



Reproductive suppression in female Alpine marmots, *Marmota marmota*

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We studied mechanisms responsible for reproductive skew in female Alpine marmots. In each social group, only dominant females produced weaned young although subordinate females had similar body condition, were fertile as indicated by high levels of oestradiol during the mating season, and occasionally started pregnancies. During the period of gestation, dominant females initiated significantly more agonistic interactions against subordinate females, resulting in significantly increased levels of glucocorticoids and decreased levels of progesterone in subordinates. Results suggested that reproductive suppression in female Alpine marmots is mediated by the negative effects of stress (glucocorticoids) on the activity of the hypothalamic-pituitary-gonadal axis. The strength of competition between subordinate and dominant females was affected by their relatedness. Dominant females attacked unrelated subordinate females more, whereas amicable behaviour was observed mainly between dominant females and their daughters. These differences could be explained by differences in indirect fitness: related subordinate females benefited from warming the offspring of the dominant female during hibernation. Reproductive suppression was apparently costly for dominant females, because their reproductive success decreased as the number of adult subordinate females in a group increased.

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In many cooperatively breeding mammals, reproduction is not equally distributed among members of social groups. The degree of reproductive skew can vary considerably and is most pronounced in species where reproduction is restricted to one or a few individuals (Keller & Reeve 1994; Clutton-Brock 1998; Reeve et al. 1998). Suppression of subordinate reproduction in species with high reproductive skew is often considered to be controlled by dominant individuals. Among females, reproduction may be suppressed or less successful because of delayed puberty, earlier menarche, or impaired lactation (reviewed by Faulkes & Abbott 1997). Behavioural interventions of dominant females can either directly prevent copulations of subordinate females (e.g. Creel et al. 1992), or impair reproduction indirectly by inducing stress responses. Stressed animals typically secrete more glucocorticoids, which often negatively affect reproduction

and health, especially when this elevation is chronic (Chrousos & Gold 1992; Sapolsky 1992; von Holst 1998). Reduced reproductive success in losers of conflicts has been demonstrated in many laboratory studies (e.g. Louch & Higginbotham 1967; Schuurman 1980). However, there is increasing evidence that high levels of glucocorticosteroids do not necessarily impair reproduction. Creel (2001) pointed out that in 12 of 14 studies on cooperatively breeding species, glucocorticoid levels of dominant individuals were higher than or the same as in subordinates.

An exception to the predominant pattern according to Creel (2001) is the male Alpine marmot. Alpine marmots are highly social, cooperative breeders with high social complexity (as defined by Blumstein & Armitage 1998) within the genus *Marmota*, with a relatively high degree of reproductive skew (Allainé 2000). They form extended family groups of one dominant pair and several subordinate offspring up to 5 years old (Arnold 1990b). Because of territory take-overs, groups frequently contain unrelated subordinates. Reproductive suppression of subordinate males is incomplete, and sons of the dominant male may have some direct reproductive success. About 17% of

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juveniles are not fathered by a group's dominant male (Hackländer et al. 1999). Dominant males predominantly attack unrelated individuals, which show a subsequent glucocorticoid increase and androgen suppression, but sons above a critical body mass are left alone (Arnold & Dittami 1997). Glucocorticoid responses of dominant males increase with increasing numbers of unrelated males but decrease with increasing numbers of sons in a group. The functional explanation of reproductive suppression of unrelated males and lack of suppression of older sons offered by Arnold & Dittami (1997) relies on the cooperative breeding system of alpine marmots. Adult sons are the most effective helpers in warming young marmots during their first hibernation (Arnold 1993). Dominant males may maximize their reproductive success despite allowing subordinate sons to reproduce if such behaviour recruits valuable helpers.

In contrast to males, female subordinate Alpine marmots are less important for juvenile survival during hibernation (Arnold 1993), and reproductive skew among females is high, that is, only dominant females produce weaned young (Arnold 1990a; Perrin et al. 1993a; Lenti Boero 1999). However, the mechanism of this high reproductive skew has not yet been studied. Therefore, our aims in this study were (1) to determine the reproductive status of subordinate and dominant female Alpine marmots by measuring levels of oestradiol and progesterone and (2) to assess female interactions and glucocorticoid levels during reproduction.

METHODS

Study Animals and Site

Alpine marmots are large burrow-dwelling rodents inhabiting high alpine regions (Mann et al. 1993). Females are monoestrous and reach sexual maturity during their third summer (Hackländer et al. 1999). To avoid age-related effects, we included in this study only adult females 3 or more years old. Alpine marmots mate within about 2 weeks of emergence from hibernation but are obviously receptive for only 1 day (Müller-Using 1957; Psenner 1957). After 34 days of gestation a female marmot gives birth to, on average, four juveniles, which are suckled for about 4 weeks. Litters are weaned in late June or early July (Psenner 1960; Arnold 1990a), when juveniles can be observed above ground for the first time.

