

Reproductive suppression in male alpine marmots

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Abstract. Social groups of alpine marmots, *Marmota marmota*, often contain several adult males only one of which is a dominant territorial male. How reproductive competition may be expressed among adult group males during mating was investigated, in particular whether reproduction is suppressed in subordinate males. Among adult subordinate males at least 3 years old, potential offspring of the territorial male ('sons') had androgen levels as high as those of territorial males whereas non-related group males ('non-sons') had significantly lower vernal levels, similar to those of 2-year-old individuals. Plasma androgen and corticosteroid titres were negatively correlated in subordinates at least 2 years old but were positively correlated in territorial males. Corticosteroids correlated negatively with body mass in sons and were high regardless of body mass in non-sons. Androgens mirrored these relations. Injuries from intraspecific fighting were more frequent among non-sons than among sons. Androgens and corticosteroids of territorial males correlated positively with the number of non-sons in the group, whereas the number of sons in a group had no comparable or at best the opposite effect. These results indicate that territorial males attempt to inhibit reproduction in other group males but adjust their effort according to inhibition costs (presumably increasing with a subordinate male's body size) and benefits (which are lower in sons). Marmots with high corticosteroid levels in spring gained less mass during the following summer. This could impair winter survival or reproductive success in the next year. Body-mass loss during hibernation correlated positively with vernal androgen levels in adult males. Only males with sufficient summer mass gain may be capable of sustaining energetically costly interruptions of torpor at the end of winter, necessary for gonadal development. The interactions between group members around mating time may reflect general patterns throughout the year that lead to selective reproductive inhibition in the group via effects on mass gain, hibernation mass loss and gonadal development.

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The alpine marmot, *Marmota marmota*, is a social mammal, which lives in groups of up to 20 individuals. These groups typically consist of a dominant, territorial pair and their subordinate offspring of various age classes. In addition to this pattern, groups often contain subordinates that are less related or even unrelated to the territorial animals. This happens when territorial males tolerate offspring of previous tenants in the group, when litters of neighbouring groups intermingle,

or after the territorial male has been cuckolded (Arnold 1990a; Arnold et al. 1994). An important aspect of alpine marmot sociality has been presumed to be the advantages of communal hibernation (Arnold 1990b, 1993a), but a negative consequence of this communality appears to be reproductive competition. Subordinate females do not reproduce and the majority of the offspring seem to stem from territorial males (Arnold 1990a). Actual reproductive suppression of other males in the group by the territorial male, however, has not been documented. Instead, polyandrous matings have occasionally been observed (Müller-Using 1957; Hembeck 1958; Arnold 1990a).

Investigation of the mating system of alpine marmots by paternity analysis has been severely

Dedicated to Professor Dr Wolfgang Wickler on the occasion of his 65th birthday.

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hampered by low genetic variability (Arnold 1990a; Rassmann et al. 1994). None the less, enzyme electrophoresis and DNA fingerprinting have shown that individuals other than the territorial male, predominantly group males, compete and sire offspring (Arnold 1990b; Arnold et al. 1994). This cuckoldry of territorial males by subordinate group males stimulated us to investigate the mechanisms involved in reproductive competition among group males. Our aim was to compare various aspects of condition and reproductive physiology during the mating season in the first 2 weeks after emergence from hibernation (Müller-Using 1957; Psenner 1957). Important parameters were body mass, which affects reproductive activity and gonadal size in ground squirrels (Barnes 1984), and plasma corticosteroids. We expected to find high levels of corticosteroids as indicators of behaviourally induced stress and correspondingly low levels of androgens in reproductively suppressed males.

The underlying questions were whether all subordinate males are reproductively active, and if not, whether the interactions between territorial and subordinate males or effects of body condition might result in reproductive suppression of subordinates. In addition, we investigated how territorial males were physiologically affected by the presence of other adult males in the group.

METHODS

Study Population and Animals

We studied alpine marmots from 1982 to 1992 in the Berchtesgaden National Park, Germany (47°36'N, 13°0'E, 1100–1500 m above sea level). Details of the study population, capture and marking techniques can be found in Arnold (1990a). Territorial males could be identified behaviourally in most groups. They regularly 'patrolled' the borders and initiated and won most aggressive interactions among group males (186 of 189 observed interactions, J. Hottinger & W. Arnold, unpublished data). In a few groups it was not possible to identify a single territorial male with certainty, for example when intruding males could not evict the territorial male and the intruder could not be repelled. We excluded data from such individuals with uncertain status (territorial or not) from analysis.

We discriminated three age classes. Marmots are yearlings after the first hibernation, 2 years old after the second hibernation, and 3 or more years old after the third hibernation. The age of most marmots investigated was known exactly because they were trapped within a few days of first emergence from the natal burrow and marked permanently by tattoos on the inguinal skin. The 'adults' class contained some individuals of unknown age. 'Sons' were males born during the territorial occupancy of the dominant male, 'non-sons' were born either before the territorial occupancy or they were immigrants from another group. Hence most sons were presumably offspring of the territorial male whereas non-sons were definitely not.

Body Measurements

At emergence from hibernation, animals were captured, weighed to the nearest 50 g, and testes width and length were measured with a sliding calliper as an indirect measure of gonadal development. We determined mass gain during the active season for individuals reweighed at least 40 days after the first measurement. We estimated body mass at immergence into hibernation (end of September) by extrapolating a Gompertz growth curve fitted to an individual's mass data. The date of snow melt in a territory determines the onset of food availability and mass gain and was therefore used to approximate a growth curve's inflection point (for further details see Arnold 1990a). We calculated mass loss during hibernation by subtracting the measured vernal mass from the estimated immergence mass in the previous autumn. Mass loss is expressed as percentage decrease of immergence mass.

