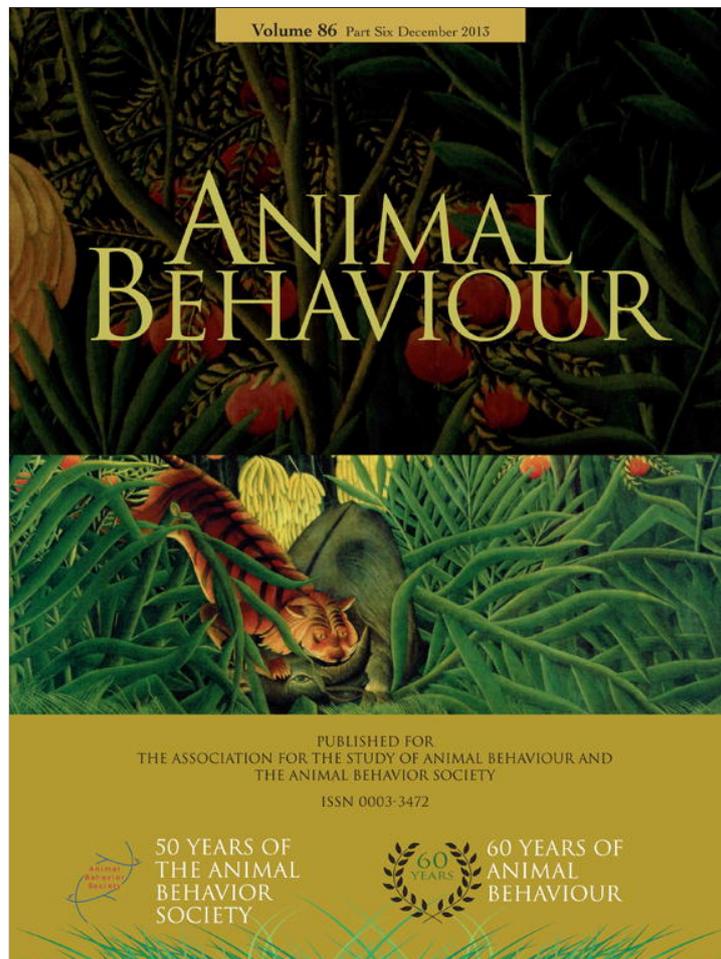


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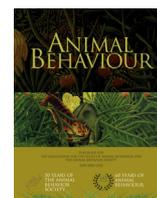
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# Intrasexual competition and female dominance in a singular breeding mammal, the Alpine marmot



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Although long neglected, female competition is widespread and may have stronger evolutionary consequences than previously thought. In singular breeders, reproductive success is conditional on social status, and intrasexual competition for the dominant position can be particularly severe in females. Because the ability of females to secure the dominant position may strongly influence their fitness, a better understanding of the determinants of dominance maintenance is needed. Using a 21-year data set on Alpine marmots, *Marmota marmota*, we investigated the potential drivers of female dominance loss in a singularly breeding mammal. Particularly, we tested whether the dominant females' ability to retain their social position depended on the number and the characteristics (age, relatedness to dominant individuals) of potential competitors in the social unit. To identify the potential underlying mechanism, we further investigated how the number of subordinate females affected females' competitive ability. We found that the risk of losing the dominant position increased with the number of subordinate adult females in the group, but that the age of the subordinate females and their parentage relationships to the dominant individuals were unlikely to be driving dominance loss in this species. Moreover, when the number of potential competitors in the social unit increased, we observed a difference in body mass increase between the dominant and her subordinates leading to a decrease in the body mass difference between dominant females and their subordinate adult females, and ultimately to a higher risk of females losing the dominant position. Overall, our results showed that the number of potential competitors in a social group affects the females' ability to secure their dominant position, and suggested that this effect is mediated through changes in female body mass.

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The process of intrasexual competition has been widely studied in males whereas female–female competition has received much less attention. However, recent work on mammals suggests that competition between females for mating or for resources required for producing and raising offspring (such as food, territory, nesting or social status) is more widespread than previously thought (Clutton-Brock 2009; Stockley & Bro-Jørgensen 2011). Although female intrasexual competition may constitute a general and strong selective pressure, its mechanisms and evolutionary consequences are still poorly understood.

In social species with a strong social hierarchy, reproduction is generally biased towards dominant individuals. In these systems, reproductive success is strongly linked to social rank, and competition for social position between the dominant and same-sex subordinates of the group is particularly intense (Alexander

1974). Intrasexual competition for reproduction is expected to be maximal in species with a large reproductive skew, such as singular breeding species, where a single dominant monopolizes reproduction and prevents other same-sex group members from reproducing (Emlen 1994; Solomon & French 1997). Additionally, the intensity of competition for social status should increase with the number of same-sex subordinates in the group (i.e. potential competitors), their age and their body condition (Emlen 1994). As a consequence, the number of same-sex subordinates, that is, potential competitors, in the social unit can be used to assess the intensity of competition in a social group. Evidence of increased frequency of aggressive behaviour with an increase in number of same-sex subordinates in the group indeed suggests that the two are correlated (Balshine et al. 2001; Kutsukake & Clutton-Brock 2008; Cheney et al. 2012).

Dominance tenure is an important determinant of male and female reproductive success (Fedigan 1986; Hodge et al. 2008; Lardy 2012). In males, the dominants' ability to retain their social position is affected by the intensity of competition in the social group. For instance, in mandrills, *Mandrillus sphinx*, and Alpine

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marmots, *Marmota marmota*, dominant male tenure decreases as the number of potential competitors in the social unit increases (Setchell et al. 2006; Lardy et al. 2012). In females, although social hierarchies have been described in several species (Stockley & Bro-Jørgensen 2011), the underlying mechanisms of competition for dominance and factors influencing females' ability to retain their social position are still poorly understood.

