Social, maternal, and environmental influences on reproductive success in female Alpine marmots (*Marmota marmota*)

Wendy J. King and Dominique Allainé

Abstract: We examined the social, maternal, and environmental factors affecting the reproductive success of female Alpine marmots (*Marmota marmota*) during 8 years in the French Alps. Successful production of juveniles was almost entirely limited to dominant females. Production of juveniles increased with maternal body condition and experience. Female body condition was positively correlated with body mass and negatively correlated with dominant-male takeovers in spring, while experience increased with age. We found little evidence for a pregnancy block with takeover of dominant males because male replacement occurred mostly after mid-May, when juveniles were susceptible to infanticide. Production of yearlings depended on the number of juveniles produced, dominant-male takeovers in summer, and exposure of the site. We found no significant influence of group size or composition on production of yearlings. Climatic conditions varied little and had no measurable effect on reproduction. Social factors such as female dominance and dominant-male takeovers that could lead to infanticide have a strong effect on female reproductive success in Alpine marmots.

Résumé : Nous avons examiné les facteurs sociaux, maternels et environnementaux affectant le succès reproducteur des femelles de marmottes alpines (*Marmota marmota*) lors d'une étude de 8 ans dans les Alpes françaises. La production de juvéniles était presque exclusivement assurée par les femelles dominantes. La production de juvéniles augmentait avec la condition corporelle et l'expérience des mères. La condition corporelle des femelles était positivement corrélée à la masse et négativement corrélée au remplacement du mâle dominant au printemps, tandis que l'expérience augmentait avec l'âge. Nous n'avons pas vraiment trouvé de preuves d'un blocage de la gestation à la suite des remplacements du mâle dominant car ceux-ci ont eu lieu la plupart du temps après la mi-mai, lorsque les juvéniles étaient nés et soumis à l'infanticide. La production de jeunes de 1 an dépendait du nombre de juvéniles produits, du remplacement du mâle dominant pendant l'été et de l'exposition du site par rapport au soleil. Nous n'avons pas trouvé d'influence significative de la taille ni de la composition du groupe sur la production de jeunes de 1 an. Les conditions climatiques ont peu varié et n'ont pas affecté la reproduction. Les facteurs sociaux tels que la dominance de la femelle et le remplacement du mâle dominant qui pourrait être associé à l'infanticide affectent fortement le succès reproducteur des femelles de marmottes alpines.

Introduction

Reproductive success can be viewed as the result of several factors of differing origin that influence production and survival of offspring at different stages of development, and as offspring approach breeding age, measures of reproductive success become approximations of fitness (Clutton-Brock 1988). Reproductive success of female vertebrates is generally thought to increase with female body condition (see Clutton-Brock 1988). Body condition, in turn, can be influenced by maternal characteristics such as age and reproductive experience and by environmental factors such as habitat quality and climate. In social species, social factors such as dominance, aggressive interactions, and group size may also affect reproductive success.

Much interest has focused on how aggressive male behaviour affects the reproduction of female mammals. Aggression may involve infanticide (Hausfater and Hrdy 1984) or a pregnancy block mediated through male pheromones (Bruce 1959). Infanticide is difficult to document in the field, but killing of juveniles by adult males has been described for several mammalian species, especially ground-dwelling sciurids (McLean 1983; Coulon et al. 1995; Hoogland 1995; Blumstein 1997). Infanticide often occurs in association with male immigration into or takeover of social groups and has been interpreted as an adaptive male strategy to increase reproductive success by removing another male's offspring and by increasing the chance that the infanticidal male will soon mate with the mother of the young he has killed (van Schaik 2000).

Recently, Hackländer and Arnold (1999) have shown that dominant-male takeovers and female body mass in the spring affect the probability of producing offspring in female Alpine marmots (*Marmota marmota*). However, litter production is only one component of reproductive success, since success depends on both the number and the survival of

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W.J. King.[1] Département de biologie, Université de Sherbrooke, Sherbrooke, QC J1K 2R1, Canada.
D. Allainé. Laboratoire de biométrie et biologie evolutive, Unité mixte de recherche 5558, Centre national de la recherche scientifique (CNRS), Université Lyon 1, 43 boulevard du 11 novembre 1918, F-69622 Villeurbanne, France.

[1]Corresponding author (e-mail: Wendy.King@USherbrook.ca).

