; Storey, 1990).

Most authors considered male-caused failure of female reproduction an adaptive male strategy instead of assuming an accidental or pathological origin (review in Hrdy, 1979). Essentially, it has been suggested that females start the next reproductive episode earlier if the current period of maternal investment is interrupted. Therefore, males killing dependent juveniles sired by other males or blocking such gestations can reproduce earlier and thereby increase their lifetime reproductive success. However, in contrast to many descriptive reports, theoretical models (Breden and Hausfater, 1990; Glass et al., 1985), and experimental work in the laboratory (review in Brooks, 1984), data on the adaptive value of direct or in-

direct infanticide in free-ranging mammals are rare (e.g., Dorges et al., 1992; Packer et al., 1990). Reasons are the lack of long-term observations of known individuals, insufficient knowledge about the relationships among these individuals (Brooks, 1984), and the difficulty of observing infanticide in the field, especially in burrow-dwelling rodents (Labov, 1984).

In contrast to the widely accepted and empirically supported view that infanticide can be advantageous for males, the situation is less clear from the female’s point of view. At first glance, a conflict of interest should exist, because infanticide implies a waste of reproductive investment for females. In the case of direct infanticide, females may just not be able to defend their offspring, because of the difference in physical strength between males and females (e.g., in lions: Packer et al., 1990). However, this constraint argument cannot explain why females volunteer in the case of indirect infanticide. There must be a net fitness benefit for females for a Bruce effect to evolve. The common argument is that females may anticipate that a new male will be infanticidal or that it will not provide paternal care. Females therefore should do better by interrupting the current reproductive cycle immediately after a male takeover to minimize the inevitable loss of reproductive investment (Huck, 1984; Schwagmeyer, 1979). Furthermore, subsequent reproduction may even be improved after a pause in species that depend on body fat reserves for reproduction (e.g., Andersen et al., 1976; Grizzel, 1955; Rogers, 1976; Samson and Huot, 1995; Snyder et al., 1961). Although these arguments are logical, there is virtually no evidence from field studies that females indeed make the best of a bad job by interrupting gestation after a male takeover.

We report in this paper increased reproductive failures of females after territory takeovers by males in a free-ranging, highly social ground squirrel, the alpine marmot. We further present evidence suggesting that reproductive failures may be caused by pregnancy blocks and demonstrate the adaptive value of male-caused failures in female reproduction in this species for both sexes.

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MATERIALS AND METHODS

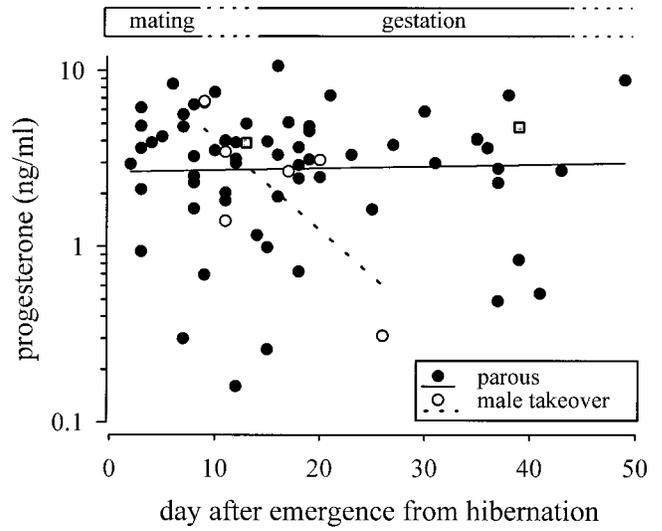


Figure 1
 Plasma progesterone changes of territorial females from emergence from hibernation to late gestation. Parous females: $\log(y) = 0.424 + 0.001x$, $n = 63$, n.s.; nonparous territorial females from groups with male takeovers during the time window of gestation: $\log(y) = 1.138 - 0.052x$, $n = 6$, $F_{1,65} = 3.81$, $p = .055$.

Table 1
Effect of male takeovers and time of takeover on female reproduction

Male territory takeover	Production of weaned young (%)	p^a	N
None	64		230
During mating period	50	n.s.	8
After mating period	8	<.001	13

^a p values refer to chi-square tests comparing proportions of reproductive females from groups with and without a change of the territorial male.

13 territorial females should have weaned young, but only 1 of them reproduced successfully. This is a significantly reduced reproductive rate ($p < .001$).