Radioimmunoassays

From 1988 to 1992 we collected blood samples from males, during the first 2 weeks after emergence, from the saphenal vein without anaesthesia. Samples were taken between 0900 hours and 1700 hours, the main activity period of marmots at this time of year. Traps were checked at least every second hour. Captured animals were transferred into a cone-shaped, cotton handling bag. We took 4 ml of blood within 5 min of approaching the trap. After addition of a few drops of EDTA, samples were centrifuged and stored at

Table I. Variables measured and sample sizes

Variable	Individuals sampled	Number of samples	<i>F</i>	<i>df</i>	<i>P</i>
Androgens	70 (59)*	119	0.90	(69, 118)	0.651
Corticosteroids	70 (59)	119	0.79	(69, 118)	0.794
Testis length	54 (44)	99	0.77	(53, 98)	0.808
Testis width	54 (44)	98	1.06	(53, 97)	0.428
Vernal body mass	149 (126)	416	2.55	(148, 415)	<0.001
Mass loss during last winter	89 (71)	198	0.00	(88, 197)	1.000
Mass gain during following summer	110 (91)	235	0.69	(109, 234)	0.956

Intra-individual variation of measurements was compared with variation between individuals with two-way ANOVAs with factors 'age' and 'individual ID'; *F* and *P* values are given for the factor 'individual ID'.

*Numbers in parentheses indicate the number of individuals of exactly known age (see text for details).

– 70°C. Steroid concentrations were measured using standard RIA techniques and antisera from Vienna Lab. N.Y. lot number 01916 for testosterone (cross-reactivity with DHT and androstenediol) and lot number 01197 for glucocorticosteroids (cross-reactivity with cortisol > cortisone > desoxycortisol > corticosterone) after a petroleum benzene/diethyl ether (1:1) extraction on 0.5 g Extralut columns (Merck, Frankfurter Straße 250, D-64293 Darmstadt, Germany). This method produced recoveries of approximately 85% for androgens and 45% for glucocorticosteroids and eliminated possible lipid interference in the assay. Inter-assay variance with this method is 11%; intra-assay variance was held under 5%. The extraction and high cross-reactivity of the antisera respectively with other androgens and corticosteroids is the basis of our terminology: total androgens and total corticosteroids.

Statistical Analysis

We used SPSS for Windows, release 6.0. Parametric tests were applied whenever the assumptions were met. For some analyses this was the case only after logarithmic transformation of the original data. Significance values were obtained from two-tailed tests. Twenty males were sampled twice during one mating season and one three times. Within-season intra-individual differences of androgens averaged 0.61 ng/ml (*SD*=0.51) and of corticosteroids 0.91 ng/ml (*SD*=0.79). From individuals sampled multiply during one mating season, we selected the maximal values of the hormone and, for consistency, of all other factors measured for analyses. In our opinion, maxima

indicate condition and reproductive potential better than means. However, the use of means instead of maxima did not change the results significantly. Many individuals were sampled in several years. We checked for all variables with two-way ANOVAs for factors 'age' and 'individual ID'. Intra-individual variation between years differed from the variation between marmots only in vernal body mass (Table I). Hence except for vernal body mass, samples were considered as the appropriate, statistically independent unit of analysis. For comparing vernal body masses between individual classes (Table II), the mean of repeated measurements of an animal in different years was used for males 3 or more years old.

RESULTS

Differences in Body Mass and Gonadal Size

Mass and gonadal size changed during development (Table II). Body mass increased with age until year 3 as did the summer mass gain. No differences were found between sons and non-sons in either vernal body mass or summer mass gain. The same trend was observed with testes development. Summer mass gain, body mass and gonadal size of subordinate males reflected developmental patterns that were not different for different levels of relatedness to the territorial male. In addition, males 3 or more years old did not differ from territorial males in these parameters. Hence, reproductive suppression is not evident here. Nevertheless, sons seemed to lose more mass during hibernation than non-sons among males 3 or more years old whereas 2-year-old sons and

Table II. Reproductive and physical parameters of male alpine marmots

Variable	Yearling		2-year-old		≥3-year-old		Territorial males	P of kin effect	P of age effect	P of age-kin interaction
	Non-sons	Sons	Non-sons	Sons	Non-sons	Sons				
Androgens (ng/ml)	0.18 (8) ^a 0.16–0.34	0.16 (7) ^{a,b} 0.14–0.44	0.44 (10) ^{a,b} 0.36–0.94	0.65 (6) ^b 0.38–1.11	0.60 (12) ^{a,b} 0.27–0.82	1.40 (16) ^c 0.76–2.06	1.51 (60) ^e 1.03–2.11	0.014 (0.003)	<0.001 (NS)	0.058 (NS)
Corticosteroids (ng/ml)	3.85 (8) ^a 1.64–6.29	1.49 (7) ^b 0.90–2.63	2.82 (10) ^{a,c} 1.79–3.94	2.65 (6) ^{a,c} 2.24–3.01	2.85 (12) ^a 2.40–3.34	1.43 (16) ^b 0.95–1.55	2.23 (60) ^{b,c} 1.12–3.08	<0.001 (0.010)	NS (0.026)	0.045 (0.013)
Testis width (mm)			10.2 (6) ^a 9.7–11.4	11.5 (4) ^a 8.7–12.5	13.5 (13) ^b 12.2–14.7	13.3 (16) ^b 11.7–14.7	13.9 (59) ^b 12.9–15.0	NS	<0.001	NS
Testis length (mm)			23.1 (7) ^a 20.0–25.0	23.3 (4) ^a 19.2–25.4	27.7 (12) ^{b,c} 25.1–29.0	27.4 (16) ^b 24.8–29.4	28.7 (60) ^e 26.2–30.4	NS	<0.001	NS
Vernal body mass (g)	1200 (23) ^a 1050–1350	1050 (74) ^a 950–1150	2450 (30) ^b 2250–2650	2350 (47) ^b 2200–2600	2950 (21) ^c 2700–3050	2900 (40) ^c 2800–3050	3000 (55) ^c 2800–3150	NS (NS)	<0.001 (<0.001)	0.054 (NS)
Mass loss during last winter (%)	35.3 (1)	39.1 (8) ^a 33.4–43.7	28.5 (19) ^{b,c} 26.2–34.5	26.6 (26) ^b 23.9–31.3	28.8 (17) ^{b,c} 26.6–32.7	32.1 (41) ^{c,d} 29.8–35.0	33.8 (84) ^d 29.8–37.7	NS (NS)	0.005 (0.025)	0.073 (0.029)
Mass gain during following summer (g)	2350 (10) ^a 2200–2500	2200 (43) ^a 2000–2350	1800 (21) ^b 1600–2100	1950 (37) ^b 1750–2200	1350 (10) ^c 1200–1750	1450 (30) ^c 1250–1750	1500 (84) ^c 1300–1650	NS (NS)	<0.001 (<0.001)	NS (NS)