We studied Alpine marmots intensively from 1982 to 1996 in the Berchtesgaden National Park, Germany (47°36'N, 13°0'E, 1100–1500 m above sea level). The study population consisted of about 20 family groups per year. Marmots were captured with live-traps (Model 608, National Live Trap Corp., Tomahawk, Wisconsin, U.S.A.) in spring after emergence from hibernation and in July after weaning of juveniles. Upon first capture, we permanently marked marmots by tattooing numbers into the skin of the inguinal region. For visual identification over a distance, we dyed numbers on to the back fur and unique markings on the face (Nyanzol D). We trapped on average 141 individuals per year (about 95% of all marmots on the study site) and hence got

comprehensive information about the composition of groups and relatedness among group members. We did not include in our analyses families with uncertain social dominance relationships during the reproductive period, for example if the dominant female or male had changed during this time (Hackländer & Arnold 1999).

We identified females' attempts at breeding, in the absence of observable young, by their enlarged nipples (Arnold 1990a) or late moult (Psenner 1957). By July, nearly all females in our study population that had reproduced successfully had not finished their moult (93%; $N=55$) or had enlarged nipples (95%; $N=21$). In May 1994, we also used ultrasonography (Model SSD-500, Aloka, Tokyo, Japan; 5 MHz convex sector/linear scanner) to determine the reproductive status of three subordinate females. Litter size of parous females was determined by extensive observation and trapping around the time of weaning (for details see Arnold 1990a, b). Because only one female per group reproduced, false assessment of maternity could occur only if juveniles were present in neighbouring groups and intermingled (Arnold 1990b). Such groups were not included in this study.

Behavioural Data

Marmots were continually observed during the active season from emergence from hibernation in April until immergence into hibernation in October. In 1996 we observed five families more intensively (about 100 h each) during the period of reproduction, that is, in the first 11 weeks after emergence from hibernation (mating: weeks 1–2; gestation: weeks 3–7; lactation: weeks 8–11). Each family group consisted of a dominant pair and at least one adult subordinate female of known relatedness to the dominant female (daughter=offspring of the dominant female; nondaughter=offspring of another female). The group compositions were as follows: groups A and B: one daughter each; groups C and D: one nondaughter each; group E: one daughter and one nondaughter.

Observations took place during hours of peak activity: 0900–1800 hours (Türk & Arnold 1988). Each observation period lasted at least 2 h in which we noted all interactions between dominant and subordinate females (using the definitions of Perrin et al. 1993a, b, see below) as well as the identity of initiators and recipients. Differentiation between agonistic and amicable interactions was sometimes difficult (see also Barash 1973, 1974). For instance, playfighting, often interpreted as sociopositive (e.g. Perrin et al. 1993b), could result in friendly behaviour such as grooming or in serious fighting. On the other hand, marmots appeared to use nose-to-nose contact ('greeting'), often considered as sociopositive (e.g. Perrin et al. 1993b), to recognize an individual as an opponent. We therefore chose a conservative approach and discarded ambiguous interactions from analysis. We considered interactions as 'agonistic' if distinct signs of aggression such as severe biting and screaming were observed, and allogrooming as the only clearly 'amicable' interaction. Playfighting and greeting were classified as 'neutral'.

Endocrinological Data

We sampled blood from trapped marmots without anaesthesia between 1988 and 1996. Traps were checked at least every 2 h. About 4 ml of blood was taken from the femoral vein into a polyethylene vial immediately after we removed an individual from a trap, that is, within a few minutes of approaching a trap. We added two or three drops of anticoagulant (EDTA) to each blood sample, separated plasma and blood cells after centrifugation, snap-froze both fractions in dry ice and stored samples at -70°C until analyses. The concentrations of unconjugated oestrogens, progesterone, corticosterone and cortisol were measured with enzyme immunoassays (Palme & Möstl 1994, 1997; Schwarzenberger et al. 1996).

Statistical Analysis

The majority of the adult females were trapped repeatedly each year and in several consecutive years. However, the number of samples per individual differed. Thus, our data set consisted of repeated measurements with unbalanced replicates. As age, body weight, social status and other parameters may change between years, the unit for all analyses was the 'individual-year'. To compare body condition between subordinate and dominant females during the mating period (first 2 weeks after hibernation) we used linear mixed-effects modelling in S-Plus 2000 Professional Release 2 (Venables & Ripley 1999; Pinheiro & Bates 2000) with the independent fixed effect social status and the dependent fixed effects body mass, hindfoot length and age. The group variable for random effects was the individual-year.

We used Pearson chi-square to test whether the distribution of reproduction between dominant females from groups with differing numbers of subordinate females was consistent with a random sample drawn from a specific theoretical distribution and to evaluate the effect of social status or kinship on the initiation and type of a behavioural interaction between a dominant and a subordinate female.