Mechanisms of reproductive failure

In none of the reported cases of reproductive failure after a change of the territorial male did we obtain evidence of direct infanticide. We never found injured juveniles or carcasses, nor did we observe fights between the new territorial male and the territorial female. For five territorial females that did not wean any young after a territory takeover, we have further evidence that they indeed attempted to reproduce, because they were trapped during the typical time window of advanced gestation or observed later in the season. All of them either had enlarged nipples, or molted late during July/August like dams. In contrast, clearly nonparous females always had little nipples and molted simultaneously with males during June.

Progesterone in parous territorial females remained high from the mating period until the approximate time of littering (Figure 1). Progesterone data were also available from six territorial females failing to reproduce after a male takeover. Two values matched the pattern found in parous females (gray squares in Figure 1) and came from a female that lived in a group where the new dominant male took over on June 13 (i.e., certainly after the typical period of littering in alpine marmots). In contrast to parous females, progesterone concentrations of the remaining five females seemed to decrease during the time window of gestation from initially high levels (Figure 1), indicating either a failure to conceive or a block of gestation. One should not overestimate this borderline significant difference because the sample of territorial females from groups with male takeovers is rather small, and exceptionally low levels of progesterone have been found in parous females as well (Figure 1). Low levels may be due to sampling outside of the period of gestation because we did not know the exact time of conception and parturition, or due to the fact that progesterone secretion between pregnant individuals can vary substantially (Concannon et al., 1984; Sinha Hikim et al., 1991). However, the course of progesterone in the two groups of females is certainly not contradictory to the view that reproductive failures after male takeovers were caused by block of gestation.

Body mass and reproduction

Sufficient vernal body mass (body mass measured within 14 days after emergence from hibernation) was apparently mandatory for successful reproduction in females. In groups without male takeovers, emergence body mass of territorial females was on average 141 g (SD = 182 g) higher in years with successful reproduction than in years when the same individ-

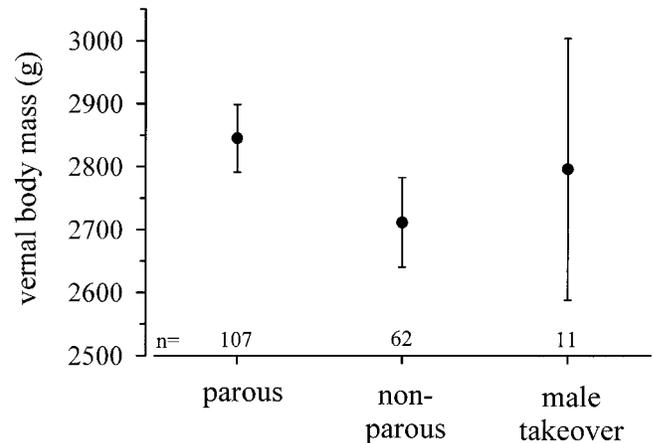


Figure 2
Vernal body mass of territorial females in reproductive years (parous), in nonreproductive years (nonparous), and in nonreproductive years associated with a change of the territorial male (male takeover) during gestation. Means \pm 95% confidence intervals; ANOVA: $F_{2,177} = 4.388$, $p = .014$; significant differences between subgroups parous/male takeover or nonparous/male takeover, n.s. (Tukey-HSD multiple post-hoc comparisons).

uals did not wean young (t test for paired comparisons, $t = -4.043$, $df = 26$, $p < .001$, see also Figure 2). However, vernal body mass of territorial females from groups with male takeovers during the time window of gestation corresponded to the grand mean of parous and nonparous females (Figure 2). Therefore, one would expect that their reproductive rate should approximate the population mean as well (64%; Table 1). Hence, other reasons than condition may have been responsible for the reproductive failure of these females. Logistic regression analysis revealed that a male takeover during gestation was such a reason for reproductive failure of territorial females. Independent of the positive effect of vernal body mass on reproduction (logistic partial correlation statistic $R = .165$, $p = .003$, $n = 181$), a change of the territorial male after the mating season significantly decreased the probability that a territorial female produced weaned young ($R = -.163$, $p = .004$).