Medians and quartile range (below, Harshbarger 1977), sample size in parentheses. Individual groups differed significantly in all variables (Kruskal–Wallis tests, all $P<0.001$, groups with $N>1$ differing at $P<0.05$ are denoted with different superscripts: multiple post-hoc comparisons; Conover 1980). Data for subordinates were analysed for effects of age (age effect) and relatedness to the territorial male (kin effect) by two-way ANOVAs. Androgen and corticosteroid data were log-transformed for these analyses in order to meet the assumption of homoscedasticity. P -values in parentheses refer to differences between 2-year-old and 3-or-more-year-old sons and non-sons living in groups in which the territorial male had not changed recently (see text).

non-sons had similar mass loss as indicated by a significant age-kin interaction. However, the direct post-hoc comparison of sons and non-sons did not show a significant difference (Table II).

Endocrine Differences

Androgen levels increased with age and were maximal in territorial males and sons 3 or more years old while corticosteroid levels varied between groups independent of age (Table II). Corticosteroid levels were high but similar among all 2-year-old males and non-sons 3 or more years old. Corticosteroid titres of territorial males were also relatively high. Yearling sons and sons more than 3 years old had significantly lower corticosteroid titres than all other subordinate males. Yearling non-sons are not easily compared with other groups because the territorial changes that lead to the non-son status all occurred in spring shortly before capture. The elevated corticosteroid levels of yearling non-sons were presumably an immediate result of the social change. Subordinate individuals sampled within a day of a change of the territorial male ($N=10$) had significantly higher corticosteroid ($P=0.029$) and lower androgen titres ($P=0.009$) than others ($N=49$, U -tests). Restricting the analyses to data of subordinate animals from groups with settled social relations (no data from yearlings were available then) produced different results. No age- but only kin-related differences in circulating androgens were evident in this reduced data set and a now highly significant age-kin interaction was found in corticosteroids (Table II).

The effects of corticosteroid-androgen interactions together with developmental patterns could explain the endocrine differences between the various individual groups (Table II). Androgens and corticosteroids were positively correlated in territorial males (Fig. 1a) but the relationship in subordinate males 2 or more years old was negative. There was no difference in slopes of regressions between sons and non-sons but androgen levels were generally higher in sons (Fig. 1b).

Factors Involved in Reproductive Competition

Body mass and group composition

The results so far indicate a reproductive suppression of non-sons and an age- and/or body-mass-dependent reproductive suppression of sons,

which can be seen in the endocrine state but not in gonadal size or vernal body mass. Reproductive function (in terms of vernal androgen levels) of territorial males was not similarly impaired, even in the presence of high corticosteroid titres (Fig. 1a). Following this, we investigated (1) the role of an individual's body mass and hence competitive abilities in these endocrine effects and (2) whether the number of subordinate sons or non-sons (potential competitors) in a group affected the physiology of the territorial male. In non-sons corticosteroid levels were high regardless of body mass; in sons they decreased significantly with body mass (Fig. 2a). Androgens mirrored this relationship (Fig. 2b) as would have been expected from the negative correlation between androgens and corticosteroids in subordinate males (Fig. 1b).

In territorial males we found a positive relationship between the level of corticosteroids and the number of non-sons (Fig. 3a), but a (borderline-significant) negative relationship with the number of sons in the group (Fig. 3b). Androgens again showed correlations in the direction that would have been expected from their positive relation to corticosteroids in territorial males although only the correlation with the number of sons in a group was significant (Fig. 3).

Hibernation mass loss

Because body mass played an important role in the reproductive competence in subordinate sons, we further analysed whether mass loss during the preceding hibernation was critical. There was no significant correlation between hibernation mass loss and corticosteroids and no difference between sons, non-sons, or territorial animals (Fig. 4a). However, higher hibernation mass loss seemed to be positively related with corticosteroid titres during the following mating season in non-sons and negatively in sons (difference between regression slopes of sons/non-sons: $F_{1,27}=4.05$, $P=0.060$; Fig. 4a). The relation between hibernation mass loss and vernal androgen levels was clearer than that for corticosteroids. Here, positive relations were found in all categories of males and the regression was significant in the pooled data set (Fig. 4b).

Aggressive interactions

An important question now was whether territorial males achieve reproductive suppression of