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young produced. The purpose of this study, then, was to measure reproductive success of female Alpine marmots in terms of production and survival of offspring and to assess the relative influence of social, maternal (phenotypic), and environmental factors. We were particularly interested in the influence of potentially infanticidal males, and by monitoring the reproductive success of several social groups over 8 years, we were able to take into account environmental influences and year-to-year variability, which can play an important role in the reproductive success of long-lived species (Clutton-Brock 1988).

Alpine marmots present an interesting combination of large territorial groups with extreme reproductive skew among females in a harsh mountainous environment. They can live in groups of up to 20 individuals, but typically, a group is composed of the dominant pair, three yearlings (range 1–9), and two subordinate adults (range 1–10) (Arnold 1990*b*). Only one litter emerges per group per year, since only the alpha female reproduces (Arnold 1990*a*; Goossens et al. 1998*a*). Females can become reproductively mature at age 2 but usually delay dispersal to the age of 3 or 4 (Arnold 1990*a*; Magnolon 1999). Infanticide has been observed when a new male takes over a territorial group (Coulon et al. 1995). Alpine marmots are considered cooperative breeders with alloparental care (Emlen 1997) because positive correlations have been found between numbers of subordinate adults and over-winter survival of juveniles (Arnold 1993; Allainé et al. 2000). No significant effect of spring, summer, and fall climate has been found on juvenile survival (Farand et al. 2002), but marmots prefer south-facing slopes where snow melts relatively early (Allainé et al. 1994).

We expected that maternal factors such as dominance, body condition, age, and experience would positively influence fecundity. We supposed that social factors could have positive or negative effects on female reproduction through influences on juvenile survival. Survival of the mother, group size, and number of subordinate adults should increase juvenile survival, whereas dominant-male takeovers should decrease juvenile survival. Environmental factors such as climate and site exposure could affect both juvenile survival and maternal condition. Harsh winters characterized by low temperatures and little snow cover, very rainy or very dry conditions, and north-facing locations with late snowmelt should have a negative effect on reproduction.

Methods

We studied Alpine marmots from April to September 1990–1997 in the Grande Sassière Nature Reserve, France (45°29′N, 6°59′E). The study site comprised approximately 57 ha of continuous alpine meadow at an elevation of 2350 m.

Marmots were captured in double-door traps baited with dandelions (*Taraxacum officinale*) and anaesthetized with a zolazepam–tiletamine mixture (Zoletil) for handling. Individuals were permanently marked subcutaneously using an electronic microchip (TROVAN) and numbered metal ear tags. A coloured plastic flag was attached to one ear tag and the pelage was dyed with black human hair dye (various commercial brands) for visual identification during observations. We weighed captured adults to the nearest 25 g using a spring scale and measured total body length (from the tip of the nose to the first caudal vertebra) to the nearest 0.25 cm. Body length was generally only recorded at the first capture each year for adults. Marmots were aged by mass at the first capture as juveniles, yearlings, or adults (2 years of age and older) (see Arnold 1990*a*). Trapping efforts were concentrated in the spring (early April to mid-May) and around the time of juvenile emergence (late June to mid-July) to ensure that all group members were marked. Hair samples were collected from all captured individuals from 1992 onwards for DNA analysis (see Goossens et al. 1998*b*) to verify that litters were correctly assigned to potential parents.

Behavioural observations to determine social grouping took place at a distance of 80–200 m using binoculars and 20–60× telescopes. Number of observation hours varied from group to group, but each group was observed, on average, for approximately 1 h per day for a minimum of 30 h per year. Dominant individuals were identified by their scent-marking behaviour because both the dominant male and female made daily scent-marking tours of the territory (Bel et al. 1995). Dominance relationships among adult females of the same group were confirmed by the outcome of aggressive interactions (chases and fights), if they occurred. When a new adult male entered a social group, it challenged the previously dominant male through prolonged and intensive chases and fights. If the new male won, the old male was usually evicted. This process was termed a dominant- male takeover. Occasionally, a subordinate male within the group would assume dominance when the dominant male disappeared. This process lacked aggression and was not considered a male takeover. Takeovers could occur in the spring during the breeding and gestation periods (early April to mid-May) or in summer after juveniles are born and susceptible to infanticide (mid-May to July).