The females' ability to retain their social position probably depends on their body mass and that of their challengers. Body mass may be an important attribute of females' competitive ability and a correlation between body mass and social rank exists in females of several mammalian species (see Rusu & Krackow 2004; Pusey et al. 2005; Archie et al. 2006; Hodge et al. 2008 for examples; but see Stockley & Bro-Jørgensen 2011 for discussion). In singular-breeding meerkats, *Suricata suricatta*, dominant females able to maintain a sufficient difference between their body mass and that of the heaviest subordinate of the group stay dominant for longer (Clutton-Brock et al. 2006). Reproductive competition results in a high frequency of aggressive interactions between the dominant and her subordinate females, leading to increased risk of injuries and energy expenditure for the dominant in order to control the challengers (Faulkes & Abbott 1997; Hackländer et al. 2003; Sharp & Clutton-Brock 2011; Nelson-Flower et al. 2013). This energy expenditure may result in body mass loss that in turn may impair the competitive ability of the dominant female. One can thus expect the number of potential competitors to affect the dominant female's competitive ability and thus her capacity to maintain a sufficient difference in body mass from her subordinates. Nevertheless, the hypothesis that the number of potential competitors influences female body mass needs to be tested.

We examined the effect of the number of same-sex subordinates, used as a proxy of female reproductive competition, on females' ability to maintain the dominant position in a mammalian singular breeder, the Alpine marmot. In this long-living cooperative rodent (up to 16 years for females and 14 for males in the study population), individuals live in family groups of 2–16 individuals. Each family group is composed of a dominant breeding pair, sexually mature subordinates of each sex, yearlings, and pups born that year (one to seven in a litter per year: Arnold 1990; Perrin et al. 1993) with all individuals being highly related (Lardy 2012). Individuals reach sexual maturity at 2 years old but they never attain dominance before reaching their adult size at 3 years old. From 3 years old, individuals may either disperse or delay their dispersal for a few years (up to 3 years in the study site). Dispersers can gain a dominant position in an existing territory by evicting the dominant or, in rare cases, they can found a new territory (only five territories founded in 21 years in the study site), but they never join a new group as subordinate. Once established, the new dominant generally chases away most of the same-sex subordinates of the family group (Lardy et al. 2011). Individuals delaying dispersal may either reach dominance in their natal group or disperse later.

Dominant females monopolize reproduction, and competition between females for reproduction is thus expected to be particularly acute. Dominant females inhibit subordinate reproduction through repeated aggressive behaviour (Hackländer et al. 2003) and only five cases of subordinate reproduction have been witnessed in the study population in 21 years (630 reproductive events). Dominant females lose their social status following eviction, either by one of their adult female subordinates or by a dispersing female, or natural death, the last being rare (dominant females' survival rate is equal to 0.92, Stephens et al. 2002).

Using long-term data on a natural population of Alpine marmots, we first investigated whether the females' ability to reach dominance depended on their body mass. If body mass is a good indicator of females' competitive ability, the heaviest females

should be more likely to take over a dominant position than the lightest ones (prediction 1). Second, we focused on the determinant of dominance maintenance. We studied how the number of subordinate adult females in the group, their age and their relatedness to the dominant affected the risk of females losing dominance. We expected this risk to increase with an increase in the number and the age of adult female subordinates in the family group and when the subordinates are not related to the dominant individuals (prediction 2). Third, to identify the potential underlying mechanism, we also investigated the impact of the number of adult female subordinates on female body mass. Given that the Alpine marmot is a cooperative species, both dominant and subordinate females potentially benefit from cooperation. Within a family group, individuals cooperate for territory defence (Barash 1973), vigilance against predators (Barash 1973) and thermoregulation (Arnold 1990) leading to an increase in dominant male and female reproductive success until the optimal group size and composition are reached (Allainé & Theuriau 2004; Lardy 2012). Nevertheless, because the dominant female needs to control the reproduction of her subordinates through aggressive behaviour, the cost associated with reproductive competition should be higher for the dominant female than for her subordinates and should increase as the number of adult female subordinate increases. We thus expected a lower difference in body mass between a dominant female and her subordinates when the number of adult females present in the social group increased (prediction 3). Finally, if ability to retain dominance relies on the dominant female's body mass, we expected the risk of the female losing the dominant position to increase when she was lighter (if absolute body mass is more important than relative mass) or when the difference between dominant and subordinate females' body mass decreased (if relative body mass is more important; prediction 4).

## METHODS

### Field Methods

The study is based on long-term monitoring of the natural population of Alpine marmots located in La Grande Sassièrre Nature Reserve in the French Alps (45°29'N, 6°59'E). Between 1990 and 2011, marmots were monitored on 30 territories. Each year, between mid-April and mid-July, individuals were trapped using two-door live-capture traps baited with dandelion, *Taraxacum officinale*, placed in front of the entrance of the main burrow of the territory. Once caught, individuals were tranquilized with an intramuscular injection of Zolétil 100 (0.1 ml/kg), then sexed, aged, weighed and individually marked with a transponder chip (model ID100, 0.9 cm long, <0.1 cm in diameter, Trovan Ltd, [www.Trovan.com](http://www.Trovan.com), Identifikationssysteme, Metternicher Straße 4, 53919 Weilerswist, Germany) injected under the skin of the neck for permanent individual recognition, and a numbered ear tag (1 cm × 3 mm). For genetic analyses, we collected hair from all individuals captured since 1992, and tissue biopsies from the flank of individuals since 1997; a piece of skin (<1 mm<sup>3</sup>) was removed with a biopsy punch (Alcyon, 'Les Echets' – ZAC de Follioues, rue du Beaujolais, 01706 Miribel Cedex, France). The social status of each adult individual was determined based on scrotal development for males and teat development for females, and was confirmed by behavioural observations (Bel et al. 1995) and by maternity and paternity analyses. We used capture–mark–recapture protocols and daily observations to count the adults, 2 year olds, yearlings and pups of each sex in each family group.