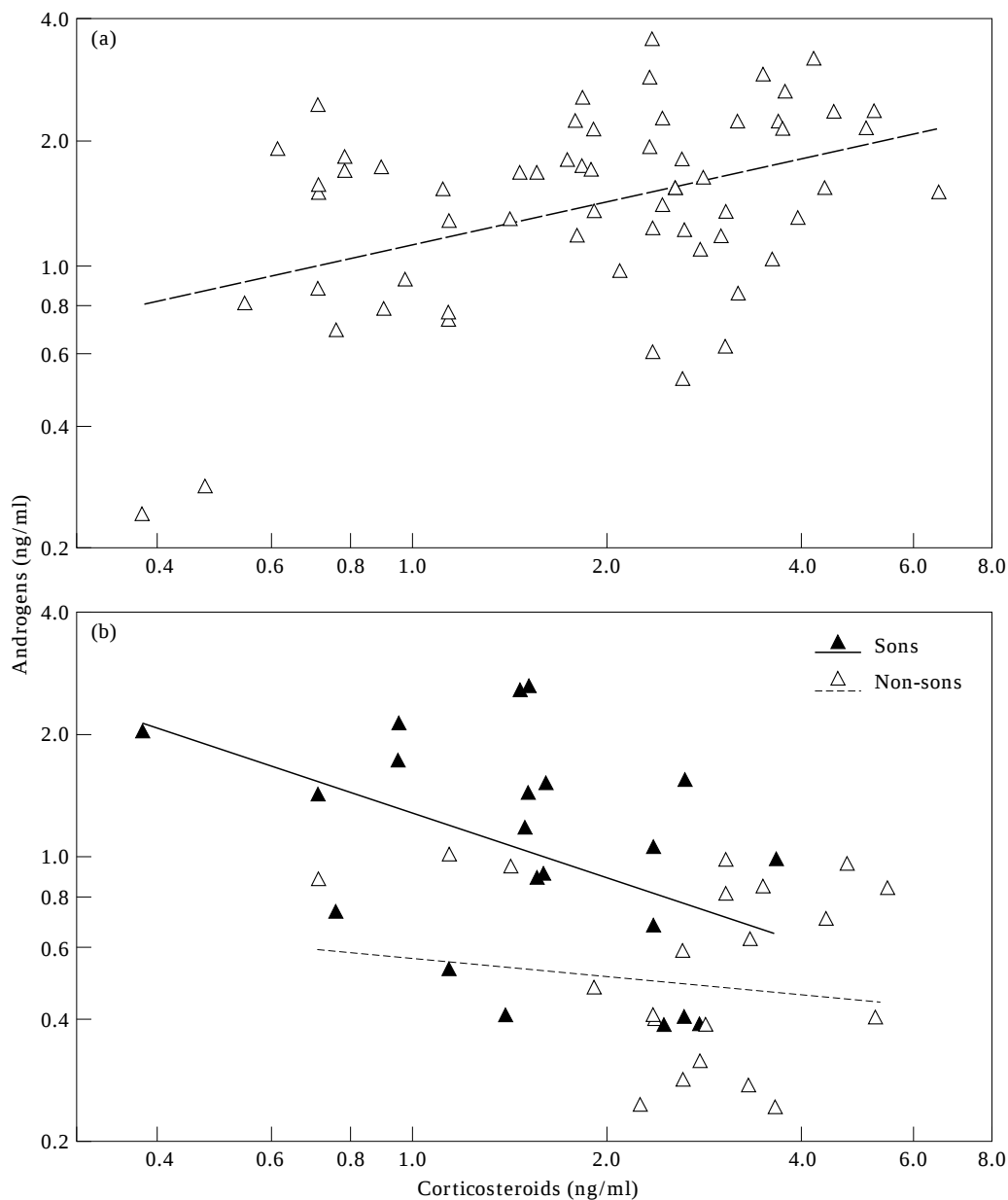


Figure 1. The relationship between androgen and corticosteroid plasma titres in (a) territorial and (b) subordinate male marmots 2 or more years old. Overall difference between slopes of regressions: $F_{2,97}=8.1$, $P=0.001$. Difference between slopes of regressions of territorial males/sons: $F_{1,78}=14.07$, $P<0.001$; territorial males/non-sons: $F_{1,77}=4.55$, $P=0.036$; sons/non-sons: $F_{1,39}=1.08$, ns. Difference between Y -axes intercepts of sons/non-sons: $F_{1,39}=5.12$, $P=0.029$. Individual regressions: (a) territorial males: $\log(Y)=0.047+0.345 \log(X)$, $F_{1,58}=13.41$, $P<0.001$; (b) sons: $\log(Y)=0.104-0.519 \log(X)$, $F_{1,20}=4.90$, $P=0.039$; non-sons: $\log(Y)=-0.201-0.174 \log(X)$, $F_{1,19}=0.57$, ns; pooled data of sons/non-sons, $\log(Y)=0.041-0.562 \log(X)$, $F_{1,41}=14.21$, $P<0.001$.