Levels of hormones were tested with linear mixed-effect statistics with the independent fixed effects social status and reproduction. We also tested the effect of relatedness between subordinate and dominant females on hormonal levels. Data are given as means \pm SEs. Because not all data could be measured in all individuals, error degrees of freedom varied. Error degrees of freedom resulting from linear mixed-effect modelling were calculated as number of observations minus number of groups (in this case the individual-year) minus 1.

Ethical Note

We trapped marmots and took blood with permission of the Berchtesgaden National Park Administration. At the beginning of our study we tried to trap marmots by using baits (e.g. peanut butter, seeds, salt) but trapped

individuals regularly ignored these. Thereafter we did not use baits nor did we provide any food or water in the traps. However, we checked the traps at least every 2 h and covered them with plant material to hide them from predators and to provide shade from the sun.

Captured animals were transferred into a cone-shaped, cotton handling bag. Because of the thick cotton material, trapped individuals were in the dark and appeared to be relaxed with normal heart rate and breathing. The cotton bag enabled us to avoid immobilization, which would have burdened an animal's circulation and which could have led to competitors evicting recovering animals from the group. The cotton bag had a longitudinal velcro fastener, giving us access to any body region of the animal without scaring it. Thus, we were able to handle the hindleg of the animal to tattoo it, to check the tattoo number in marked individuals, and to take a blood sample. For other investigations and marking, we grabbed an animal in the bag and pulled it out by holding its neck. This enabled us to put on Nyanzol-D for dyeing and check the animal for bite wounds (as a result of severe fights between marmots within a group). Altogether, this handling lasted no longer than 10 min. Animals appeared to resume their former behaviour after hiding in a burrow for a few minutes, regardless of trapping frequency. During our 14-year study we did not identify any negative effect of trapping on the individuals.

RESULTS

Social Status and Reproduction

During the first 2 weeks after hibernation (mating period), we detected no significant differences between subordinate ($N=36$) and dominant females ($N=104$) with respect to body mass (2670 ± 558 and 2750 ± 318 g, respectively; $F_{1,117}=0.01$, $P=0.94$) and hindfoot length (85 ± 3 and 86 ± 8 mm, respectively; $F_{1,74}=0.11$, $P=0.74$), although subordinate females were on average 2.9 years younger than dominants (3.4 ± 0.6 and 6.3 ± 2.2 years, respectively; $F_{1,117}=85.30$, $P<0.0001$). Using ultrasonography we found a dead fetus in the uterus of a subordinate female, which had bloody mucus inside her vagina, indicating an abortion. Three subordinates showed signs of reproduction indicated by both enlarged nipples and late moult. We also found a copulatory plug in the vagina of a subordinate female after it had spent the night in a burrow together with the dominant male of the group. However, none of the subordinates ($N=60$) produced weaned young. In contrast, 111 (ca. 64%) of 174 dominant females reproduced successfully during the study period.

Reproduction in dominant females ($N=174$) was affected by the number of subordinate females (range 0–8) in the group ($\chi^2_6=13.13$, $P<0.05$; Fig. 1). More detailed analysis revealed a negative association of dominant reproduction with the number of unrelated subordinate females in a group ($\chi^2_4=10.60$, $P<0.05$), whereas the number of daughters present had no effect ($\chi^2_3=4.26$, $P=0.18$).

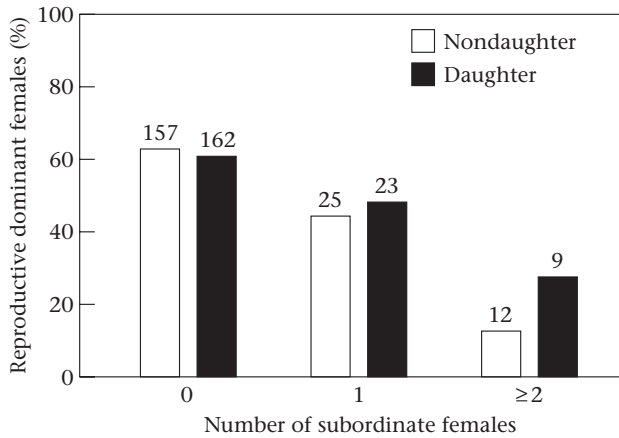


Figure 1. Percentage of dominant females that reproduced in groups with different numbers of adult subordinate daughters and nondaughters. Sample sizes are given above the bars.

Behavioural Interactions

Interactions between dominant and subordinate females occurred most frequently during the gestation period (84% of all interactions, $N=386$). In this period the pattern of initiation and character of interaction differed between dominant and subordinate females ($\chi^2_2=35.89$, $N=325$, $P<0.001$). Dominant females initiated far more of the agonistic interactions (69%, $N=131$) than amicable (1%, $N=25$) or neutral (47%, $N=169$) ones. A more detailed analysis where each group was analysed separately showed that this result was significant in three groups (group A: $\chi^2_2=12.55$, $N=76$, $P<0.01$; group C: $\chi^2_2=10.49$, $N=32$, $P<0.01$; group D: $\chi^2_2=9.97$, $N=62$, $P<0.01$), almost significant in group E ($\chi^2_2=5.12$, $N=141$, $P=0.077$) and not significant in group B ($\chi^2_2=4.20$, $N=14$, $P=0.12$). After intensive fights, subordinate females (losers) often rested lethargically for several minutes, whereas dominant females typically began to feed.