Individuals were genotyped at 16 microsatellite loci and neither departure from Hardy–Weinberg equilibrium for any of the loci (all

$P > 0.05$ ) nor genetic linkage disequilibrium among any of the loci (all  $P > 0.05$ ) was evidenced. Maternity and paternity were determined using both exclusion analyses and the software CERVUS 3.0.3 (Kalinowski et al. 2007). The genotype of each subordinate female and that of the dominant individuals were compared. A subordinate female was considered as the daughter of the dominant female if no mismatch was observed between their genotypes. Similarly, a subordinate female was considered as the daughter of the dominant male if no mismatch was observed between their genotypes. We set the level of parentage confidence to 98%. Further details of the genotyping method and parentage analyses may be found in Cohas et al. (2008).

#### Ethical Note

Traps were checked every half hour to limit the time a marmot spent in a trap and thus exposure to predators and the weather. Once trapped, marmots were placed in an opaque bag and brought to a cabin where handling occurred. They were placed in a calm and cool room for 5 min to recover from the stress of transport and were then tranquillized. The marking and biopsies did not cause any bleeding. The implantation of the chip under the skin of the neck and the tissue removal by biopsy were superficial and did not require the use of analgesic. The implantation of the transponder has no obvious adverse effects and no migration of the chip from the implantation site or infection has been observed. Handling lasted a maximum of 10 min. The recovery did not require the use of an antidote. To recover, marmots were placed again in a calm and cool room for 15 min until they were able to walk. All tranquillized marmots recovered well and no adverse effects have been noticed: all individuals were observed alive the day after their capture. Tranquillizing pregnant or lactating females did not have any obvious impact on offspring as all the females successfully raised offspring to weaning. Overall, individuals were absent from their territory for a maximum of 40 min. We never observed exclusion from the territory for any individual of any age following capture. Marmots were tranquillized no more than once a year and in case of recapture the same year, the marmot was weighed and released without additional handling.

All the handling and sampling were done by S.L. and A.C. who are authorized for experimentation with animals by the French Ministry of Agriculture and Fisheries (diploma nos OETRY20090520 and 433R45GRETA110). The protocol was approved by the ethical committee of the University of Claude Bernard Lyon 1 no. BH2012-92 V1.

#### Statistical Analyses

Details of sample sizes are given in Table 1. Between 1990 and 2011, 69 dominant females and their 62 subordinate adult females were followed. Each year, whether the female stayed dominant (encoded as 0 or 1) and the number of subordinate adult females present in the family group were recorded ( $N = 332$  observations in total). The complete dominance tenure was known for 43 females ( $N = 204$  observations) while the beginning (left censored data), the end (right censored data) or both the beginning and the end (left and right censored data) of the tenure were unknown for 12 ( $N = 52$  observations), 12 ( $N = 71$  observations) and two females ( $N = 5$  observations), respectively.

#### Test of prediction 1

To test the effect of body mass on females' ability to take over the dominant position, we compared the residual body mass of females acquiring dominance in a given year with that of females staying subordinate the same year. In a given year, the number of females reaching dominance is often lower than the number of

**Table 1**

Characteristics of the subordinate adult females in the 30 family groups followed between 1990 and 2011 (332 observations in total)

|                                    | Number of subordinate adult females |           |           |           | Total     |
|------------------------------------|-------------------------------------|-----------|-----------|-----------|-----------|
|                                    | 0                                   | 1         | 2         | 3         |           |
| <i>N</i> (observations)            | 277                                 | 44        | 10        | 1         | 332       |
| <i>N</i> dominance loss            | 36                                  | 13        | 5         | 0         | 54        |
| <i>N</i> subordinate adult females | —                                   | 40        | 19        | 3         | 62        |
| Average age (year) (mean±SE)       | —                                   | 3.52±0.10 | 3.18±0.03 | 3.00±0.00 | 3.37±0.03 |
| Maximal age (year)                 | —                                   | 6         | 4         | 3         | —         |
| Daughter of the dominant female    | —                                   | 25        | 17        | 0         | 39        |
| Unrelated to the dominant female   | —                                   | 3         | 2         | 3         | 8         |
| Daughter of the dominant male      | —                                   | 8         | 2         | 3         | 13        |
| Unrelated to the dominant male     | —                                   | 18        | 13        | 0         | 31        |

females staying subordinate. In the analysis, a dominant female thus needs to be compared to several subordinates and therefore contributes more than one observation, leading to problems of pseudoreplication ('pooling fallacy', see Kramer & Schmidhammer 1992 for a discussion on this topic). To overcome this problem, we used a bootstrap procedure ( $N = 5000$ ) to provide independent replicates of pairs of dominant/subordinate females. We then performed a paired  $t$  test.

#### Test of prediction 2

Cox's proportional hazard models with time dependence, allowing censored data (Kleinbaum & Klein 2005), were used to test whether the risk of females losing dominance depended on the number of subordinate adult females in the family group. A Cox regression assumes that the probability per unit of time that a female will lose her dominant status (i.e. the leaving tendency or hazard rate =  $h[t]$ ) is the product of a baseline leaving tendency ( $h_0[t]$ ) and a ( $\exp\{\sum_{i=1}^p \beta_i z_i\} \cdot t$ ) factor representing the joint effect of the  $p$  explanatory variables ( $z_i$ ) over the time elapsed since the dominant female acquired the dominant status ( $t$ ). The  $\beta$  values (the regression coefficients) express the contribution of each explanatory variable to the overall loss of dominance tendency. These coefficients are interpreted through the exponential term (i.e. the hazard ratio). A hazard ratio higher than one indicates that the corresponding explanatory variable has an increasing influence on the tendency of a dominant female to lose her position. Conversely, a hazard ratio lower than one corresponds to a negative influence on the tendency of a dominant female to lose her position. Regression coefficients were estimated by maximization of the partial likelihood (for details, see Kalbfleisch & Prentice 2002). Clusters were incorporated into the model and the within-cluster correlation was used to estimate the variance parameter to take into account repeated measurement on a female as well as a potential effect of territory quality (Kleinbaum & Klein 2005).

