Sex-specific determinants of fitness in a social mammal

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Abstract. Sociality should evolve when the fitness benefits of group living outweigh the costs. Theoretical models predict an optimal group size maximizing individual fitness. However, beyond the number of individuals present in a group, the characteristics of these individuals, like their sex, are likely to affect the fitness payoffs of group living. Using 20 years of individually based data on a social mammal, the Alpine marmot (*Marmota marmota*), we tested for the occurrence of an optimal group size and composition, and for sex-specific effects of group characteristics on fitness. Based on lifetime data of 52 males and 39 females, our findings support the existence of an optimal group size maximizing male fitness and an optimal group composition maximizing fitness of males and females. Additionally, although group characteristics (i.e., size, composition and instability) affecting male and female fitness differed, fitness depended strongly on the number of same-sex subordinates within the social group in the two sexes. By comparing multiple measures of social group characteristics and of fitness in both sexes, we highlighted the sex-specific determinants of fitness in the two sexes and revealed the crucial role of intrasexual competition in shaping social group composition.

Key words: Dominance; fitness; French Alps; intrasexual competition; optimal group size; reproductive skew; sexual conflict; singular breeder; sociality.

INTRODUCTION

Social living is widespread in the animal kingdom, ranging from temporary aggregations of individuals to stable and complex social structures (Sherman et al. 1995). Although social living may provide individuals with fitness benefits through processes such as cooperation, group members may also incur costs as they compete for food or reproduction. Because costs of group living should increase with group size faster than benefits, theoretical models predict a bell-shaped relationship between group size and fitness, whereby an optimal group size maximizes individual fitness (Giraldeau 1988).

The cost–benefit balance of group living may, however, depend on other group characteristics such as its composition and stability (reviewed in Silk 2007). In many species, the nature and intensity of social interactions vary between group members. For instance, in the bonnet macaques (*Macaca radiata*), both aggressive and affiliative behaviors between group members vary with kinship or social rank of individuals involved in social interactions (Silk et al. 1981). Consequently, the fitness payoffs of group living may change with the focus individual and the group members it interacts with (Silk 2007).

Sex is another likely determinant of fitness payoffs. Within social groups, reproduction is often highly skewed toward dominant individuals (Alexander 1974) and competition for reproduction is expected to be particularly acute among same-sex individuals in both sexes (Clutton-Brock 2009, Stockley and Brø-Jorgensen 2011). In male meerkats (*Suricata suricatta*), for example, the proportion of offspring sired by the dominant male decreases with the number of competitors in the group, whereas in females, litter survival decreases with the number of adult females in the group. As a result, fitness components such as reproductive life span, fecundity, and offspring survival (Clutton-Brock 1988) should depend on the number of males in the group for dominant males, whereas fitness components of females should depend on the number of females (Clutton-Brock et al. 2006). In addition, the relative contribution of fitness components to fitness variation also varies between the sexes (Clutton-Brock 1988) because males and females differ in their reproductive strategies to maximize fitness (Bateman 1948). For instance, in lions (*Panthera leo*), offspring survival is the component contributing the most to fitness variation in females (84%) when male fitness variation is mostly affected by fecundity (46%; Packer et al. 1988). These empirical results suggest that the sex of individuals should determine what group characteristics affect fitness components the most, but it should also influence the relative contribution of reproductive life span, fecundity, and offspring survival to fitness. Ultimately,

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the effect of group characteristics on fitness should differ between males and females in social species.

Despite the numerous studies investigating the relationships between group characteristics and individual performance in social species, reported results are contrasting in magnitude and direction (Silk 2007), and evidence for optimal group characteristics for fitness remains scarce (but see Armitage and Schwartz 2000). Moreover, whether fitness determinants are sex specific has not been investigated yet. Such a disparity in empirical results (reviewed in Ebensperger et al. 2012) may be due to the limitation of the previous analyses to one sex, the short time scale over which fitness is often measured, the consideration of few fitness components, and the partial description of the social groups.