Female interactions were affected by the relatedness between the dominant and the subordinate female ($\chi^2_2=34.74$, $N=325$, $P<0.001$; Fig. 2). Between dominant females and their daughters, amicable and neutral interactions predominated during the gestation period, whereas agonistic interactions between dominant females and unrelated subordinate females increased fourfold from the 3rd to the 6th week after emergence from hibernation (Fig. 2). A further analysis on the group level was possible only in group E (where the dominant female lived together with both a non-daughter and a daughter). In this group the pattern was also significant ($\chi^2_2=24.97$, $N=141$, $P<0.0001$). Within subordinate females, nondaughters initiated significantly more agonistic interactions towards the dominant female than did daughters ($\chi^2_2=25.59$, $N=154$, $P<0.001$).

Nevertheless, we found no evidence during the study period that dominant females tried to prevent subordinate females from copulating. Subordinate females

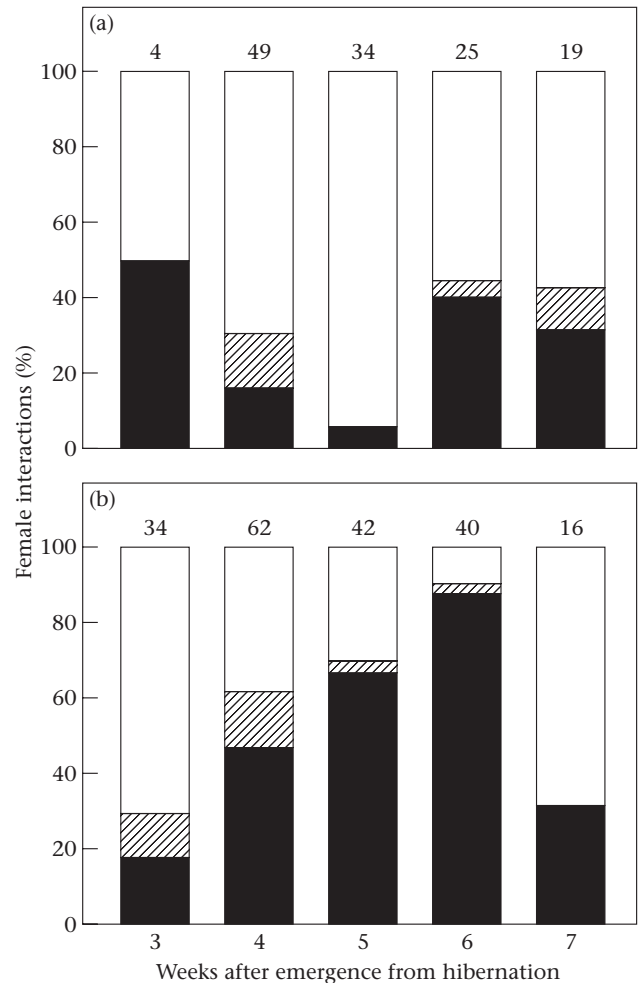


Figure 2. Pattern of interactions during the gestation period between dominant females and (a) daughters and (b) non-daughters. □: Neutral; ▨: amicable; ■: agonistic. Sample sizes are given above the bars.

apparently had unrestricted access to males, and were occasionally even observed to copulate.

Oestradiol and Progesterone

Circulating oestradiol could be traced with our assay predominantly during the first 2 weeks after emergence from hibernation, that is, during the mating season. During this period, there was no significant effect of social status (subordinates: 8.30 ± 1.84 pg/ml, $N=61$; dominants: 10.49 ± 16.68 pg/ml, $N=93$; $F_{1,83}=0.72$, $P=0.40$) or subsequent reproduction (nonparous females: 8.02 ± 1.49 pg/ml, $N=103$; parous females: 12.87 ± 2.34 pg/ml, $N=51$, $F_{1,83}=2.53$, $P=0.16$) on oestradiol concentrations. During the gestation period, circulating plasma progesterone levels increased in parous females resulting in higher progesterone levels than in nonparous females ($F_{1,34}=15.53$, $P<0.001$; Fig. 3). Daughters did not have significantly lower progesterone

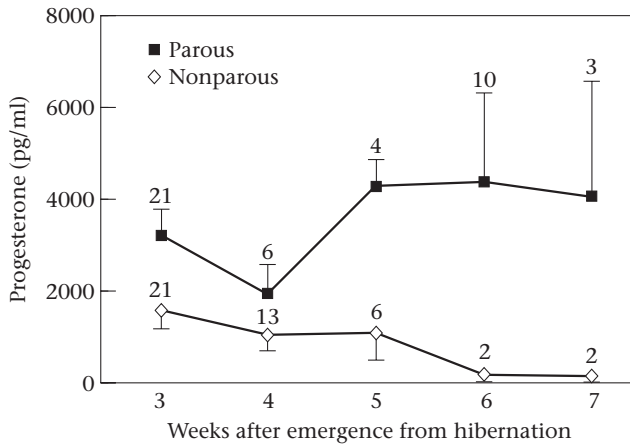


Figure 3. Levels of plasma progesterone in adult females during the gestation period. Means are given \pm SE. Numbers are sample sizes.