To test whether the risk of losing dominance is affected by the presence of subordinate adult females in the family group or by their number, we built three different models. A binary variable (presence/absence of subordinate adult females) was entered as the explanatory variable in the first model. To test whether the risk of losing dominance is affected by the number of the subordinate adult females, the number of subordinate adult females was entered as a continuous variable in a second model and as a three-modalities categorical variable (none, one and two or more subordinate adult females) in a third model. For each model, the Akaike

information criterion (AIC) was used to assess the relative quality of the model.

Owing to their low variability, the relatedness between the dominant and her subordinate females and the age of the subordinates (Table 1) are unlikely to influence the risk of the dominant female losing her position and statistical analyses with these variables were not meaningful. However, the absence of relatedness between the subordinate adult females and the dominant male, that is, their potential future partner, may increase competition for breeding position and thus affect the risk of losing dominance. To account for this potential confounding effect, we tested the effect of the relatedness, as a binary variable (daughter/nondaughter), on the risk of losing dominance. Because of the high number of observations without subordinate adult females (and therefore no corresponding data for the parentage link between the male and the subordinate) we tested this effect in a separate model to that used to test the effect of the number of subordinate adult females. We used a Cox model with time-dependent data with the relatedness between subordinate adult females and dominant male (binary variable) entered as the explanatory variable. Clusters were incorporated into the model and the within-cluster correlation was used to estimate the variance parameter to take into account repeated measurement on a female as well as a potential effect of territory quality (Kleinbaum & Klein 2005).

#### Test of prediction 3

We investigated the effect of the number of adult females in the family group on body mass of both subordinate ( $N = 163$  measures on 101 females) and dominant females ( $N = 211$  measures on 69 females). Nonsexually mature females (age 1 year) were excluded from the analysis. To correct the female body mass for nonlinear effects as well as pseudoreplication, we used generalized additive mixed models (GAMMs) with the following explanatory variables: a categorical variable for the year of capture (21 modalities), a smooth term for the date of capture (continuous variable) in interaction with the gestation status (four-level categorical variable: subordinate, nonreproductive, pregnant, lactating), a binary variable (2 versus 3 years old) for the age of the female and a smooth term for the number of adult females in interaction with the social status (two-level categorical variable: subordinate or dominant). The identity of the female nested in the territory was included as a random term in both models to take into account repeated measurement on a female as well as a potential effect of territory quality (for details see Tafani et al. 2013). Variance components were estimated using the restricted maximum likelihood (RELM) method.

We then tested for the effect of the number of subordinate adult females on the difference in residual body mass between the dominant female and the adult female subordinates of the group. For that, a linear mixed model was fitted with the difference in residual body mass as the dependent variable and the number of subordinate adult females as the explanatory variable ( $N = 17$ ,  $N = 19$ ,  $N = 6$  observations for cases with one, two and three subordinate adult females, respectively, corresponding to 13, seven and one different females in each case). The dominant/subordinate pairs nested in the dominant female identity were included as random terms. The residual body mass was obtained by fitting a GAMM similar to the model described above without the last terms, that is, the effects of the number of females and social status. Residuals, representing the difference between the observed response for an individual and the population mean body mass, were calculated for each female (Maindonald & Braun 2003). The difference in residual body mass was then calculated for each possible pair of dominant and subordinate adult females in the family group ( $N = 43$  pairs with 16 dominant females and 25 subordinate females).

#### Test of prediction 4

We first tested whether the dominant female's absolute body mass affected her ability to retain dominance. Cox's proportional hazard models with time dependence, allowing censored data, were used to study the risk of losing status for the dominant female as a function of her residual body mass. To take into account the repeated measurement on the same dominant female and on the same territory, clusters were incorporated into the model and the within-cluster correlation was used to estimate the variance parameter (Kleinbaum & Klein 2005).

We then tested whether the dominant female's relative body mass affected her ability to retain dominance. Since not all females were captured and weighed each year, we had 29 observations of the difference in body mass between the dominant and her subordinates. Given the sample size, we used separate models to test the role of the absolute and the relative body mass on the female's ability to retain dominance to avoid problems of convergence in the statistical models. Cox's proportional hazard models with time dependence, allowing censored data, were used to study the risk of losing status for the dominant female as a function of the mean differential residual body mass between the dominant female and her subordinate adult females. To take into account the repeated measurement on the same dominant female and on the same territory, clusters were incorporated into the model and the within-cluster correlation was used to estimate the variance parameter (Kleinbaum & Klein 2005). We tested the effect of the difference in body mass between the dominant female and all of the subordinate adult females and between the dominant female and her heaviest subordinate adult female.

All statistical analyses were performed using R 2.12.0 (R Development Core Team 2010). The 'gamm' function of the 'mgcv' library was used for the GAMM (Wood 2008), the 'coxph' from the 'survival' library for the Cox analyses (Therneau 2011), and the 'lme' function from the 'nlme' library for the linear mixed models (Pinheiro et al. 2011). Unless otherwise stated, the parameters given are  $\pm$ SE and the level of significance is set to 0.05.