We took advantage of a detailed, long-term (20 years), and individually based monitoring of a wild population of the Alpine marmot, *Marmota marmota*, a social and singularly breeding species, to test whether optimal group characteristics (size or composition) maximize fitness and whether fitness determinants are sex specific. In Alpine marmots, the social group is composed of a dominant breeding pair, one or several sexually mature (older than one year old) and immature (one year old) subordinates of both sexes, and the pups of the year. Being social breeders, group members cooperate for territory defense, vigilance against predators, and thermoregulation (Arnold 1988, Allainé 2000). We used the lifetime reproductive success (LRS; Clutton-Brock 1988) and individual lambda (λ_i; McGraw and Caswell 1996) as proxies of fitness for males and females, and decomposed it into contribution of tenure length, breeding rate, average number of pups produced, and pup survival. We then investigated the effects of size, composition, and instability of groups on fitness and its components to test the following predictions: (1) group size and fitness should be linked by a quadratic relationship (Giraldeau 1988); (2) group characteristics influencing fitness and its components should be contingent upon the sex of the dominant individual; and (3) the number of same-sex subordinates in the group should be the major determinant of fitness of dominant males and females (Clutton-Brock et al. 2006).

Material and Methods

Model species

The Alpine marmot is a monogamous and singular-breeding species in which individuals compete for breeding (Lardy et al. 2012, 2013). Within the study population, males remain dominant for 1–11 years and females for 1–14 years, until natural death or eviction by another individual (Lardy et al. 2011). After an eviction, a dominant individual never becomes subordinate again. Eviction of the dominant is generally followed by its death and usually leads to the loss of the litter produced, either by infanticide by the incomer or by abandonment of the pups (Hacklander 2003, Lardy et al. 2011).

Eviction also has strong consequences for group composition and social bonds because it leads to the departure of most subordinates of the same sex as the intruder (Lardy et al. 2011). As a consequence, relatedness between group members is extremely high in marmot social groups (Lardy 2012, Lardy et al. 2013), with low variability of average relatedness among groups.

The dominant female gives birth to 1–7 pups once a year. Dominants inhibit reproduction of same-sex subordinates through aggressive behavior (Arnold 1997, Hacklander 2003), resulting in a high level of corticosteroids that reduces testis maturation and spermatogenesis in subordinate males (Arnold 1997), and causes the failure of embryo implantation and development in subordinate females (Hacklander et al. 2003). Although dominant females generally monopolize reproduction in their family group, dominant males may lose paternity to the benefit of sexually mature subordinates of the family group or transient individuals, accounting for 46% and 54% of extrapair paternities, respectively (Cohas et al. 2006; Appendix A).

Study site and data collection

We collected data from a wild population of Alpine marmots located in the Grande Sassière nature reserve in the French Alps (2340 m above sea level; 45°29′ N, 6°59′ E) from 1990 to 2010. Every year, marmots from up to 24 territories were monitored from mid-April to mid-July, using both capture–mark–recaptures and observations. From 1990, 19 territories were permanently occupied. Five additional ones appeared during the course of the study and have been permanently occupied since then. At each capture, marmots were aged, sexed, and their social status determined according to scrotal development for males and teat development for females. All individuals were marked using a transponder and a numbered metal ear tag on one ear. The number of subordinates was assessed for each family according to sex and age class (pup, yearling, and adult) by behavioral observations. Marking behavior was used to confirm the identity of the dominant pair (Bel et al. 1995). The number of weaned pups in each family was determined from daily observations. Because neonates stay in the burrow until weaning and are not accessible for census, the occurrence of reproduction and the number of pups produced were respectively assessed by the presence and number of weaned pups ~40 days after birth, at emergence.

Description of groups

We characterized each group by three quantities: (1) group size, defined as the number of individuals one year old or older in the group (including the dominant pair) averaged over the dominant's tenure length; (2) group composition, characterized by the number of sexually immature and mature subordinate males and females (i.e., males or females aged one year or older) averaged

over the dominant's tenure length; and (3) group instability, estimated as the number of times a dominant faced a partner change divided by tenure length (Appendix B).