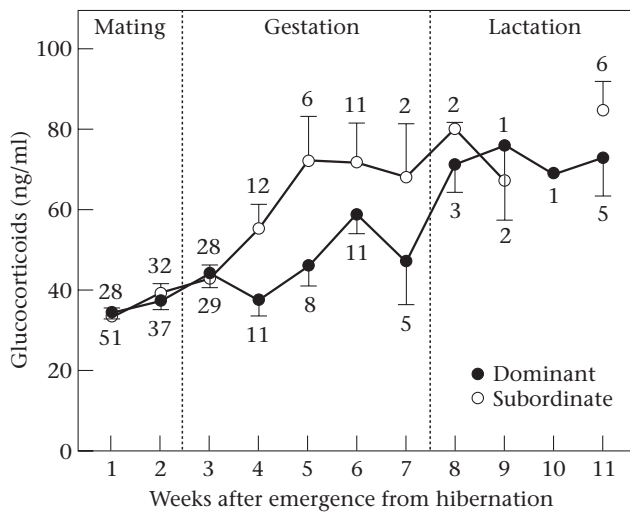


Figure 4. Levels of plasma glucocorticoids of adult dominant and subordinate females during the reproductive period. Means are given \pm SE. Numbers are sample sizes.

levels (538 ± 134 pg/ml, $N=22$) than nondaughters (1032 ± 248 pg/ml, $N=25$; $F_{1,17}=2.37$, $P=0.14$).

Glucocorticoids

Glucocorticoids increased in all adult females more than twofold from emergence from hibernation to July, the end of lactation (effect of week: $F_{1,207}=164.57$, $P<0.0001$; Fig. 4). However, these changes differed in magnitude between subordinate and dominant females (interaction of week and status: $F_{1,205}=6.38$, $P<0.05$; Fig. 4). During the gestation period, subordinate females had significantly higher levels of circulating glucocorticoids than dominant females ($F_{1,62}=4.98$, $P<0.05$; Fig. 4). Glucocorticoid levels did not differ between nonparous dominant females (44.68 ± 3.89 ng/ml, $N=24$) and parous dominant females (46.55 ± 2.59 ng/ml, $N=40$; $F_{1,26}=0.17$, $P=0.68$) or between daughters (49.75 ± 6.21 ng/ml, $N=22$) and nondaughters (56.93 ± 6.21 ng/ml, $N=25$; $F_{1,16}=0.81$, $P=0.38$).

DISCUSSION

Occurrence of Reproductive Suppression

In Alpine marmot family groups with a stable social structure only dominant females produce weaned young (e.g. Arnold 1990a, b; Perrin et al. 1993a; Lenti Boero 1999). Our results show that this high reproductive skew is not due to differences between subordinate and dominant females in reproductive ability or body condition. Adult subordinate and dominant females did not differ in body mass, hindfoot length or level of plasma oestradiol after hibernation. Thus, virtually all adult female marmots came into oestrus, regardless of social status. Furthermore, because all females had access to males, every female should have been able to mate and to become pregnant (see also Goossens et al. 1996, 1998). Oestrous female Alpine marmots copulate with all males present in rapid succession, and males show no obvious rivalry over mates (reviewed in Arnold 1990a). Consistent with this finding, we observed copulations between males and subordinate females (see also Arnold 1990a) and had indirect evidence that subordinate females mate, as we found a copulatory plug in a trapped individual. We also found indirect cues of reproduction (enlarged nipples and late moult) in three subordinates, and one subordinate female's pregnancy was confirmed by ultrasound. However, we never trapped a lactating subordinate female in a family group with a stable social structure. One possibility of reproductive suppression, infanticide, a widespread phenomenon in ground-dwelling sciurids (reviewed in Hackländer & Arnold 1999), was apparently rare in our study population, although we may have failed to detect it because juveniles remain in the natal burrow until weaning.

During our 14-year study, we recorded only once a subordinate female that had given birth; only one litter emerged above ground in this group, and only one female, an adult daughter of the dominant female, showed clear signs of lactation. The failure of reproductive suppression in this case of competing mother and adult daughter seemed to be caused by similar body strength and hence an equivocal dominance relationship. Attempts at reproductive suppression apparently continued here even beyond weaning because the subordinate daughter's offspring had been seriously attacked. Four juveniles appeared above ground in this group, and all were trapped within a few days. Two of them had severe injuries from bites and one disappeared for several weeks and resided temporarily in a neighbouring group. The undecided dominance relation between the females apparently existed until the end of July and eventually resulted in the eviction of the older female and the previously subordinate adult daughter taking over the dominant position.