We monitored reproduction in 4–15 groups each year, and groups were followed for 4.9 years, on average. Reproductive success was calculated for each adult female in three different ways. First, we examined the production of juveniles by counting the juveniles that emerged around the time of weaning (for 1990–1997, 8 years of data). Second, we recorded the number of yearlings produced by counting the juveniles that survived their first hibernation (born 1990–1997, 8 years of data). Third, we examined the number of 2-year-olds produced by counting the yearlings that survived hibernation to age 2 (born 1990–1996, 7 years of data). Production of juveniles is a measure of fecundity, whereas production of independent offspring (yearlings or 2-year-olds) approximates fitness and includes both fecundity and offspring survival (Clutton-Brock 1988). Thirty-three individual "breeding" females (see Results) contributed, on average, 2.3 years (range 1–6 years) to the overall dataset.

Analysis

We compared differences in reproductive success against phenotypic (i.e., maternal), social, and environmental factors. Production of juveniles was evaluated in relation to maternal spring body mass, spring body condition, age, and experience (see below). Social factors examined included dominant-male takeovers in spring and spring group size (April to mid-May), whereas environmental factors included

site exposure (north-facing, south-facing, or valley), winter snow depth, winter temperature, and spring precipitation.

Factors chosen to test against production of yearlings and 2-year-olds were primarily social and environmental. Social factors included survival of the mother, takeover of the dominant male in summer, fall group size, and numbers of subordinate adults and subordinate males in the fall. Environmental factors were the same as those examined for production of juveniles but included summer precipitation. The number of juveniles produced was included in the analysis to assess whether the different variables affected offspring survival to yearling age. Similarly, the number of yearlings produced was tested against production of 2-year-olds.

Multivariate analyses for each level of reproductive success were performed using ANCOVA, with discrete variables as factors and continuous variables as covariates. Certain variables, such as female age and dominant-male takeovers in spring, could not be included in the ANCOVAs because of small sample sizes, and their relationship with reproductive success was tested individually using one-way ANOVA or Student's t tests. Correlations between variables were investigated using Pearson's correlations for continuous variables and Student's t tests, one-way ANOVAs, or χ^2 tests for discrete variables.

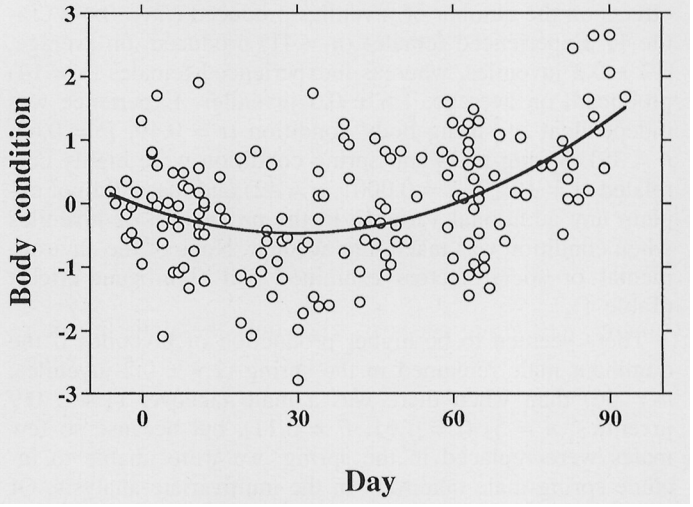
Female body condition was assessed by the standardized residual of the linear regression of body mass on total body length for all captures of adult females (n = 167, r^2 = 0.38). Body condition decreased in the spring but improved significantly following about day 60 (11 June) (Fig. 1) in mid to late lactation. Thus, spring body condition measured up to day 60 was used to compare individual females. Body condition was available for only 57% of the 74 female-years for dominant females because not all adults were captured during the required time period. Since each adult female was only captured one to four times each year ($\bar{x}$ = 1.3 captures per year), we could not determine lactation status for most females.

Female experience was assessed by whether or not the female was dominant within a group for the first time. Therefore, unmarked adult females that entered a group and assumed the dominant position but that could have been previously dominant in another group were excluded from analyses involving experience.

