



## 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 Follieuses, 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

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