However, in groups of stable social structure, signs of advanced gestation were rare in subordinate females, as indicated by low levels of progesterone and the few subordinate females with enlarged nipples or late moult. Thus, we suggest that reproductive suppression leading to high reproductive skew occurred predominantly during

the weeks between mating and advanced gestation, that is, before or immediately after implantation.

Mechanisms of Reproductive Suppression

Most of the agonistic interactions between females occurred during the gestation period. Dominant females were more often initiators of agonistic interactions (see also Barash 1976; Naef-Daenzer 1984; Goossens et al. 1996) but they rarely initiated amicable behaviour towards subordinates, whereas 15% of the interactions initiated by subordinates were amicable. Probably because of increased aggression by dominants, subordinates had significantly higher levels of glucocorticoids during the gestation period than dominant females. This result fits into the classical scheme of winner–loser contests known from laboratory studies (Louch & Higginbotham 1967; Schuurman 1980): after a fight glucocorticoid levels increase over several hours in losers but decrease rapidly in winners. Evidence suggests that glucocorticoids interfere with the stimulatory action of gonadotropins on sex steroid-producing cells and decrease pituitary responsiveness to GnRH (Rivier & Rivest 1991). It is not surprisingly, therefore, that subordinate females showed only basal concentrations of circulating progesterone instead of increasing levels, as parous dominants did. Therefore, we suggest that the proximate mechanism of reproductive suppression in female Alpine marmots lies in the negative effect of stress on the activity of the hypothalamic-pituitary-gonadal axis.

Why do Subordinates Stay at Home?

Subordinates should be able to move away to terminate an attack if behavioural appeasement does not work. As described for Olympic marmots, *Marmota olympus* (Barash 1973), subordinate females of Alpine marmots did not choose their sleeping burrow by chance. Especially during the gestation period, these individuals slept apart from the group and hence apart from the dominants (K. Hackländer & F. Frey-Roos, unpublished data). Nevertheless, this strategy of avoidance is limited because of the relatively small size of an Alpine marmot group's territory in our study area (mean 2.6 ha, Arnold 1993).

The majority of studies on the relation between glucocorticoids and social status in cooperatively breeding species have shown that glucocorticoid levels are not significantly higher in subordinates (Creel 2001). Only two field studies on cooperatively breeding species have shown that subordinate individuals had higher levels of glucocorticoids; these results are similar to the findings of several captive winner–loser studies. Both species are ground-dwelling rodents (naked mole-rats, *Heterocephalus glaber*: Faulkes & Abbott 1997; male Alpine marmots: Arnold & Dittami 1997) for which a territory is crucial for survival and dispersal is limited. For example, Alpine marmots rely on their burrow system to provide shelter from predation (mainly red fox, *Vulpes vulpes*, and golden eagle, *Aquila chrysaetos*) and a hibernaculum for winter

survival. Dispersal in Alpine marmots is related to high costs. In a study of 22 dispersing Alpine marmots (Frey-Roos 1998; Arnold & Frey-Roos 1999) seven died during summer. Three of seven dispersing individuals that entered hibernation survived winter. These risks result in delayed dispersal in Alpine marmots. Nearly all 2 year olds and about one-third of the 3- and 4-year-old group members remain an additional year in the family group (Arnold 1990a, b; Perrin et al. 1993b). Because avoidance of social aggression within a group is limited in Alpine marmots (and in mole-rats) dominant–subordinate relationships within a group could be considered similar to that of winner–loser contests in captive laboratory studies.

The Effect of Relatedness

In general, additional adult group members increase the survival rate of juveniles during hibernation by producing heat (Arnold 1993). Hence, dominant females should have an interest in keeping the number of adult individuals in the group high. However, daughters and nondaughters should show different strategies (Armitage 1987). Daughters of the dominant female could increase their indirect fitness by staying at home and warming their siblings. Although these gains of indirect fitness are low compared with the benefits of direct fitness, daughters should be more likely to forgo their own reproduction than nondaughters. Thus, dominant females should be less aggressive towards their daughters. This prediction is consistent with our result that the number of agonistic interactions between dominant females and daughters was relatively low and peaked at the beginning of the gestation period.

Even if the dominant male is the father of a dominant female's nondaughter, this nondaughter cannot be sure of gaining indirect fitness benefits, because young in the group may be fathered by several males. Thus, nondaughters should be more willing to start a pregnancy and to expel the dominant female. In line with this, we found that daughters were more amicable to dominant females, that dominant females directed their aggression mainly towards unrelated subordinate females, and that nondaughters initiated more agonistic interactions than daughters. These behaviour patterns were not reflected by the endocrinological data, as we found no differences in hormonal levels between nondaughters and daughters, although this was probably because of the low sample size.