## RESULTS

### Characteristics of Subordinate Adult Females

In the 30 family groups observed, there were zero to three subordinate adult females (median 0, mean  $\pm$  1 SE =  $0.45 \pm 0.03$ ). The subordinate adult females were 3–6 years old with the vast majority being 3 years old ( $N = 37$  of 51). In groups with two or more subordinate adult females, variation in subordinate age was very low. In the 11 cases with two or more subordinate adult females, subordinates had the same age in nine cases, and in two cases one of the subordinate females was 1 year older than the other. Subordinate females tended to be older when alone in the family group (Kendall's rank correlation:  $z = -1.80$ ,  $N = 51$ ,  $P = 0.07$ ). The majority of the subordinate adult females (92.9%) were the daughter of the dominant female (Table 1). Conversely, the dominant male was the father of the subordinate adult female in only 30% of cases.

### Dominance Take-over

Dominant females held tenure for 1–14 years (median 4, mean  $\pm$  SE =  $4.38 \pm 0.03$ ). Among family groups with zero, one and at least two subordinate adult females, a dominant female lost her status in 13%, 30% and 45.5% of cases, respectively (Table 1). Among the 45 cases in which both the former and the new dominant females were known, 31 dominant females (69%) were replaced by a female from another territory and 14 (31%) were replaced by one of her subordinate females. In 12 cases, the subordinate female was a

daughter of the dominant female while in two cases the subordinate female was unrelated to the dominant female. Body mass of all subordinate adult females present in a family was known in only one case, and here the lightest female became dominant. In the one case in which we could compare the ages of all the subordinate females the oldest became dominant. We knew the parentage relationship between the dominant male and the subordinate adult females that became dominant in six cases: in five cases they were unrelated and in one case the subordinate female was the daughter of the dominant male but he was evicted the same year. This did not differ from the proportion of adult female subordinates being the daughter of the dominant male observed in the population ( $\chi^2_1 = 0.0012, P = 0.97$ ).

**Test of Prediction 1**

In a given year, females reaching dominance had a higher residual body mass than the females staying subordinate the same year ( $N = 5000$  replicates, mean difference in body mass  $\pm$  SE =  $157.27 \pm 0.01; P < 0.01$ ).

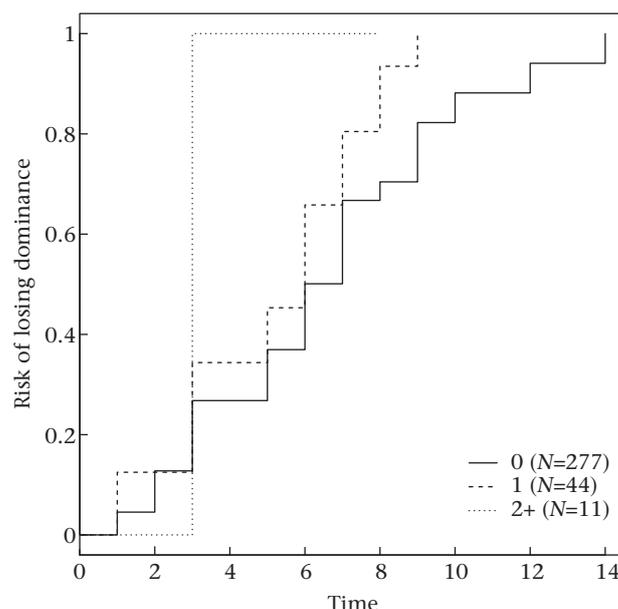
**Test of Prediction 2**

The presence of at least one subordinate adult female in a family group multiplied the risk for the dominant female of losing her status by 2.16 (95% confidence interval, CI: 1.17–3.99;  $\beta = 0.77 \pm 0.31, Z = 2.46, N = 332, P = 0.01, AIC = 341.78$ ; Table 2). When the number of subordinate adult females in the family group increased by one female, the risk of a dominant female losing her status was, on average, multiplied by 1.82 (95%CI: 1.24–2.66;  $\beta = 0.60 \pm 0.22, Z = 3.07, N = 332, P = 0.002, AIC = 341.08$ ; Fig. 1, Table 2). When the number of subordinate adult females was entered as a categorical variable (Wald  $\chi^2_2 = 9.27, N = 332, P = 0.009$ , model AIC = 343.03), the risk of losing her status for a dominant female was multiplied by 1.93 (95%CI: 0.96–3.89) when one subordinate adult female was present ( $\beta = 0.66 \pm 0.34, Z = 1.85, N = 44, P = 0.06$ ) and by 3.14 (95%CI: 1.42–6.91) when two or more subordinate adult females were present ( $\beta = 1.14 \pm 0.50, Z = 2.84, N = 11, P = 0.004$ ; Table 2) as compared to when subordinate adult females were absent ( $N = 277$ ). The three models had similar AIC indicating that the presence of subordinate adult females was not a better predictor of the risk of losing dominant status than the number of subordinate adult females.

**Table 2**  
Comparison of the different models used to test the effect of the number of subordinate adult females on the risk of losing dominance ( $N = 332$ )

| Model tested  | Odds ratio (95%CI)      | Estimate $\pm$ SE | Z    | P     | AIC    |
|---|-------------------------|-------------------|------|-------|--------|
| Presence/Absence of adult subordinate adult females         | 2.16 (95%CI: 1.17–3.99) | 0.77 $\pm$ 0.31   | 2.46 | 0.01  | 341.78 |
| Number of subordinate adult females (continuous variable)   | 1.82 (95%CI: 1.24–2.66) | 0.60 $\pm$ 0.22   | 3.07 | 0.002 | 341.08 |
| Number of subordinate adult females (categorical variable)* |                         |                   |      |       | 343.03 |
| No vs 1 subordinate   | 1.93 (95%CI: 0.96–3.89) | 0.66 $\pm$ 0.34   | 1.85 | 0.06  |        |
| No vs 2 or more subordinates                                | 3.14 (95%CI: 1.42–6.91) | 1.14 $\pm$ 0.50   | 2.84 | 0.004 |        |

\* Wald  $\chi^2_2 = 9.27, P = 0.009$ .