Maternal effort and future reproduction

The energetic consequences of reproduction influenced future reproduction. Female vernal body mass was on average 177 g (SD = 272 g) lower after a year of reproduction (t test for paired comparisons, $t = -2.759$, $df = 17$, $p = .013$) than after years when the same females failed to wean young. Apparently, the annual energetic demands of reproducing females exceeded the amount of body fat that could be accumulated during one summer, due to the additional costs for gestation/lactation and the cost of warming juveniles during winter (Arnold, 1993). Without the burden of maternal investment, females not only reestablished their energy reserves during summer to meet the energetic requirements for the next hibernation, but emerged in the subsequent spring with higher body masses compared to the previous spring (Figure 3). The difference of vernal body mass from year to year, a measure of the body fat reserves available after hibernation, was positive in nonparous but negative in parous females, and significantly influenced the next reproductive output (Table 2). Parous females were less likely to produce a litter in the following year (56% of 110) than pausing females (69% of 81, $\chi^2 = 3.22$, $df = 1$, one-tailed $p = .036$).

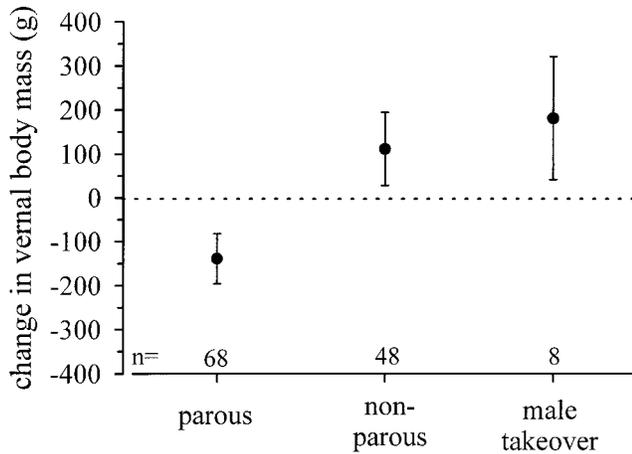


Figure 3

Change in vernal body mass of territorial females after reproductive years (parous), after nonreproductive years (nonparous), and after nonreproductive years associated with a change of the territorial male (male takeover) during gestation. Means \pm 95% confidence intervals; ANOVA: $F_{2,121} = 16.494$, $p < .001$; significant differences between subgroups (Tukey-HSD multiple post-hoc comparisons): parous/nonparous territorial females $p < .001$, nonparous territorial females of groups with a change of the territorial male (male takeover)/parous females $p = .002$.

DISCUSSION

Mechanisms of female reproductive failure

Alpine marmots typically emerge from hibernation before the thaw is completed, and no food is available for up to 53 days after emergence (median 16 days; Arnold, 1990a). Hence, the energetic cost of reproduction must to a considerable degree be paid from the fat reserves that remained after hibernation. Many females apparently emerged with an insufficient vernal body mass to fulfill these requirements and forfeited reproduction in order to replenish their fat reserves.

Besides body condition, social relations within and between the sexes influenced female reproduction. In line with previous reports (Arnold, 1990a; Lenti Boero, 1994; Perrin et al., 1993), we never found more than one reproductive female per group in our study, and this was without any doubt the dominant, territorial female (exceptions under conditions of unclear dominance; Barash, 1976; Goossens et al., 1998). Three-year-old and older subordinate females did not show any signs of lactation and never weaned young, although they emerged with body masses similar to those of successfully reproducing territorial females. However, we frequently noticed signs of estrus and gestation in subordinate females and sometimes observed copulations. Therefore, territorial females are apparently not able to prevent subordinate females from copulation and fertilization but achieved complete reproductive suppression of subordinate females during gestation (Arnold, 1990b; Hackländer et al., 1998).

Female reproduction is further affected by males. Almost all territorial females failed to reproduce in years when the territory owner was replaced by a new male after the mating season. Insufficient body mass could be excluded as a reason for these failures. There are three possibilities for how new territorial males could manipulate female reproduction: (1) by killing juveniles, (2) by causing the mother to commit infanticide, or (3) by blocking gestation.