Winter weather data were obtained from the ski hill at Tignes, approximately 8 km to the west, elevation 2100 m. Mean daily snow depth was calculated for December to March for each of seven winters, from 1990–1991 to 1996–1997, and ranged from 85 to 146 cm. Marmots emerged through the snowpack in the spring. Absolute snow depths on the median date of emergence for 1995–1997 were 164 cm (15 April), 88 cm (15 April), and 107 cm (7 April), respectively. Average daily mean temperature in winter for the same seven 4-month period as for snow depth ranged from –4.1 to –5.8°C. Spring and summer precipitation data were obtained from Météo France for the 8 years, 1990–1997, at Tignes. Precipitation in spring (April to June) ranged from 199 to 384 mm and in summer (July to September) ranged from 188 to 345 mm.

ANCOVAs were performed using GLM (SPSS Inc. 1999) and univariate statistical tests were run using StatView (Abacus Concepts Inc. 1991). A probability level of 5% was considered statistically significant. Means are presented with standard errors.

Fig. 1. Standardized residuals of the regression of body mass versus total body length in adult female Alpine marmots (*Marmota marmota*) graphed against date at La Sassière, France, from 6 April to 14 July 1990–1997. Day 0 = 12 April and day 60 = 11 June. The line equation is $y = -0.029x + 0.000492x^2 - 0.041$ (n = 161, r^2 = 0.23).



Results

Alpine marmots at La Sassière lived in territorial groups of 2–15 individuals, excluding juveniles. Median spring group size was six with 78% of groups ranging in size from two to eight individuals. There was much variation in group composition and both males and females aged 2 and older moved between groups (Magnolon 1999). Dominant-male takeovers were documented for 20 of 78 (26%) group-years. Five takeovers (25%) occurred between early April and mid-May, before juveniles were born. Of those five spring takeovers, only three occurred in April during the breeding season. Most takeovers (75%) occurred between mid-May and late July, while juveniles were at risk of infanticide (Coulon et al. 1995). Of the 15 summer takeovers, 11 occurred after late June, when juveniles had emerged from natal burrows. Fall group sizes, excluding juveniles, were somewhat smaller than spring group sizes, with a median of 5 individuals (range 2–13 individuals). Most fall groups consisted of a dominant pair plus zero to three subordinate adults (85% of groups) and zero or two to four yearlings (83% of groups). Maximum numbers of subordinate adults and yearlings in fall groups were six and seven, respectively.

We were able to calculate production of juveniles for 147 female-years. Mean production of juveniles was much higher for dominant females ($\bar{x}$ = 2.9 ± 0.2 juveniles, n = 73) than for subordinate females. Litters emerged for 71% of 73 dominant females and litter sizes of dominant females ranged from two to seven juveniles ($\bar{x}$ = 4.0 ± 0.2, n = 52). Only 1 of 74 (1%) subordinate females raised a litter, consisting of three juveniles. Survival of juveniles to yearling age was 67% (n = 213 juveniles), whereas survival of yearlings to age 2 was 63% (n = 126 yearlings). The following analyses were performed on the dominant females plus the

one subordinate mother, together termed breeding females. Females were thus considered to occupy the "breeding position" in a group if they were dominant or if they were a subordinate mother.

Only maternal factors were associated with production of juveniles. Spring body condition and experience had positive effects on the number of juveniles produced ($R^2 = 0.44$) (Table 1). Experienced females ($n = 41$) produced, on average, 3.3 ± 0.3 juveniles, whereas inexperienced females ($n = 14$) produced, on average, 1.6 ± 0.5 juveniles. Experience was independent of spring body condition ($t = 0.49$, $P = 0.63$, $n = 38$). Spring mass and spring condition were highly correlated ($r = +0.73$, $P = 0.0001$, $n = 42$) and mass did not explain any additional variance in the production of juveniles when condition was taken into account. None of the environmental or social factors examined had significant effects (Table 1).

There seemed to be higher production of juveniles if the dominant male remained in the spring (2.9 ± 0.2 juveniles, $n = 66$) than when there was a male takeover (1.4 ± 0.9 juveniles, $n = 5$) ($t = 1.61$, $P = 0.11$), but because so few males were replaced in the spring, we were unable to include spring male takeovers in the multivariate analysis. Of the five spring takeovers, three occurred in April during the breeding period with a result of one litter of three juveniles produced, and two spring takeovers occurred in gestation in early May with one litter of four juveniles produced. Females were in better body condition when the dominant male remained in spring ($\bar{x} = +0.158 \pm 0.121$, $n = 39$) than when there was a male takeover in spring ($\bar{x} = -1.228 \pm 0.238$, $n = 3$) ($t = 3.12$, $P = 0.003$). Using maternal age as a variable was problematic because although production of juveniles increased with age from 2 through 5 years and older ($F_{[3,27]} = 7.15$, $P = 0.001$, $n = 31$), few females were of known age. Experience increased with age ($\chi^2 = 17.85$, df = 3, $P = 0.0005$, $n = 31$), and since experience was known for almost twice as many females as was age, we used experience in the ANCOVA.