Costs of Reproductive Suppression

Dominant females incurred costs related to the reproductive suppression of subordinate group members. The more subordinate females there were in the group, the lower was the probability of the dominant female reproducing successfully. A diminishing effect of competing individuals on female reproductive output has also been described for several other marmot species (Grizzel 1955; Svendsen 1974; Wasser & Barash 1983; Armitage 1986).

The reduced reproduction of dominant females in our study was due to unrelated subordinate females, which confirms that there is intense competition between unrelated females within an Alpine marmot family group.

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References

- Allainé, D. 2000. Sociality, mating system and reproductive skew in marmots: evidence and hypotheses. *Behavioural Processes*, **51**, 21–34.
- Armitage, K. B. 1986. Individuality, social behaviour, and reproductive success in yellow-bellied marmots. *Ecology*, **67**, 1186–1193.
- Armitage, K. B. 1987. Social dynamics of mammals: reproductive success, kinship and individual fitness. *Trends in Ecology and Evolution*, **2**, 279–284.
- Arnold, W. 1990a. The evolution of marmot sociality: I. Why disperse late? *Behavioral Ecology and Sociobiology*, **27**, 229–237.
- Arnold, W. 1990b. The evolution of marmot sociality: II. Costs and benefits of joint hibernation. *Behavioral Ecology and Sociobiology*, **27**, 239–246.
- Arnold, W. 1993. Social evolution in marmots and the adaptive value of joint hibernation. *Verhandlungen der Deutschen Zoologischen Gesellschaft*, **86**, 79–93.
- Arnold, W. & Dittami, J. 1997. Reproductive suppression in male Alpine marmots. *Animal Behaviour*, **53**, 53–66.
- Arnold, W. & Frey-Roos, F. 1999. Verzögerte Abwanderung und gemeinschaftliche Jungenfürsorge: Anpassungen des Alpenmurmeltieres (*Marmota marmota*) an eiszeitliche Lebensbedingungen. *Stapfia (Kataloge des Oberösterreichischen Landesmuseums)*, **NF**, **63**, 33–42.
- Barash, D. P. 1973. The social biology of the Olympic marmot. *Animal Behaviour Monographs*, **6**, 173–245.
- Barash, D. P. 1974. The social behaviour of the hoary marmot (*Marmota caligata*). *Animal Behaviour*, **22**, 256–261.
- Barash, D. P. 1976. Social behaviour and individual differences in free-living Alpine marmots (*Marmota marmota*). *Animal Behaviour*, **24**, 27–35.
- Blumstein, D. T. & Armitage, K. B. 1998. Life history consequences of social complexity: a comparative study of ground-dwelling sciurids. *Behavioral Ecology*, **9**, 8–19.
- Chrousos, G. P. & Gold, P. W. 1992. The concepts of stress and stress system disorders: overview of physical and behavioral homeostasis. *Journal of the American Medical Association*, **267**, 1244–1252.
- Clutton-Brock, T. H. 1998. Reproductive skew, concessions and limited control. *Trends in Ecology and Evolution*, **13**, 288–292.
- Creel, S. R. 2001. Social dominance and stress hormones. *Trends in Ecology and Evolution*, **16**, 491–497.
- Creel, S. R., Creel, N. M., Wildt, D. E. & Monfort, S. L. 1992. Behavioural and endocrine mechanisms of reproductive suppression in Serengeti dwarf mongooses. *Animal Behaviour*, **43**, 231–245.
- Faulkes, C. G. & Abbott, D. H. 1997. The physiology of a reproductive dictatorship: regulation of male and female reproduction by a single breeding female in colonies of naked mole-rats. In: *Cooperative Breeding in Mammals* (Ed. by N. G. Solomon & J. A. French), pp. 302–334. Cambridge: Cambridge University Press.
- Frey-Roos, F. 1998. Geschlechtsspezifisches Abwanderungsmuster beim Alpenmurmeltier (*Marmota marmota*). Ph.D. thesis, Philipps-University Marburg/Lahn.
- Goossens, B., Coulon, J., Allainé, D., Graziani, L., Bel, M.-C. & Taberlet, P. 1996. Immigration of a pregnant female in an Alpine marmot family group: behavioural and genetic data. *Comptes Rendus de l'Académie des Sciences—Serie III—Sciences de la Vie*, **319**, 241–246.
- Goossens, B., Graziani, L., Waits, L. P., Farand, E., Magnolon, S., Coulon, J., Bel, M.-C., Taberlet, P. & Allainé, D. 1998. Extra-pair paternity in the monogamous Alpine marmot revealed by nuclear DNA microsatellite analysis. *Behavioral Ecology and Sociobiology*, **43**, 281–288.
- Grizzel, R. A. 1955. A study of the southern woodchuck, *Marmota monax monax*. *American Midland Naturalist*, **53**, 257–293.
- Hackländer, K. & Arnold, W. 1999. Male-caused failure of female reproduction and its adaptive value in Alpine marmots (*Marmota marmota*). *Behavioral Ecology*, **10**, 592–597.
- Hackländer, K., Bruns, U. & Arnold, W. 1999. Reproduktion und Paarungssystem bei Alpenmurmeltieren (*Marmota marmota*). *Stapfia (Kataloge des Oberösterreichischen Landesmuseums)*, **NF**, **63**, 21–32.
- von Holst, D. 1998. The concept of stress and its relevance for animal behavior. *Advances in the Study of Behavior*, **27**, 1–131.
- Keller, L. & Reeve, H. K. 1994. Partitioning of reproduction in animal societies. *Trends in Ecology and Evolution*, **9**, 98–103.
- Lenti Boero, D. 1999. Population dynamics, mating system and philopatry in a high altitude colony of alpine marmots (*Marmota marmota* L.). *Ethology, Ecology and Evolution*, **11**, 105–122.
- Louch, C. D. & Higginbotham, M. 1967. The relation between social rank and plasma corticosterone levels in mice. *General and Comparative Endocrinology*, **8**, 441–444.
- Mann, C. S., Macchi, E. & Janeau, G. 1993. Alpine marmot (*Marmota marmota*, L.). *Ibex, Journal of Mountain Ecology*, **1**, 17–30.
- Müller-Using, D. 1957. Die Paarungsbiologie der Murmeltiere. *Zeitschrift für Jagdwissenschaft*, **3**, 24–28.
- Naef-Daenzer, B. 1984. Sozialverhalten und räumliche Organisation von Alpenmurmeltieren (*Marmota m. marmota*). Ph.D. thesis, University of Bern.
- Palme, R. & Möstl, E. 1994. Biotin-Streptavidin enzyme immunoassay for the determination of oestrogens and androgens in boar faeces. In: *Advances of Steroid Analysis '93* (Ed. by S. Görög), pp. 111–117. Budapest: Akademiai Kiado.
- Palme, R. & Möstl, E. 1997. Measurement of cortisol metabolites in faeces of sheep as a parameter of cortisol concentration in blood. *Zeitschrift für Säugetierkunde*, **62**, Suppl. II, 192–197.
- Perrin, C., Allainé, D. & Le Berre, M. 1993a. Socio-spatial organization and activity distribution of the Alpine marmot *Marmota marmota*: Preliminary results. *Ethology*, **93**, 21–30.
- Perrin, C., Coulon, J. & Le Berre, M. 1993b. Social behavior of Alpine marmots (*Marmota marmota*): seasonal, group, and individual variability. *Canadian Journal of Zoology*, **71**, 1945–1953.
- Pineiro, J. C. & Bates, D. M. 2000. *Mixed Effects Models in S and S-plus*. Berlin: Springer.