There are numerous reports of observed or assumed infanticide in other ground-dwelling sciurids (Armitage et al., 1979; Balfour, 1983; Betts, 1991; Blumstein, 1997; Brody and Melch-

Table 2
Changes in vernal body mass of territorial females from the previous year to the present year and median of produced young

Change in body mass	Litter size (median with 1st and 3rd quartile)	N
Increase	3 (0, 4)	49
Decrease	0 (0, 3.5)	53

Mann-Whitney U test: $U = 975$, $p = .025$.

er, 1985; Dobson and Kjellgaard, 1985; Hare, 1991; Hoogland, 1985; Lacey, 1992; McLean, 1983; Perrin et al., 1994; Sherman, 1982; Steiner, 1972; Trulio, 1996; Trulio et al., 1986; Vestal, 1991; Waterman, 1984; Wiggert and Boag, 1986). Coulon et al. (1995) observed that a new territorial alpine marmot male killed a juvenile and assumed that infanticide by new males was responsible for the death of juveniles in several other cases. However, we have no evidence for direct infanticide after a male takeover in our study population. We never found carcasses of juveniles killed by conspecifics. During 14 years of study we only once detected juveniles that had been attacked by other marmots. In this case, the juveniles were offspring of a former subordinate female who expelled the previous territorial female, her mother, from the territory. Two of four juveniles became severely injured during the struggle for dominance between the two females. Furthermore, we have no evidence for defense behavior of territorial females, a possible indication for infanticidal new males (Elwood et al., 1990). Nevertheless, the lack of evidence for direct infanticide in our study does not exclude this possibility. Infanticide would not be detected if it occurred inside burrows, nor would cannibalism, a widespread behavior in ground-dwelling sciurids (Armitage et al., 1979; Hare, 1991; Holmes, 1977; McLean, 1983; Plotnikov, 1997; Trulio et al., 1986; Vestal, 1991). In fact, one of the females from groups with male takeovers presumably lost her young after parturition (gray squares in Figure 1), suggesting that her juveniles had been killed.

The third explanation for female reproductive failure, male-caused blocking of gestation, is well documented for a variety of rodent species under laboratory conditions (reviews in Huck, 1984; Schwagmeyer, 1979). However, apart from one study about pregnancy interruption in *Microtus ochrogaster* under seminatural conditions (Heske and Nelson, 1984), there is to our knowledge only one study showing the existence of this cryptic pathway of reproductive suppression in wild rodent populations under natural conditions (in *Microtus pennsylvanicus*; Mallory and Clulow, 1977). Three lines of evidence suggest that in alpine marmots a block of gestation is a likely reason for the lack of successful reproduction after a change of the territorial male. First, territorial females failing to reproduce after a male takeover showed clear signs of pregnancy early in the season, but did not wean any young. Second, direct infanticide seems to occur infrequently (Coulon et al., 1995; this study). Third, the decrease in circulating progesterone in these females after the mating season suggests abortion or resorption of litters, a common phenomenon in marmots (Bibikow, 1996).

The adaptive value of male-caused reproductive failure

Darwin (1871) pointed out that killing unrelated juveniles is advantageous for males if females then come into estrus earlier, offering the infanticidal male an immediate chance for reproduction. This specific advantage does not exist in monoestrous species like marmots. However, infanticide would still

be beneficial for a male if females are more likely to produce young (or have larger litters) after a year with no or negligible maternal investment (Hoogland, 1985; Michener, 1982). Parous female alpine marmots bear not only the considerable energetic costs of gestation and lactation, they also have higher mass loss during winter because juvenile alpine marmots must be warmed during their first hibernation (Arnold, 1990b). This is energetically costly for dams even when supported by their mate or by offspring from previous years (Arnold, 1993). Consequently, parous females had a lower vernal body mass in the year after reproduction and therefore had less reproductive output. In contrast, nonparous females, and in particular females failing to reproduce because of a male takeover, had a higher chance of producing young in the following year. Hence, by blocking gestation new territory owners most likely increased their lifetime reproductive success. The cases of successful reproduction despite a male takeover further support the view of an adaptive male manipulation of female reproduction. Female reproduction was not impaired if the new male was probably the sire of the young because the former territory owner had been expelled during the mating season.

However, gestation is under female control, in contrast to male infanticide. Why should females abort or resorb their unborn young after a male takeover? A frequently offered answer is that females avoid useless maternal investment by interrupting gestation if infanticide by the new male is expected (Huck, 1984; Schwagmeyer, 1979). This explanation may hold for alpine marmots, too. Mothers presumably could not protect their young from infanticidal males because juveniles are active in the group's entire territory within a few days upon emergence from the natal burrow. On the other hand, we have to consider that females may interrupt gestation not only to minimize inevitable losses of reproductive investment. Reproduction with the new male could have additional advantages. An intruding male that repelled the territorial male is typically in better condition (Arnold, 1990a), possibly indicating superior genetic quality. To summarize, as long as the residual reproductive value of a female does not become too small, it may well be advantageous for females to give up the present reproduction and mate with the new territorial male as early as possible.

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