One social and one environmental factor were associated with production of yearlings ($R^2 = 0.66$) (Table 2). Females in groups where the dominant male remained throughout the summer produced, on average, 2.2 ± 0.2 yearlings ($n = 56$), whereas those that experienced a summer male takeover produced only 0.5 ± 0.3 yearlings ($n = 13$). Because females located in the valley bottom produced more yearlings ($\bar{x} = 2.3 \pm 0.3$ yearlings, $n = 35$) than those on either north-facing or south-facing slopes ($\bar{x} = 1.2 \pm 0.4$ yearlings, $n = 15$, and $\bar{x} = 1.7 \pm 0.3$ yearlings, $n = 25$, respectively), data from north-facing and south-facing slopes were combined. Takeover of the dominant male in the summer and site exposure both influenced production of yearlings after accounting for the number of juveniles produced the previous year (Table 2). Dominant-male takeover in summer was not correlated with site exposure ($\chi^2 = 0.75$, $P = 0.39$, $n = 69$). All other variables tested did not contribute significantly to the model (Table 2).

Production of yearlings is the product of the number of juveniles produced (or fecundity) multiplied by juvenile survival. Thus, we investigated the potential effects of several factors on juvenile survival to yearling age. We documented

Table 1. ANCOVA for the production of juveniles by breeding female Alpine marmots (*Marmota marmota*), 1990–1997.

Type of factor	Variable	df	F	P
Phenotypic	Spring body mass	1	0.32	0.58
	Spring body condition	1	5.00*	0.03
	Experience	1	7.08*	0.01
Social	Spring group size	1	1.43	0.24
Environmental	Exposure	2	0.93	0.41
	Previous winter snowfall	1	0.18	0.68
	Previous winter temperature	1	0.86	0.36
	Spring precipitation	1	0.55	0.46

Note: Sample size is 37 female-years; $F_{[9,27]} = 2.35$, $P = 0.04$, $R^2 = 0.44$.
*$P < 0.05$.

seven cases of dominant-male takeovers during the summer in territories with juveniles. In five cases, no juveniles survived; in one case, the litter was reduced from six to two; and in the last case, all four juveniles survived. This represented a survival rate of only 18% for the 33 emergent juveniles. In contrast, survival of 163 juveniles to yearling age from groups without summer male takeovers was 77%. The effect of dominant-male takeovers during summer on juvenile survival is thus very strong ($\chi^2 = 42.38$, $P = 0.0001$). Disappearances of juveniles after dominant-male takeovers accounted for 42% of all juvenile mortality during summer. The survival rate on the valley slopes was 59% for 104 juveniles compared with 75% for 109 juveniles in the valley bottom ($\chi^2 = 6.67$, $P = 0.01$). The effect of maternal survival on juvenile survival was less than the effect of male takeovers. Forty-eight percent of 23 juveniles survived when their mother died compared with 69% of 186 juveniles whose mothers survived ($\chi^2 = 4.05$, $P = 0.04$). Juvenile survival rates did not differ according to the number of subordinate adults present in the group in fall. The percentage of juveniles surviving in groups with zero, one, a few (two or three), or many subordinates (four, five, or six) was 65, 64, 73, and 59%, respectively ($\chi^2 = 1.85$, df = 3, $P = 0.60$, $n = 200$).

It should be noted that spring body condition of females did not vary according to site exposure ($t = 0.82$, $P = 0.42$, $n = 42$). Body condition of females was also independent of takeover of the dominant male in summer ($t = 0.17$, $P = 0.87$, $n = 41$), and there was no correlation between maternal experience and male takeovers in summer ($\chi^2 = 0.10$, $P = 0.75$, $n = 55$) or between experience and exposure ($\chi^2 = 0.14$, $P = 0.70$, $n = 57$).