Measure of fitness

Fitness is related to the rate of spread of a gene in the population (Charlesworth 1994). In wild populations, lifetime reproductive success (LRS), measured as the total number of offspring that survived to sexual maturity produced throughout an individual life span, is considered a good proxy of fitness (Clutton-Brock et al. 1988, Brommer et al. 2004, Pekkala et al. 2011). Because LRS does not account for the timing of reproduction, we also used the individual lambda (λ_i, the dominant eigenvalue of an individual-based Leslie matrix, where i represents different individuals; McGraw and Caswell 1996), a common rate-sensitive measure of individual fitness (Gaillard et al. 2000, McAdam et al. 2007). All of the methods and the results relative to λ_i, as well as a discussion comparing our results with LRS and λ_i, are presented in Appendix C.

Alpine marmots reach sexual maturity at the age of two years, but survival during the first hibernation is a critical stage in the marmots' life history cycle (Cohas et al. 2009). Additionally, because dispersal may occur from two years of age, we were unable to obtain a reliable estimate of the number of individuals surviving to sexual maturity. Hence, we measured the LRS of each individual ($N = 52$ males and $N = 39$ females) as the total number of pups produced (≥ 1) surviving to the age of one. We confirmed field observations of parentage by genetic analyses for all offspring (Appendix A).

Given that only dominants can be monitored throughout their reproductive life span, individual fitness was estimated for dominant individuals only. In the Alpine marmot, fitness while dominant is a good proxy of individual fitness because (1) staying subordinate is not an alternative strategy in this species. Dispersal occurs from two to six years old in females and seven years old in males. Marmots become dominant in their natal territory, or disperse and become dominant on another territory, or disperse and die. (2) Reproduction as subordinate is a rare event in this species (Cohas et al. 2006; Appendix A). Overall, we reported successful reproduction of subordinates for at most one reproductive event, representing 10 out of 505 males born on the study site (that produced in total 24 pups when subordinates), and four out of 437 females born on the study site (that produced in total seven pups when subordinates). Among these individuals, four out of the 10 males and one out of the four females became dominant on the study site. Problems arose for immigrant marmots becoming dominant on our study site ($N = 22$ males, $N = 8$ females) for which we could not monitor their subordinate life. We assume here that immigrants behave the same as residents while subordi-

nates. Given the very low occurrence of subordinate reproduction and its limited consequences on the estimated fitness (Appendix D), ignoring the reproduction of immigrants when subordinates is negligible and unlikely to affect our results.

Components of fitness

We split the fitness of a given individual into four components: the reproductive life span, the breeding rate, the average number of pups produced, and the pup survival (Clutton-Brock 1988). The reproductive life span corresponded to the time spent at dominance (tenure length) and was calculated as the number of years an individual remained dominant in its family group. The breeding rate was measured as the ratio of the number of years reproduction occurred to tenure length. We measured the average number of pups produced as the total number of pups produced by an individual (genetically verified) divided by the number of successful breeding occasions. We measured pup survival as the proportion of weaned pups in year t that survived to year $t + 1$.

Statistical analyses

We analyzed male ($N = 52$) and female ($N = 39$) data sets separately and compared a posteriori the sex-specific coefficients of each of the explaining variables, using Wald tests (Agresti 2002). We also performed two-sex analyses and the results confirmed the one obtained by separate analyses of sexes (Appendix E).

Contribution of the different fitness components to variation in fitness.—To estimate the contribution of each fitness component to the variation in fitness, fitness (either LRS or λ_i) was entered as the dependent variable and tenure length, breeding rate, average number of pups produced, and pup survival as explanatory variables in generalized linear models, GLMs (for details, see Appendix F: Table F1). We then estimated the percentage of variation accounted for by each component using hierarchical partitioning of log-likelihood (Chevan and Sutherland 1991, Mac Nally 2002) implemented in the function "hier.part" of the package "hier.part" in R (Walsh and Nally 2008). This method allows an estimation of the total independent contribution of a given variable, despite the existing colinearity between the different variables of the model.