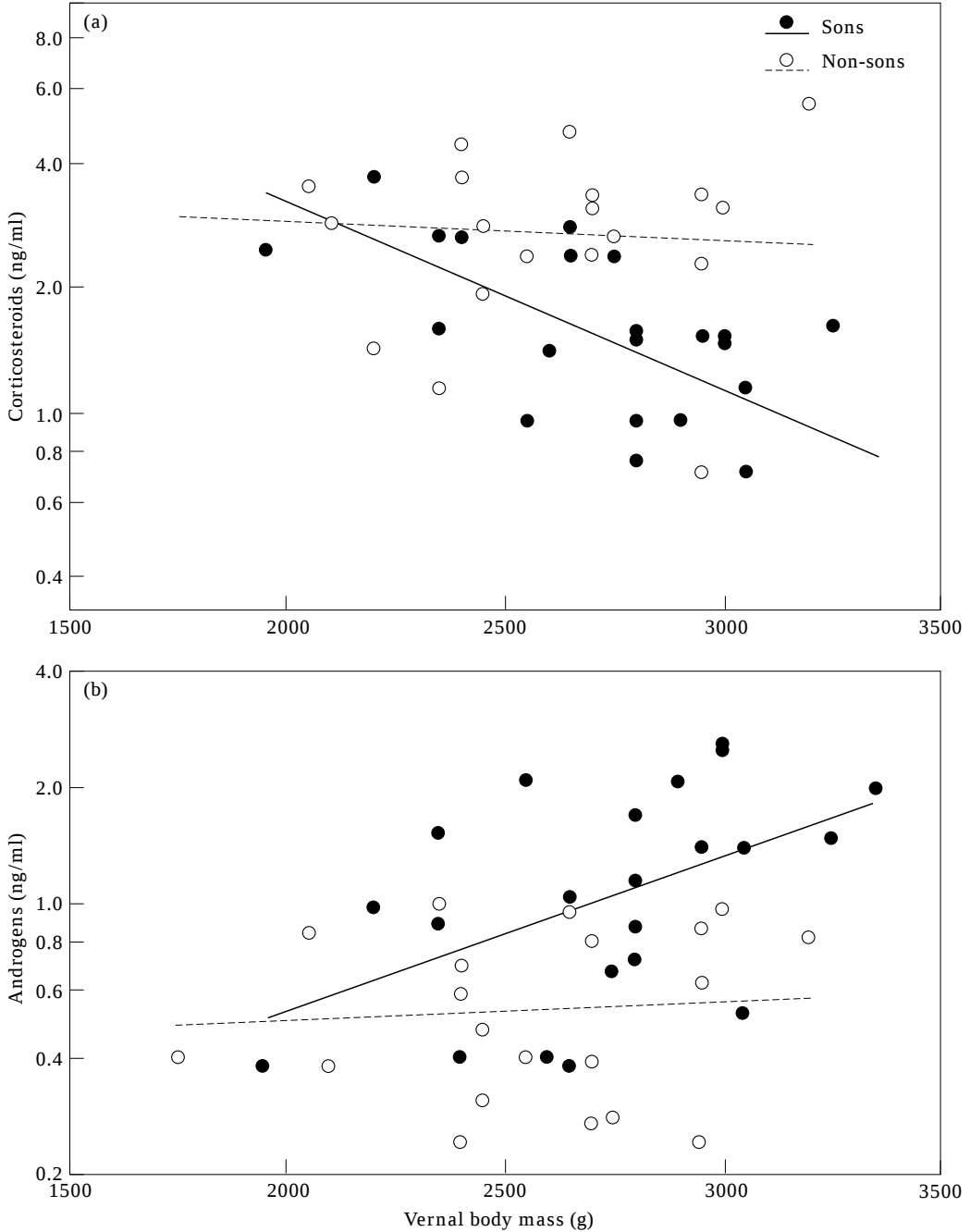


Figure 2. Corticosteroid and androgen plasma titres and their relation to vernal body mass of individual sons of the territorial male and non-sons 2 or more years old. (a) Corticosteroids. Difference between regression slopes: $F_{1,39}=9.67$, $P=0.003$; individual regressions, sons: $\log(Y)=1.416-0.00046X$, $F_{1,20}=15.66$, $P<0.001$; non-sons: $\log(Y)=0.394+0.00003X$, $F_{1,19}=0.06$, ns. (b) Androgens. Difference between regression slopes: $F_{1,38}=3.22$, $P=0.081$; individual regressions, sons: $\log(Y)=-1.079+0.0004X$, $F_{1,20}=6.56$, $P=0.019$; non-sons: $\log(Y)=-0.327+0.00002X$, $F_{1,18}=0.01$, ns.

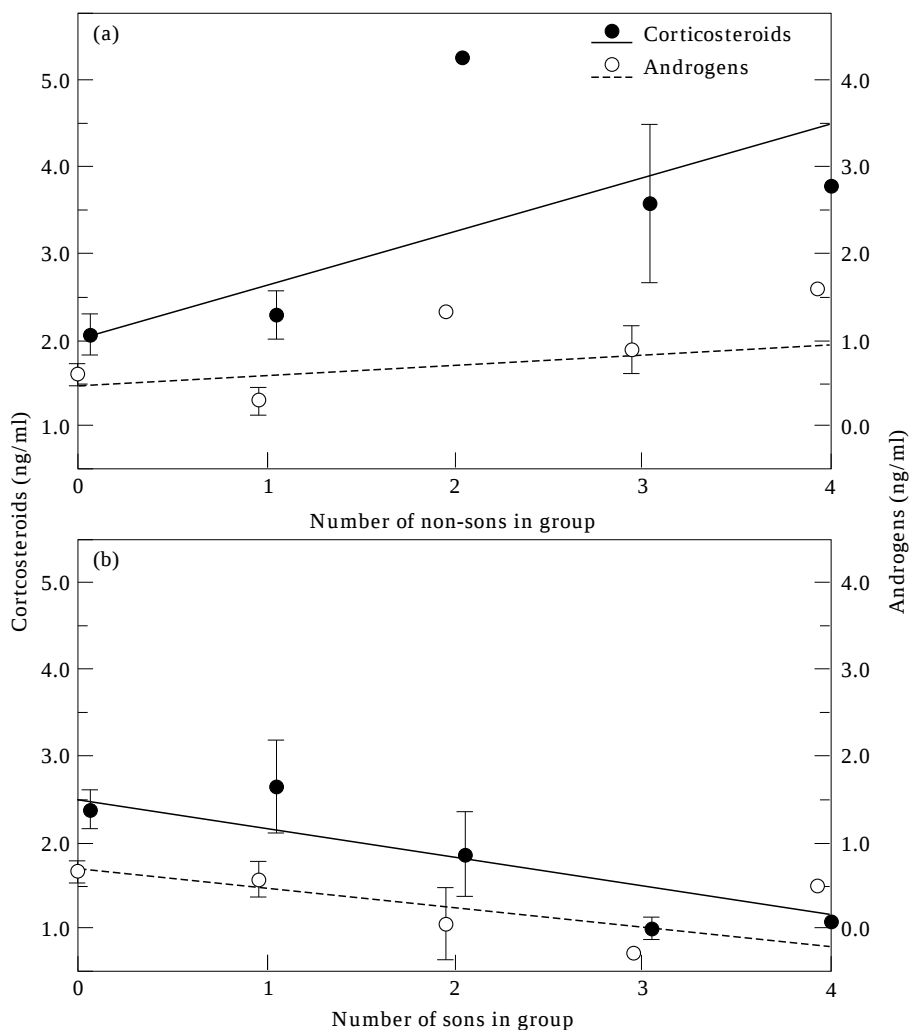


Figure 3. Corticosteroid and androgen plasma titres of territorial males and their relation to the number of non-sons and sons 2 or more years old present in the group during the mating season ($\bar{X} \pm \text{SE}$, symbols without error bars are single values). (a) Non-sons. Corticosteroids: $Y = 2.011 + 0.508X$, $F_{1,52} = 6.72$, $P = 0.012$; androgens: $Y = 1.493 + 0.101X$, $F_{1,52} = 0.88$, NS. (b) Sons. Corticosteroids: $Y = 2.488 - 0.313X$, $F_{1,52} = 2.68$, $P = 0.107$; androgens: $Y = 1.682 - 0.221X$, $F_{1,52} = 5.11$, $P = 0.028$.