No factors were found to be significantly associated with the production of 2-year-olds (Table 3). The number of yearlings produced explained 59% of the variation in number of 2-year-olds produced in a simple regression ($F_{[1,65]} = 94.29$, $n = 67$), whereas the number of juveniles produced explained 29% of the variation ($F_{[1,64]} = 26.68$, $n = 66$).

Discussion

Our results suggest that social factors, including female dominance and male takeovers, have a strong effect on the reproductive success of Alpine marmots. We recorded successful reproduction for 71% of dominant females, which is similar to the approximately 60% found by Hackländer and

Table 2. ANCOVA for the production of yearlings by breeding female Alpine marmots, 1990–1997, based on variables measured during the juvenile year.

Type of factor	Variable	df	F	P
	No. of juveniles	1	29.28**	0.0001
Social	Survival of mother	1	1.99	0.17
	Male takeover in summer	1	15.66**	0.0001
	Fall group size	1	0.69	0.41
	No. of subordinates in fall	1	2.49	0.12
	No. of male subordinates in fall	1	0.50	0.48
Environmental	Exposure (valley vs. slopes)	1	5.04*	0.03
	Winter snowfall	1	0.09	0.77
	Winter temperature	1	0.01	0.98
	Summer precipitation	1	0.72	0.40

Note: Sample size is 51 female-years; $F_{[10,40]} = 7.95$, $P = 0.0001$, $R^2 = 0.66$.
*$P < 0.05$.
**$P < 0.001$.

Table 3. ANCOVA for the production of 2-year-olds by breeding female Alpine marmots, 1990–1996, based on variables measured during the yearling year.

Type of factor	Variable	df	F	P
	No. of yearlings	1	3.33	0.08
Social	Survival of mother	1	0.03	0.85
	Male takeover in summer	1	0.78	0.38
	Fall group size	1	1.04	0.31
	No. of subordinates in fall	1	0.03	0.85
	No. of male subordinates in fall	1	0.24	0.63
Environmental	Exposure (valley vs. slopes)	1	0.15	0.70
	Winter snowfall	1	3.11	0.09
	Winter temperature	1	0.21	0.65
	Spring precipitation	1	0.01	0.98
	Summer precipitation	1	0.71	0.40

Note: Sample size is 48 female-years; $F_{[11,36]} = 4.64$, $P = 0.0001$, $R^2 = 0.59$.

Arnold (1999). Production of juveniles was essentially restricted to dominant females, confirming previous studies (Arnold 1990*a*). Dominant females apparently suppressed reproduction in subordinates. Subordinate females have been observed to mate with the dominant male, but interactions between adult females within a group are often agonistic (King and Allainé 1998). Dominant females may prevent subordinate females from conceiving, may cause them to resorb embryos, or may kill their juveniles following birth. Subordinate females occasionally raise litters by switching groups late in gestation and becoming dominant (Goossens et al. 1996) or by giving birth on the same day as the dominant female (Goossens et al. 1998*a*). Therefore, it may be that the almost complete reproductive skew was not due to the physiological inability of subordinates to breed but was maintained through dominance interactions.

As expected, variation in the production of juveniles by dominant females depended primarily on body condition and reproductive experience, two factors that influence fecundity in many ground-dwelling sciurids. Body condition influences litter size in Richardson's ground squirrels (*Spermophilus richardsonii*) (Dobson and Michener 1995) and Columbian ground squirrels (*Spermophilus columbianus*) (Dobson et al. 1999). Hackländer and Arnold (1999) used body mass as a measure of body condition in Alpine marmots and found a positive effect on the likelihood of producing a litter. Our results strengthen this relationship and show that body condition influences not only presence of young but also litter size in Alpine marmots.

Takeover of the dominant male in spring was correlated with the female's body condition: when the female was in poor condition, the dominant male was replaced. Because social groups of Alpine marmots hibernate together (Arnold 1990*b*), it was likely that members of a reproductive pair experienced the same environment during winter, and therefore had similar spring body condition (see Arnold 1993). Males in poor condition at emergence from hibernation were probably unable to defend their territory and were easily replaced by another male. Because spring male takeovers were correlated with poor female body condition, these two factors likely acted together to reduce production of juveniles.