Effect of group characteristics on fitness and its components.—To test if the group characteristics affecting male and female fitness are sex specific, fitness (LRS or λ_i) and its four components (tenure length, breeding rate, average number of pups produced, and pup survival) were modeled as a function of the average group size, or of the number of subordinate males and females and group instability using GLMs (for details, see Appendix F: Table F2). We analyzed separately the effects of group size on one side, and of group composition and group instability on the other side, because the average group size was highly correlated to

TABLE 1. Correlation matrix between the average group characteristics from (a) male ($N = 52$) and (b) female ($N = 39$) Alpine marmots (*Marmota marmota*) monitored in the Grande Sassière nature reserve (French Alps) between 1990 and 2010.

Sex and characteristic	Group size	No. males	No. females	No. partner changes
a) Males				
Group size	1	0.88*	0.80*	−0.15
No. males		1	0.43*	−0.10
No. females			1	−0.17
No. partner changes				1
b) Females				
Group size	1	0.84*	0.67*	0.09
No. males		1	0.24	0.09
No. females			1	0.14
No. partner changes				1

* Significant correlation at $\alpha = 0.05$.

both the average number of subordinate males and the average number of subordinate females (all $r > 0.67$; Table 1). The average number of subordinate males and the average number of subordinate females were also correlated, but to a lesser extent (all $r < 0.43$; Table 1).

We used a backward selection procedure to select significant explanatory variables. We tested sequentially linear and quadratic effects of the variables with type III ANOVA, therefore controlling for colinearity in predictors. For all GLMs with Poisson or binomial error distributions, we performed goodness-of-fit tests according to Agresti (2002), in which the sum of squared Pearson residuals of fitted models follows a chi-square distribution with degrees of freedom equal to the degrees of freedom of the model residual deviance.

We used the correlation coefficients between the observed data and the fitted values to approach a measure of effect size ("R"; Zheng and Agresti 2000).

Moreover, when several variables were statistically significant, we estimated the percentage of the explained variation associated with each component using hierarchical partitioning of log-likelihood values (Chevan and Sutherland 1991, Mac Nally 2002), as described previously.

Statistical analyses were performed with R 2.10.1 (R Development Core Team 2010); the function "glm.nb" in the package "MASS" was used to fit GLMs with a negative binomial distribution (Venables and Ripley 2002); and the function "glm" in the package "stats" was used to perform GLMs with other distributions (R Development Core Team 2010). We set the level of significance to $\alpha = 0.05$ and parameter estimates are given as mean $\pm$ SE.

RESULTS

Male and female LRS

In both sexes, LRS (Appendix G) ranged from 0 to 20 (Fig. 1). As expected for a monogamous species, neither the estimated median LRS ($\bar{x}_m = 4.5$, $\bar{x}_f = 6.0$; Wilcoxon $W = 1020.50$; $n_m = 52$, $n_f = 39$; $P = 0.21$) nor its variance ($\sigma_m^2 = 22.9$, $\sigma_f^2 = 28.6$, $F_{41,56} = 1.20$, $P = 0.52$) differed between sexes (subscripts m, male; and f, female).

For male and female marmots, LRS variations mainly resulted from the variations in tenure length (54.14% for males and 54.85% for females) and pup survival (30.31% and 26.57% for males and females, respectively). The contribution of breeding rate to fitness variations was slightly lower in males than in females (12.60% vs. 16.35%). Finally, the average number of pups produced had the lowest contribution in both males (2.94%) and females (2.23%).

Group size effects on the LRS of males and females and their components

For all GLMs, tests of goodness of fit indicated no over-dispersion in our models (all $P > 0.05$). We found
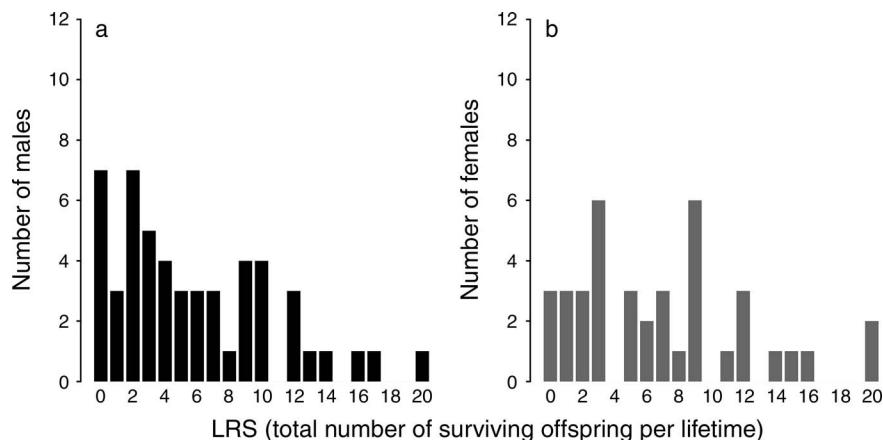