subordinate group males by aggression. Unfortunately, we did not have enough observational data available to test directly whether non-sons and light sons were the preferred target of aggression from the territorial male. Overt aggressive encounters are very rare among alpine marmot group-mates but are predominantly initiated by territorial animals (Barash 1976; Naef-Daenzer 1984). In our study population, there was only an

average of 0.6 aggressive encounters per h between territorial and subordinate males (W. Arnold & J. Hottinger, unpublished data). However, there is evidence for more intensive aggression towards non-sons than sons from injury data. Non-sons had significantly more wounds than sons and this trend was possibly more pronounced in subordinate males 3 or more years old than in 2 year olds (Table III). These data are based on

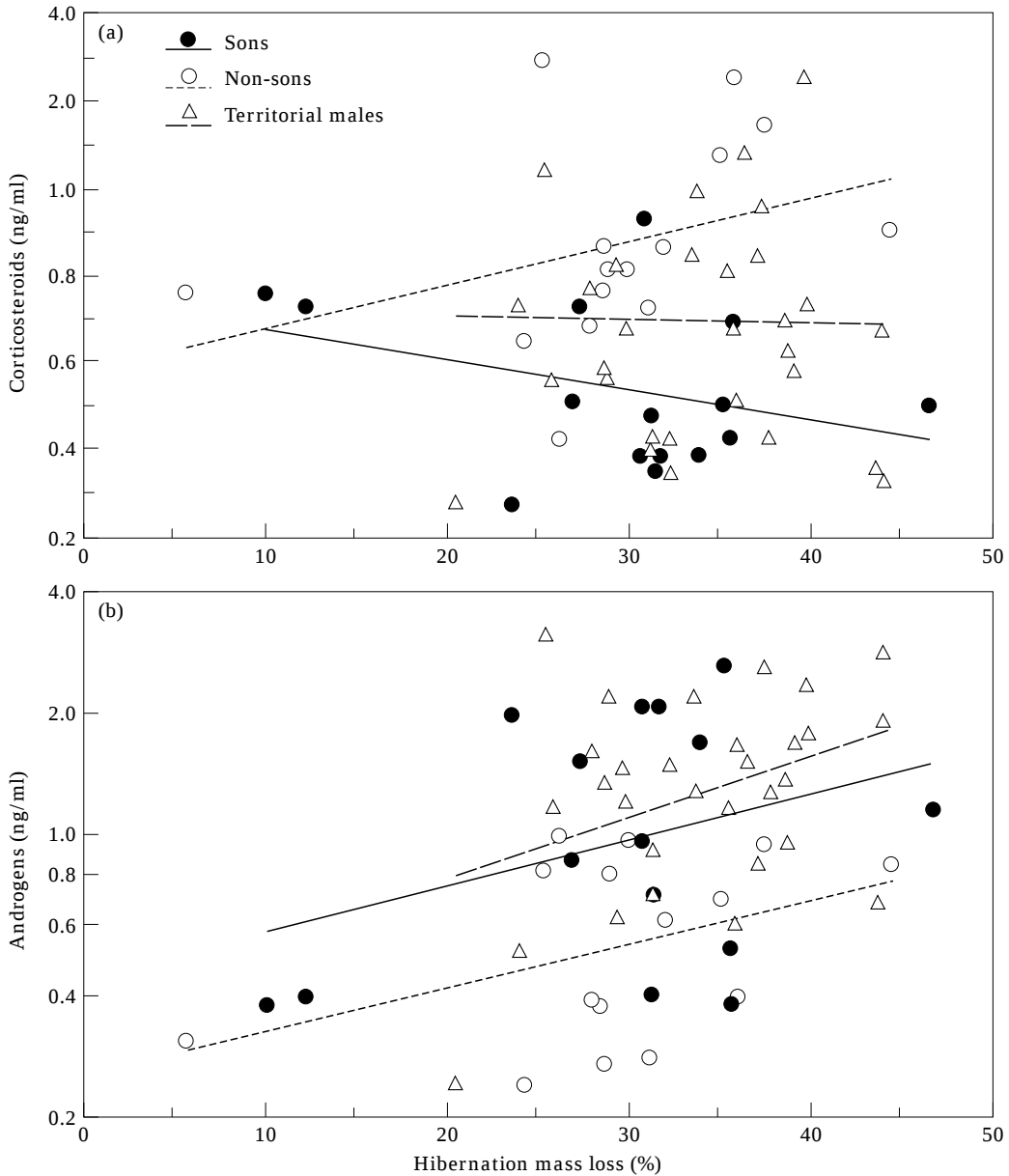


Figure 4. Corticosteroid and androgen plasma titres and their relation to mass loss during the previous hibernation in individual subordinate males 2 or more years old and territorial male marmots. (a) Corticosteroids. Differences between regression slopes: $F_{2,56}=1.33$, NS; difference between Y-axes intercepts: $F_{2,56}=0.23$, NS; overall regression, $F_{1,71}=0.01$, NS. (b) Androgens. Difference between regression slopes: $F_{2,55}=0.05$, NS; difference between Y-axes intercepts: $F_{2,55}=0.31$, NS; overall regression: $\log(Y) = -0.419 + 0.014X$, $F_{1,70}=9.54$, $P=0.003$.

recent injuries found in trapped individuals. Their conspecific source could be determined by the typical teeth marks of rodent incisors.