The Bruce effect (Bruce 1959), whereby the presence of a new, unfamiliar male leads to embryo resorption, has been suggested to occur in Alpine marmots (Hackländer and Arnold 1999). This may also take place at La Sassière, since few juveniles seemed to be produced when takeovers occurred in the spring. Embryo resorption, however, is unlikely to occur frequently because only 2 of 20 male takeovers occurred during gestation. Bruce effects have been observed in a range

of mammalian species including rodents, horses, and nonhuman primates in circumstances where subsequent infanticide is highly likely (van Noordwijk and van Schaik 2000).

After differences in the number of juveniles present a year earlier were accounted for, production of yearlings was primarily influenced by dominant-male takeovers in summer, and to a lesser extent, by site exposure. Males that invade territories after juveniles are born in mid to late May have been observed to kill juveniles in our population (Coulon et al. 1995). Documenting cases of infanticide is extremely difficult in many primate species where infanticide is a common source of juvenile mortality (Janson and van Schaik 2000). Survival of juvenile marmots to yearling age was much more dependant on the dominant male remaining than on the survival of the mother ($P = 0.0001$ vs. $P = 0.04$). Therefore, we suggest that juveniles are at great risk of infanticide following male takeovers: paternal care (in the form of defense against infanticide) appears to play a very important role in postweaning juvenile survival in Alpine marmots.

Females located in the valley bottom produced more yearlings than females located on the slopes. We could not explain this difference through social factors because there was no correlation between site exposure and dominant-male takeovers. We also had no evidence that the slopes were a poorer quality habitat than the valley in terms of both female mass and female survival (unpublished data). It is likely that snow accumulation was greater in the valley than on the slopes and that hibernacula located in the valley were better insulated than those on the slopes. Also, predation risk was possibly higher on the slopes than in the valley bottom.

We had expected to find a link between group size or composition and production of yearlings. At 1300 m elevation in Berchtesgaden, Germany, over-winter survival rates increased for juveniles in large groups of Alpine marmots, and in particular, in groups containing subordinate adults (Arnold 1990*b*). Social thermoregulation during hibernation was hypothesized to explain the positive effect of group size on over-winter survival in that study, which recorded approximately 50% annual juvenile mortality (Arnold 1990*b*). In our study population at 2350 m, we found no influence of winter weather on production of yearlings. Temperatures were consistently below 0°C but snow was abundant; thus, winter environmental conditions seemed to be relatively constant and were likely not stressful for hibernating marmots. Annual juvenile mortality in our study population was 33%, including losses associated with dominant-male takeovers. Juvenile marmots may suffer increased over-winter mortality in areas with inconsistent snow cover, such as at lower elevations. The survival of Columbian ground squirrels is also greater at high elevations with abundant snow cover than at lower elevations where snow cover is sporadic (Murie and Harris 1982).

At La Sassière, large groups of Alpine marmots likely form as a result of successful reproduction in territories where a dominant pair persists over several years. Territory quality probably varies between groups, and high-quality territories may give rise to large groups of animals, as is found for European badgers (*Meles meles*) (Woodroffe and Macdonald 2000). Because group size had no effect on production of yearlings, large groups were probably a result of successful reproduction rather than a cause of increased survival of young. A similar situation was found for kin groups in Columbian ground squirrels (King et al. 1991).

Reproductive success in Alpine marmots may be more strongly affected by social factors than in other sciurids. Infanticidal males cause substantial mortality of juveniles in golden marmots (*Marmota caudata aurea*) (Blumstein 1997), which, like Alpine marmots, are a monogamous species. In a recent review of infanticide in relation to male–female bonds in insects, birds, rodents, and nonhuman primates, Palombit (2000) concluded that heterosexual bonds have often evolved as an anti-infanticide strategy and proposed that infanticide defense selects for social monogamy when infanticidal pressure is exerted by both males and females. The influence of long-term pair bonds has not been previously addressed in analyses of the evolution of social behaviour in ground-dwelling sciurids (see Armitage 1981; Michener 1983; Blumstein and Armitage 1999), and we suggest that male–female bonds play a key role in maintaining the social cohesion of marmot groups. By lasting over several years, pair bonds can result in social groups of closely related individuals, whereas turnover of either the male or the female results in a group partly made up of unrelated individuals, likely reducing social cohesion. Future work on monogamous marmots should investigate the consequences of variability in kin relationships within groups for the survival and reproductive success of group members. Ultimately, the frequency of social disruptions caused by the disappearance of either member of the breeding pair could affect marmot population dynamics.

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