**Figure 1.** Kaplan–Meier plots showing the effect of the number of subordinate adult females in the social group on the risk that a female will lose dominance. Three levels of the number of subordinate adult females are represented: none, one and two or more.

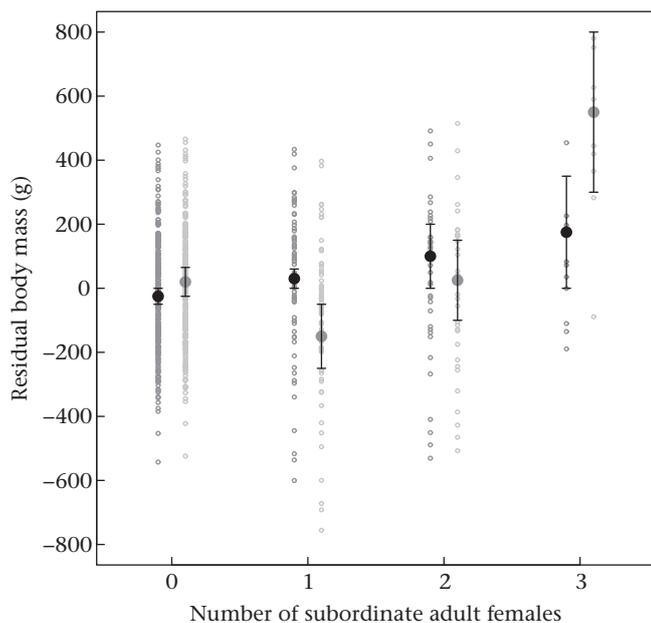
The parentage relationship between the subordinate adult females and the dominant male had no effect on the risk of a dominant female losing her status ( $\beta = -1.52 \pm 1.06, Z = -1.50, N = 37, P = 0.13$ ).

**Test of Prediction 3**

The number of adult females had a significant effect on female body mass, but as expected, this effect depended on female social status as indicated by the interaction between the number of adult females and social status. Subordinate females' body mass first decreased when only one subordinate adult female was in the group but then strongly increased with the number of subordinate adult females ( $F_{1,96,32.75} = 12.01, N = 101, P < 0.001$ ; Fig. 2) while dominant females' body mass only slightly increased with the number of subordinate adult females ( $F_{1,00,32.75} = 3.88, N = 69, P = 0.05$ ; Fig. 2). The detailed outputs of the model are presented in Appendix Tables A1 and A2. When one additional subordinate adult female was in the group, subordinate females gained up to 700 g (corresponding approximately to 20% of the average weight of a subordinate female) while the dominant gained only 150 g (corresponding approximately to 4% of the average weight of a dominant female; Fig. 2). Thus, the presence of additional subordinate adult females led to a decrease in the difference in residual body mass between the dominant female and her subordinate adult females. When three subordinate adult females were in the group, the difference in residual body mass between the dominant and her subordinate even became negative which means that the subordinate adult females became heavier than the dominant ( $\beta = -255.91 \pm 108.81, t = -2.35, N = 43, P = 0.03$ ; Fig. 3).

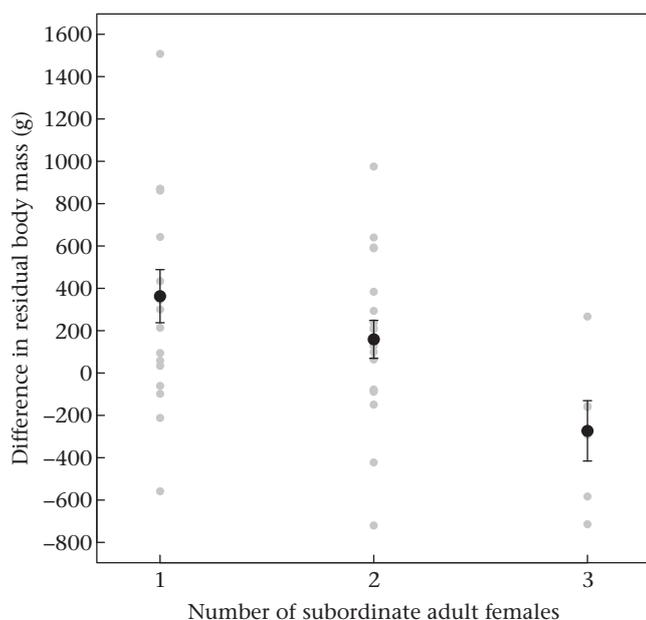
**Test of Prediction 4**

The absolute body mass of the dominant female did not influence the risk of losing her status (odds ratio = 1.001; 95%CI: 1.00–1.01;  $\beta = -0.0006 \pm 0.0007, Z = -0.72, N = 221, P = 0.47$ ). When the mean



**Figure 2.** Residual body mass of dominant females (in black) and sexually mature subordinate females (in grey) as a function of the number of subordinate adult females in the family group. The filled dots represent the mean residuals of body mass surrounded by their standard error and the empty dots represent the observed values after correction for the date and year of capture, the age and the pregnancy status of the female.

difference in body mass between the dominant and her subordinate adult females decreased by 100 g, the risk of losing her status for the dominant female tended to increase (odds ratio = 1.27; 95%CI: 0.97–1.66;  $\beta = 0.19 \pm 0.09$ ,  $Z = 2.08$ ,  $N = 29$ ,  $P = 0.08$ ). The same pattern was observed for the difference in body mass between the dominant



**Figure 3.** Difference in residual body mass between the dominant females and the subordinate adult females of the same family group as a function of the number of subordinate females. The difference was calculated as the dominant's body mass minus the subordinate's body mass. A negative difference means that subordinate females are heavier than dominant females. The grey dots represent the observed values and the black dots represent the mean differences surrounded by their standard errors.

female and the heaviest subordinate adult female (odds ratio = 1.22; 95%CI: 0.97–1.55;  $\beta = 0.20 \pm 0.16$ ,  $Z = 1.67$ ,  $N = 29$ ,  $P = 0.09$ ).