Long-term Costs of Reproductive Competition

Besides the risk of injury in aggressive encounters there was a potential long-term detrimental

Table III. Injuries of subordinate male marmots

Injury	2-year-old		≥ 3-year-old	
	Non-sons	Sons	Non-sons	Sons
No	34	57	25	61
Yes	2	1	3	1

Difference between non-sons and sons, Fisher's exact test: $P=0.05$.

effect of high corticosteroid titres: the higher the corticosteroid titre found during the mating season, the lower was the mass gain during the whole active season (Fig. 5). Only males 3 or more years old and territorial males were analysed here, because younger males were still growing and had therefore a much higher mass gain during summer (Table II). Interestingly, there was apparently no difference between territorial and subordinate males (difference between slopes of regression $F_{1,26}=2.8$, NS). However, the latter

result should not be overly stressed because the influential value from an individual territorial male with extremely low summer mass gain weakened the applicability of parametric analyses (Fig. 5).

DISCUSSION

By examining endocrine and body mass parameters of males during the mating season we have characterized some aspects of reproductive competition among male alpine marmots. Androgen levels of various groups at this time indicate that there is a degree of reproductive suppression in subordinate males that is positively related to corticosteroids. This effect depends on vernal body mass for sons but not for non-sons. From the territorial male's standpoint, this correlation looks different as androgens and corticosteroids are positively related but the latter also increase with increasing numbers of non-sons in a group. It seems overall that these endocrine effects result

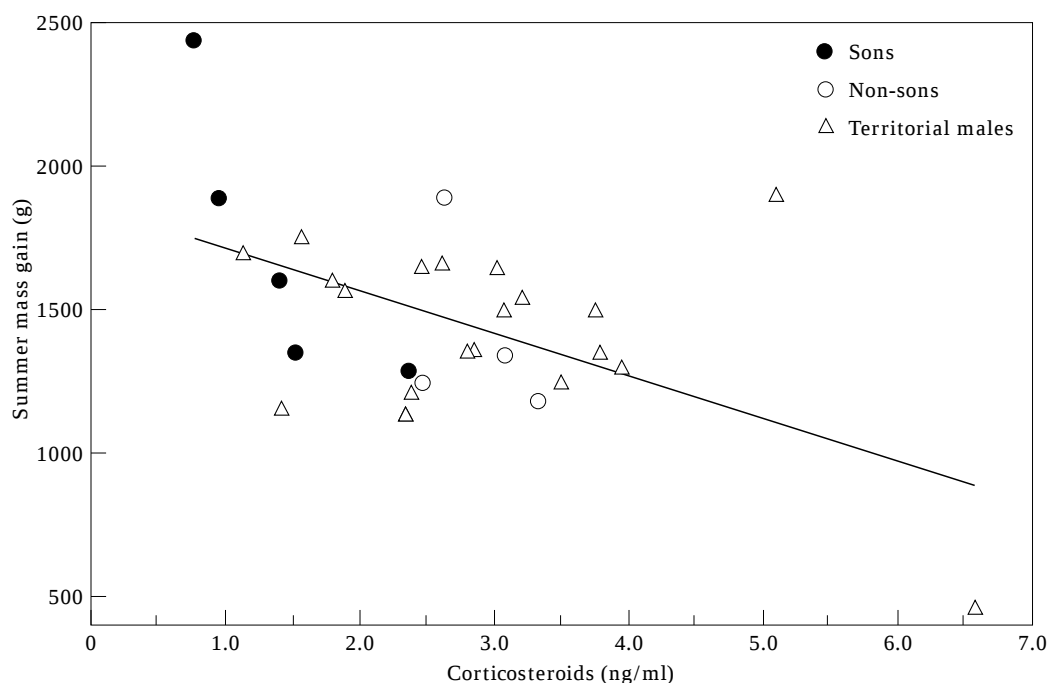


Figure 5. Corticosteroid plasma titres of males 3 or more years old during the mating season and subsequent mass gain until beginning of the next hibernation ($Y=1881.2 - 151.5X$, $F_{1,32}=12.39$, $P=0.001$; tests without the outlying value of 6.58 ng/ml corticosteroids and 450 g summer mass gain: regression: $Y=1774.3 - 101.0X$, $F_{1,32}=3.97$, $P=0.055$, Spearman rank correlation coefficient -0.364 , $P=0.037$).

from aggressive interactions among group males that apparently bear long-term costs and affect the reproductive physiology of all individuals involved. We assume here that both corticosteroid and androgen differences are a reflection of tonic levels and not a by-product of differing stress responses after capture in various groups. Alternative explanations for our results would have included adrenal exhaustion and/or coping effects. We believe that adrenal exhaustion is unlikely shortly after hibernation. Different coping responses are also unlikely in light of the absence of age- (experience-) dependent decreases in corticosteroids.

Mechanisms of Reproductive Suppression

The role of aggression

The interaction between androgens and corticosteroids is probably a direct result of conflict and social stress as has been shown for fish, birds and mammals (Rose 1985; Wingfield & Ramenofsky 1985; Sapolsky & Ray 1989; Sachser 1990; Armitage 1991; Cardwell & Liley 1991). Increased frequency of conflict is generally associated with changes in androgen and corticosteroid levels. The endocrine changes are, in addition, critically affected by the outcome of the conflict. Androgen in winners, for instance, is stimulated and in losers depressed (Ramenofsky 1984, 1985; Wingfield 1984; Sachser 1990; Sapolsky 1992). For corticosteroids, there is an immediate increase during conflict, which is greater and longer lasting in subordinates and losers (Sachser & Lick 1989; Haemisch 1990). In territorial male marmots, high androgen and corticosteroid levels are then a logical consequence of reproductive activity and frequent agonistic interactions. In addition, differences between hormone levels of sons and non-sons could be a reflection of conflict frequency and outcome. Injury data support this interpretation.