FIG. 1. Distribution of the lifetime reproductive success (LRS) for dominant (a) male ($N = 52$) and (b) female ($N = 39$) Alpine marmots (*Marmota marmota*) monitored in the Grande Sassière nature reserve (French Alps) between 1990 and 2010. LRS is measured as the total number of offspring that survived to the age of one year, per lifetime.

TABLE 2. Effects of average group size on (a) lifetime reproductive success (LRS) and (b) its components in dominant male ($N = 52$) and female ($N = 39$) Alpine marmots monitored in the Grande Sassière nature reserve between 1990 and 2010.

Model terms	Error	Link	Males				Females			
			β (SE)	z or t†	P	R	β (SE)	z or t†	P	R
a) LRS						0.51				0.50
Ave. group size	neg bin	log	**1.98 (0.47)**	**4.19**	**<0.01**		**0.99 (0.34)**	**2.93**	**<0.01**	
Ave. group size^2			**−0.17 (0.05)**	**−3.79**	**<0.01**		**−0.07 (0.03)**	**−2.29**	**0.02**	
b) LRS components										
Dominance tenure						0.35				0.35
Ave. group size	neg bin	log	**0.87 (0.32)**	**2.73**	**<0.01**		**0.63 (0.26)**	**2.38**	**0.02**	
Ave. group size^2			**−0.09 (0.03)**	**−2.75**	**<0.01**		**−0.05 (0.02)**	**−2.22**	**0.03**	
Breeding rate						. . .				. . .
Ave. group size	bin	logit	0.15 (0.09)	1.61	0.11		0.06 (0.11)	0.52	0.60	
Ave. no. pups						. . .				. . .
Ave. group size	norm	Gaus	0.06 (0.11)	0.57	0.57		0.03 (0.08)	0.46	0.65	
Pup survival						0.34				0.37
Ave. group size	bin	logit	**0.15 (0.05)**	**2.99**	**<0.01**		**0.23 (0.07)**	**3.48**	**<0.01**	

Notes: Significant variables are in boldface. Estimated parameters β are given with standard error (SE) in parentheses; R is the correlation coefficient between the observed data and values predicted by the model containing only the significant variables; R was not calculated when all variables in the model were nonsignificant. Abbreviations are: Ave., average; bin, binomial; neg bin, negative binomial; norm, normal; Gaus, Gaussian. Ellipses signify instances in which R was not calculated due to nonsignificant variables in the model.

† The z statistic was used for generalized linear models (GLM) with a logit and logarithm link functions and the t statistic was used for GLM with a Gaussian link function.

partial support for the prediction that group size and fitness should show a quadratic relationship in the Alpine marmot. As predicted, the relationship between the average group size and LRS (Table 2a) was different in males and females ($\chi^2 = 7.20$, df = 2, $P = 0.02$). The LRS of males increased until an average group size of 5.66, whereas the LRS of females peaked at an average group size of 7.29 (Fig. 2). In females, the quadratic relationship was influenced by one outlier, with an average group size (subscript g) of 10 individuals. When the outlier was removed, the relationship was linear (for quadratic relationship, $\beta \cdot g = 1.00 \pm 0.71$, $z = 1.42$, $P =$

0.16; $\beta \cdot g^2 = -0.07 \pm 0.07$, $z = -0.93$, $N = 39$, $P = 0.35$; for linear relationship, $\beta_g = 0.37 \pm 0.10$, $z = 3.72$, $N = 38$, $P < 0.01$, $R = 0.51$).