## DISCUSSION

Although female competition has been largely neglected, competition for the dominant position is strong in singular breeders (Clutton-Brock 2007) and can strongly affect female reproductive success. Our results have shown that females' ability to retain their social status depends on the number of potential competitors in the social group, used as a proxy of the level of intrasexual competition in the family group. As expected, we found that dominant females were at a higher risk of losing their position when associated with numerous subordinate adult females. Investigation of potential underlying mechanisms revealed that this increased risk was associated with a differential body mass gain between the dominant and her subordinates when these latter were numerous in the family group. Finally, our results underlined the importance of body mass in females' ability to acquire the dominant position. In species with a high female reproductive skew, dominance tenure is often the major component of female fitness and females' ability to maintain the dominant position is a source of great variation in female breeding success (Fedigan 1986; Hodge et al. 2008; Lardy 2012). More particularly in singular breeders, female competition, by largely increasing the risk of losing the dominant position, may thus have a strong impact on female fitness and therefore strong evolutionary consequences.

In contrast to some other social species (Frank 1986; Borries et al. 1991; Kutsukake 2009), dominance turnover in female Alpine marmots was influenced neither by the age of the subordinate females nor by the relatedness between dominant and subordinate females. Also, the risk of eviction for a dominant female was not affected by the relatedness between the subordinate females and the dominant male; however, this result was obtained from a small sample size. Given that a subordinate female has never been observed to become dominant while her father was still dominant, an association may potentially exist between the relatedness between subordinate females and the dominant male and the probability of a subordinate female gaining dominance in her natal group. Nevertheless, more data are needed to identify the potential effect of the relatedness between the dominant male and the subordinates on the risk of the dominant female losing her social status. Our results are thus in accordance with theoretical and empirical findings indicating that the probability of escalation of conflict increases with the number of females and the degree of reproductive suppression but not with age or relatedness between females in social hierarchies (Cant et al. 2006). We conclude that the number of subordinate adult females in family groups appears to be a major driver of female turnover in the Alpine marmot.

In several social species, subordinate individuals queue for the dominant position (see e.g. Wiley & Rabenold 1984; Cant 2000; Alberts et al. 2003). It has been proposed that future possibility of becoming dominant by queuing therefore stabilizes social hierarchies (Kokko & Johnstone 1999). However, when the probability of becoming dominant is too low, subordinates should challenge the dominant rather than remaining peacefully in the group waiting for their turn (Cant et al. 2006). In the Alpine marmot, tenure length is relatively long (more than 4 years on average, up to 14 years) and, when there is more than one subordinate adult female in a group, per capita probability of becoming dominant is low. This may explain why the maximal age of subordinate females is lower in groups with two or three subordinate adult females. Conversely, when only one adult subordinate is present, her probability of inheriting the territory is high and for this reason, it is possible that females stay subordinate longer when they are alone (up to 6 years old). This also may explain why there is such a low variability

in the age of subordinate adult females. Indeed, if one old adult female is present, the youngest adults have a low probability of becoming dominant. The youngest adults may therefore either disperse and attempt to become dominant elsewhere or be chased away by the oldest female of the group; the latter would thus keep her chance of becoming dominant high. However, more behavioural data would be needed to test these hypotheses.

Our results showed that body mass is likely to be a determinant of females' competitive ability and that the impact of the number of subordinate adult females on the risk of the dominant female losing her social status is mediated through body mass. Both dominant and subordinate females' body mass increased with the number of subordinate adult females. This pattern is unlikely to be the consequence of an effect of territory quality because the number of same-sex subordinate females varied within a given territory across years and we controlled for a year effect. This positive effect of the number of same-sex subordinates on female mass gain is likely to be the result of cooperative behaviour between group members. Benefits associated with social thermoregulation have been proposed to play a key role in the evolution of sociality in hibernating species (Ebensperger 2001; Armitage 2007). In Alpine marmots, joint hibernation and nights spent together in the same burrow strongly limit energy expenditure and the females' body mass may be higher when they are numerous (Arnold 1988, 1990, 1993).

However, the increase in body mass when numerous subordinate females were present was much less important in dominants than in subordinates. Litter size does not vary with the number of subordinate females (Lardy 2012) suggesting that the lower body mass gain in dominant females is not due to higher investment in reproduction in the presence of numerous subordinates. We suggest that the mass gain in dominant females is lower because of an increasing investment in reproductive competition when the number of subordinate females in the group is high (Hackländer et al. 2003). As in many singularly breeding species, Alpine marmot dominant females need to inhibit the reproduction of other females in the family group and to maintain their social status (Bercovitch 1987; Woodroffe & Macdonald 2000; Cooper et al. 2004; Scantlebury et al. 2004; Rubenstein & Shen 2009; Clutton-Brock et al. 2010). Specifically, the maintenance of dominant status and the inhibition of subordinate reproduction involve repeated physical conflicts with subordinate females of the group (Wasser & Barash 1983; Faulkes & Abbott 1997; Hackländer et al. 2003) that probably represent an important cost for the dominant. As the number of conflicts increases with the number of subordinates (Kutsukake & Clutton-Brock 2008), this cost should also increase with the number of subordinates. As a consequence, the difference in body mass between the dominant female and her subordinates in this study decreased and the dominant females were at a higher risk of losing their dominant position. A similar pattern has been observed in meerkats in which female tenure increases with a higher difference in body mass between the dominant and her subordinates (Clutton-Brock et al. 2006).