Physiological pathways

The differences in levels of androgens during the mating season in alpine marmots may indicate different spermatogenetic activity. In other ground squirrels sperm maturation is closely (temporally) related to an increase in testosterone after hibernation (Barnes et al. 1986, 1988), and low

androgens can suppress testes maturation and spermatogenesis without affecting somatic growth (e.g. Follet & Maung 1978). Androgen suppression could also have behavioural effects impairing a male's capacity to compete for reproductively active females (Rose et al. 1969; Bernstein et al. 1983; Wingfield 1984; Wingfield & Ramenofsky 1985; Sachser & Pröve 1986). Another behavioural factor could be the response threshold for sexual activity which again is androgen dependent (e.g. Michael et al. 1973), although the expression of sexual behaviour can occur independently of steroids in experienced animals (reviewed in Crews & Moore 1986). Still, further investigations are needed to discern whether the effects of androgen on spermatogenesis or behaviour, or both, are responsible for the suppression.

Body mass and testes size increased with age and were virtually identical in non-sons and sons in all age classes. Hence, we conclude that preferential reproductive suppression of unrelated subordinate male marmots does not occur via developmental suppression. Impaired reproductive function may instead result from constraints on gonadal development due to energetic constraints during hibernation. In other ground squirrels arousals from hibernation at the end of winter are critical for testes development (Barnes 1984, 1986; Barnes et al. 1986, 1988). Arousals are energetically costly (Bailey & Davies 1965; Wang 1978; Heldmaier et al. 1993), and only marmots in good condition may be capable of sustaining euthermia sufficiently long for the proper development of gonadal function. In line with this, hibernation body-mass loss was positively related to vernal androgen titres (Fig. 4b) and mass loss of subordinates was presumably highest in sons 3 or more years old (Table II). An attractive hypothesis here would be that autumnal body mass affects testicular development at the end of winter, and that territorial males impair pre-hibernatory fattening in males they wish to suppress. Our failure to find significantly smaller summer mass gains in suppressed males may be due to the considerable scatter produced by estimating autumn masses from fitted growth curves.

Aggressive interactions may then have a double role in suppression both during the mating season via androgen suppression and later in the year via impaired fattening and testicular development. High tonic adrenal activity, which is a natural consequence of frequent conflicts, has detrimental

effects on body mass increases via changes in intermediary metabolism (reviewed in Sapolsky 1992; Vinson & Whitehead 1992; Fig. 5).

Differential Suppression

The data supporting reproductive suppression indicate that it varies with age and status of an individual. Our major conclusion is that physiological depression of reproductive potential does occur in 2-year-old subordinate males regardless of relatedness to the territorial male and among older subordinates in non-sons. Such suppression is not a short-term effect of turbulence associated with a turnover in the territorial position because it is also present in groups with settled social relations (Table II). An analysis of paternity supports our conclusions: exclusion of territorial males from paternity increased with the number of sons 2 or more years old in a group but not with the number of non-sons 2 or more years old and was not present in multi-male groups containing only non-sons (W. Arnold, M. Klinkicht, K. Rassmann & D. Tautz, unpublished data).

It appears that territorial males predominantly attack non-related individuals with subsequent androgen suppression and corticosteroid increase (reproductive suppression) while sons above a critical body mass are left alone. This interpretation fits in with the result that territorial corticosteroid response increases with increasing numbers of non-sons but rather decreases with increasing numbers of sons in a group. The latter even suggests that sons relieve territorial males. We have anecdotal evidence that adult sons participate in the defence of the territory.

A similar kind of kin-related tolerance suggested here for male alpine marmots with low levels of agonistic interactions and adrenal activity has been described for male and female yellow-bellied marmots, *Marmota flaviventris* (Armitage 1991). A major difference between these species is the absence of correlations between reproductive state and total corticosteroids in the latter study. Conflict, mating and androgen relationships were also reported for social carnivores (e.g. dwarf mongooses, *Helogale parvula*: Creel et al. 1992). In contrast to the results here, however, Creel et al. found no relation between conflict and androgens. They postulated a behavioural suppression due to a form of exclusion. Perhaps an important point in

the comparison of these divergent results would be the role of spatial and temporal constraints that differ for the three species.

Finally, the suppression of non-sons and the surprisingly limited suppression of sons 3 or more years old needs some functional explanation. The key here may be that aggression and its effects on corticosteroids is costly for territorial animals. It can affect subsequent mass gain, which is important for successful hibernation (marmots depend during winter entirely on body fat to fuel their metabolism: Davis 1976; Bibikov 1989). Additionally, there is the risk of losing the conflict and possibly the dominant position. Territorial animals seem to adjust their effort in suppressing reproductive function of subordinate males according to the costs and benefits of such behaviour. These costs increase with a subordinate male's body size if body size reflects competitive abilities. On the other hand, the benefits from reproductive suppression of subordinate males decrease with relatedness. A loss of a reproductive chance in favour of a son decreases the territorial male's inclusive fitness less than a loss in favour of a non-son. A second important aspect is the capacity of a subordinate male to compete for territories in the vicinity of the natal territory or elsewhere after dispersal. Dispersal of male marmots predominantly occurs after the third or fourth hibernation and peaks in May after the mating season (Arnold 1990a, 1993b). Suppression of a son's 'competitiveness' might reduce its chances of obtaining a territory and correspondingly the territorial male's fitness. Lastly, perhaps the most speculative, but not unlikely hypothesis is that territorial males try to entice their adult offspring into remaining and helping in rearing new offspring (Emlen 1982). Adult sons are indeed the most effective helpers in warming young marmots during their first hibernation (Arnold 1993a). The method of enticement here may be the absence of suppression and the chance of reproduction, a mechanism of helper recruitment reported for dwarf mongooses (Creel & Waser 1991).

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