In both sexes ($\chi^2 = 3.3$, df = 2, $P = 0.19$), the average group size affected the same two fitness components, tenure length and pup survival, similarly (Table 2b). The relationship between the average group size and the tenure length was quadratic, with the maximal tenure length reached for a group size of 4.96 and 5.65 in males and females, respectively. Pup survival increased linearly with group size (Table 2b) to the same extent in males and females ($\chi^2 = 2.3$, df = 1, $P = 0.13$).
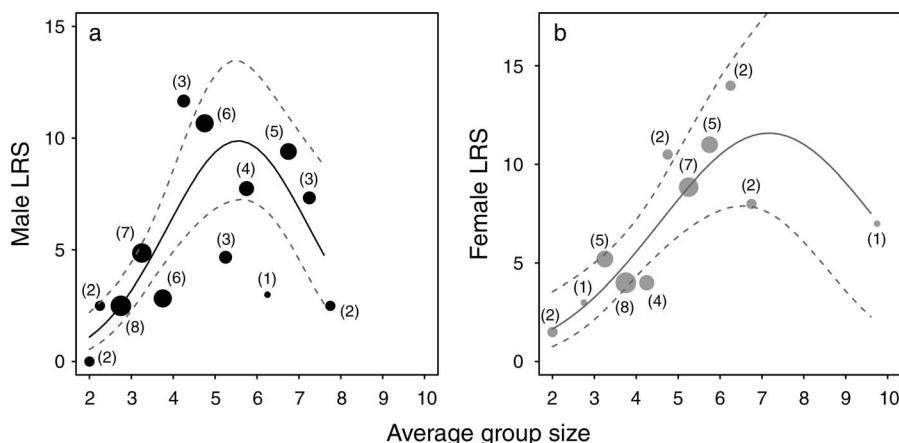

FIG. 2. Effects of the average group size on lifetime reproductive success (LRS) in dominant (a) male ($N = 52$) and (b) female ($N = 39$) Alpine marmots monitored in the Grande Sassière nature reserve (French Alps) between 1990 and 2010. Dots represent the observed data, their size being proportional to the sample size given in parentheses. Solid lines represent the model predictions; dashed lines show the associated standard errors.

TABLE 3. Effects of group composition and group instability on (a) lifetime reproductive success (LRS) and (b) its components in dominant male ($N = 52$) and female ($N = 39$) Alpine marmots monitored in the Grande Sassière nature reserve between 1990 and 2010.

			Males					Females				
Model terms	Error	Link	β (SE)	z or t†	P	Var. (%)	R	β (SE)	z or t†	P	Var. (%)	R
a) LRS							0.60					0.71
SS sub.	neg bin	log	**1.77 (0.33)**	**5.31**	**<0.01**	82.02		**1.58 (0.37)**	**4.29**	**<0.01**	72.58	
SS sub.^{2}			**−0.37 (0.08)**	**−4.41**	**<0.01**	82.02		**−0.36 (0.12)**	**−2.87**	**<0.01**	72.58	
OS sub.			**−0.28 (0.14)**	**−2.03**	**0.04**	5.42		**0.58 (0.21)**	**2.77**	**<0.01**	12.95	
OS sub.^{2}								**−0.10 (0.04)**	**−2.34**	**0.02**	12.95	
Partner			−1.68 (0.74)	−2.28	0.02	12.56		−1.03 (0.43)	−2.41	0.01	14.46	
b) LRS components												
Dominance tenure							0.50					0.46
SS sub.	neg bin	log	**0.90 (0.23)**	**3.97**	**<0.01**	36.97		**0.92 (0.30)**	**3.06**	**<0.01**	70.89	
SS sub.^{2}			**−0.22 (0.06)**	**−3.57**	**0.01**	36.97		**−0.24 (0.10)**	**−2.28**	**0.02**	70.89	
OS sub.			**−0.28 (0.10)**	**−2.79**	**<0.01**	48.97		−0.06 (0.08)	−0.86	0.39	4.35	
Partner			0.15 (0.48)	0.31	0.75	14.05		−0.59 (0.36)	−1.63	0.10	24.76	
Breeding rate							0.43					0.3
SS sub.	bin	logit	0.11 (0.16)	0.66	0.51	5.28		−0.02 (0.20)	−0.09	0.93	2.49	
OS sub.			0.09 (0.21)	0.44	0.66	1.94		0.27 (0.18)	1.47	0.14	8.00	
Partner			**−2.83 (1.02)**	**−2.76**	**<0.01**	92.78		**−1.67 (0.80)**	**−2.07**	**0.04**	89.50	
No. pups							...					...
SS sub.	norm	Gaus	−0.05 (0.18)	−0.26	0.79			0.04 (0.15)	0.27	0.79		
OS sub.			0.16 (0.24)	0.65	0.52			0.03 (0.12)	0.28	0.79		
Partner			−0.15 (0.26)	−0.59	0.56			−0.19 (0.53)	−0.35	0.73		
Pup survival							0.46					0.58
SS sub.	bin	logit	**0.83 (0.21)**	**4.03**	**<0.01**	71.19		−0.18 (0.31)	−0.57	0.57	17.89	
OS sub.			**0.63 (0.26)**	**2.44**	**0.01**	5.18		−0.39 (0.29)	−1.34	0.18	16.33	
SS sub. × OS sub.			**−0.33 (0.14)**	**−2.36**	**0.02**	22.84		**0.61 (0.22)**	**2.80**	**<0.01**	64.66	
Partner			−0.47 (0.72)	−0.66	0.51	0.79		−0.30 (0.52)	−0.57	0.56	1.12	