The strong increase in subordinate females' body mass indicates that subordinate adult females do not suffer a higher energetic cost when numerous same-sex subordinates are present in the family group. If the presence of numerous same-sex subordinates increases reproductive competition, this suggests that the energetic effect of competition for reproduction is strongly asymmetric. It is possible that subordinate females cooperate to limit the effect of aggression by the dominant by defending each other from her (Zabel et al. 1992; de Villiers et al. 2003) or that they limit energy loss by adjusting their thermoregulatory behaviour (Arnold 1988; Allainé & Theuriu 2004). Nevertheless, additional behavioural observations are needed to test these hypotheses.

Overall, these results suggest that intrasexual competition in social units has strong evolutionary consequences. The existence of strong female competition for social status in singular breeders should generate strong selective pressure on phenotypic traits that increase female competitive ability (Clutton-Brock et al. 2006). Additionally, given that dominant females face a trade-off between the benefits of cooperation and the cost of competition, an optimal number of subordinates maximizing the dominant female's fitness should exist, and strategies to control the number of subordinates in the group may have evolved (Stephens et al. 2005). Eviction of subordinate females by the dominant female has been witnessed in several species (hyaenas, *Crocuta crocuta*: Holekamp et al. 1993; house mice, *Mus domesticus*: Gerlach 1996; banded mongooses, *Mungos mungo*: Cant et al. 2001) and this behaviour might allow dominant females to control group size (Stephens et al. 2005). Nevertheless, group size regulation in social species is still poorly understood, and we recommend consideration of all factors that may affect long-term fitness, such as intrasexual competition, to understand these mechanisms better.

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### APPENDIX

**Table A1**  
Linear factors affecting female body mass in the Alpine marmot (based on 198 sexually mature females,  $\geq 2$  years old)

| Variables   | Estimate $\pm$ SE     | <i>t</i> | <i>P</i> | Comments  |
|-------------|-----------------------|----------|----------|---|
| Age (>2)    | 432.45 $\pm$ 36.08    | 11.99    | <0.1     | Correction by the age of the female (class was 2 years old or more) |
| Year (1991) | -191.32 $\pm$ 246.27  | -0.78    | 0.44     |   |
| Year (1992) | -358.62 $\pm$ 262.34  | -1.37    | 0.17     |   |
| Year (1993) | -304.26 $\pm$ 228.04  | -1.33    | 0.18     |   |
| Year (1994) | -286.84 $\pm$ 229.44  | -1.25    | 0.21     |   |
| Year (1995) | -517.19 $\pm$ 224.39  | -2.30    | 0.02     |   |
| Year (1996) | -205.93 $\pm$ 238.04  | -0.86    | 0.39     |   |
| Year (1997) | 98.71 $\pm$ 239.25    | 0.41     | 0.68     |   |
| Year (1998) | -117.55 $\pm$ 231.97  | -0.51    | 0.61     |   |
| Year (1999) | -138.60 $\pm$ 243.55  | -0.57    | 0.57     |   |
| Year (2000) | -110.01 $\pm$ 240.10  | -0.46    | 0.65     |   |
| Year (2001) | -432.98 $\pm$ 232.43  | -1.86    | 0.06     |   |
| Year (2002) | -131.64 $\pm$ 249.98  | -0.53    | 0.60     |   |
| Year (2003) | 128.73 $\pm$ 240.17   | 0.53     | 0.59     |   |
| Year (2004) | -222.87 $\pm$ 243.90  | -0.91    | 0.36     |   |
| Year (2005) | -1070.32 $\pm$ 435.41 | -2.46    | 0.01     |   |
| Year (2006) | -142.51 $\pm$ 243.63  | -0.58    | 0.56     |   |
| Year (2007) | 121.83 $\pm$ 242.73   | 0.50     | 0.62     |   |
| Year (2008) | -57.07 $\pm$ 234.08   | -0.24    | 0.81     |   |
| Year (2009) | 126.46 $\pm$ 231.93   | -0.54    | 0.58     |   |
| Year (2010) | -187.14 $\pm$ 228.59  | -0.82    | 0.41     |   |
| Year (2011) | 95.67 $\pm$ 233.47    | 0.41     | 0.68     |   |
| Intercept   | 3291.99 $\pm$ 169.39  | 19.43    | <0.01    |   |

Results are obtained from a generalized additive mixed model with female identity and territory included as random effects. Restricted maximum likelihood was used for estimations.

**Table A2**

Smooth factors affecting female body mass in the Alpine marmot (based on 198 sexually mature females,  $\geq 2$  years old)

| Variables  | df   | F     | P     | Comments   |
|--|------|-------|-------|--|
| Date $\times$ lactating                                | 1.00 | 68.64 | <0.01 | Correction by the date of capture and the pregnancy status |
| Date $\times$ pregnant                                 | 1.89 | 2.81  | 0.06  | Correction by the date of capture and the pregnancy status |
| Date $\times$ nonpregnant subordinate                  | 2.90 | 78.62 | <0.01 | Correction by the date of capture and the pregnancy status |
| Date $\times$ nonpregnant dominant                     | 1.00 | 26.52 | <0.01 | Correction by the date of capture and the pregnancy status |
| No. of subordinate adult females $\times$ dominant     | 1.00 | 3.88  | 0.05  |  |
| No. of subordinate adult females $\times$ subordinates | 1.96 | 12.10 | <0.01 |  |

Results were obtained from a generalized additive mixed model with female identity and territory included as random effects. Restricted maximum likelihood was used for estimations.

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