- Psenner, H.** 1957. Neues vom Murmeltier, *Marmota m. marmota* (Linné, 1758). *Säugetierkundliche Mitteilungen*, **5**, 4–10.
- Psenner, H.** 1960. Das Verhalten der Murmeltiere (*Marmota m. marmota*), insbesondere von Mutter und Jungen, im Bau. *Säugetierkundliche Mitteilungen*, **8**, 144–148.
- Reeve, H. K., Emlen, S. T. & Keller, L.** 1998. Reproductive sharing in animal societies: reproductive incentives or incomplete control by dominant breeders? *Behavioral Ecology*, **9**, 267–278.
- Rivier, C. & Rivest, S.** 1991. Effect of stress on the activity of the hypothalamic-pituitary-gonadal axis: peripheral and central mechanisms. *Biology of Reproduction*, **45**, 523–532.
- Sapolsky, R. M.** 1992. *Stress, the Aging Brain, and the Mechanisms of Neuron Death*. Cambridge, Massachusetts: MIT Press.
- Schuurman, T.** 1980. Hormonal correlates of agonistic behavior in adult male rats. *Progress in Brain Research*, **53**, 415–420.
- Schwarzenberger, F., Tomášová, K., Holečková, D., Matern, B. & Möstl, E.** 1996. Measurement of fecal steroids in the black rhinoceros (*Diceros bicornis*) using group-specific enzyme immunoassay for 20-oxo-pregnanes. *Zoo Biology*, **15**, 159–171.
- Svendsen, G. E.** 1974. Behavioral and environmental factors in the spatial distribution and population dynamics of a yellow-bellied marmot population. *Ecology*, **55**, 760–771.
- Türk, A. & Arnold, W.** 1988. Thermoregulation as a limit to habitat use in Alpine marmots (*Marmota marmota*). *Oecologia (Berlin)*, **76**, 544–548.
- Venables, W. N. & Ripley, B. D.** 1999. *Modern Applied Statistics with S-plus*. Berlin: Springer.
- Wasser, S. K. & Barash, D. P.** 1983. Reproductive suppression among female mammals: implications for biomedicine and sexual selection theory. *Quarterly Review of Biology*, **58**, 513–538.