Notes: Estimated parameters β are given, with standard error in parentheses; values for significant variables are boldface. Model terms are SS sub. and OS, average number of same-sex and other-sex subordinates, respectively; SS × OS, interaction between same- and other-sex subordinates; Partner, average number of partner changes. Other abbreviations are: bin, binomial; neg bin, negative binomial; norm, normal; Gaus, Gaussian; var., percentage of explained variation accounted for by the explanatory variable. The same variance value is reported for both a variable and its quadratic term. R is the correlation coefficient between observed data and values predicted by the model containing only the significant variables; R and variance was not calculated when all variables in the model were nonsignificant. Ellipses signify instances in which R was not calculated due to nonsignificant variables in the model.

† The z statistic was used for generalized linear models (GLM) with a logit and logarithm link functions and the t statistic was used for GLM with a Gaussian link function.

Group composition and instability effects on LRS of males and females and their components

For all GLMs, tests of goodness of fit indicated no over-dispersion in our models (all $P > 0.05$). As predicted, group composition did not have the same impact on male and female LRS (Table 3). The effect of the average number of same-sex subordinates in the group on males' and females' LRS was similar ($\chi^2 = 1.80$, df = 2, $P = 0.41$). Conversely, the effect of the number of opposite-sex subordinates on male and female LRS differed: the average number of subordinate males had a greater effect on males than on females ($\chi^2 = 13.10$, df = 2, $P = 0.001$), and the effect of the average number of subordinate females was greater on females than on males ($\chi^2 = 24.90$, df = 2, $P < 0.001$). Both male and female LRS increased up to an average of 2.4 and 2.2 subordinates, respectively, of the same sex in the group and then decreased (Fig. 3). The average number of same-sex subordinates contributed 82.02% and 72.58%, respectively, of the observed variation in the

LRS of males and females. The average number of the other-sex subordinates contributed relatively little to male and female LRS (5.42% and 12.95%, respectively). Both male and female LRS decreased similarly ($\chi^2 = 0.79$, df = 1, $P = 0.37$), with the average number of partner changes encountered during the dominant tenure (Table 3a) accounting for 12.56% and 14.46%, respectively, of the observed variation in male and female LRS (Table 3a).

As expected, the relationship between the social group characteristics (composition and instability) and fitness components depended on the component and the sex considered.

Tenure length.—Tenure length was affected similarly by the number of same-sex subordinates in the group for males and females ($\chi^2 = 0.71$, df = 2, $P = 0.70$). Both male and female tenure length increased until an average, respectively, of 2.1 and 1.9 subordinates of the same sex and decreased thereafter (Table 3b, Figs. 4a for males and 5a for females). The average number of same-sex subordinates contributed 36.97% and 70.89%
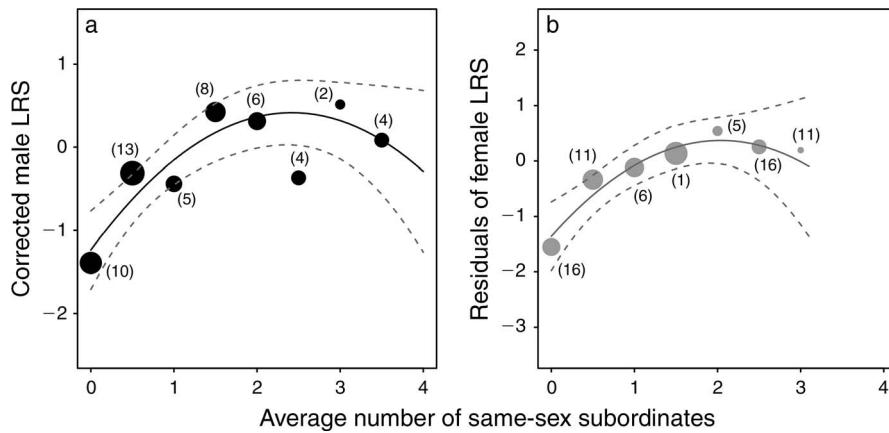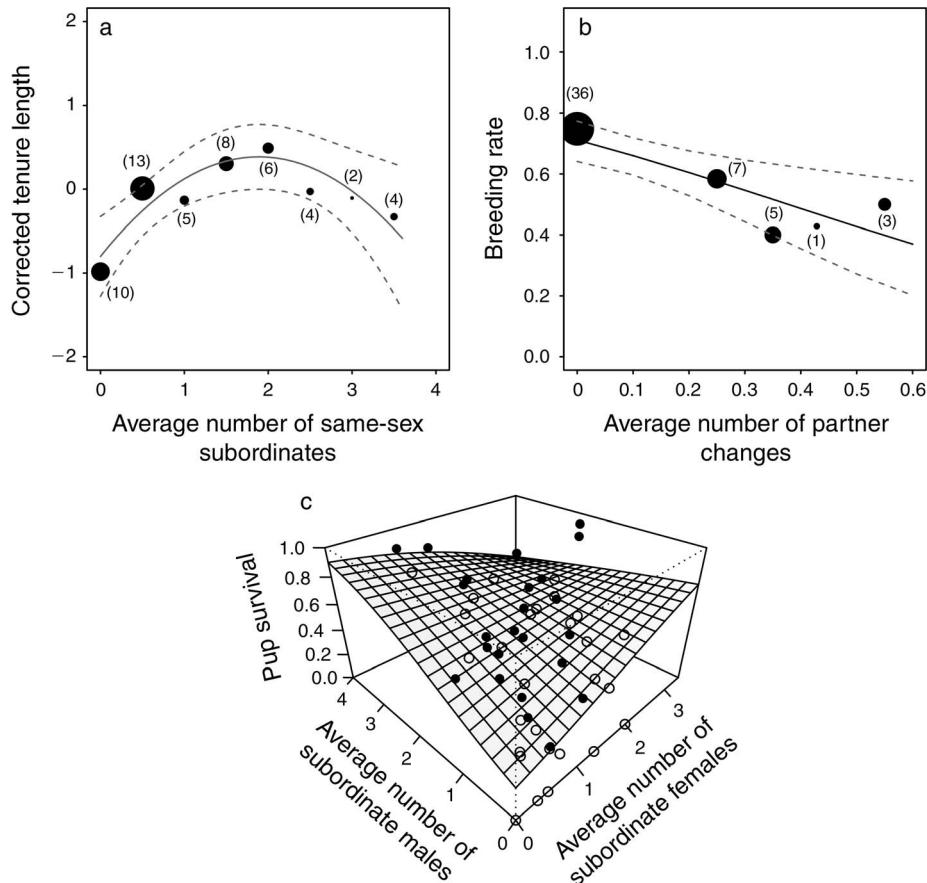
FIG. 3. Effects of the average number of same-sex subordinates on the lifetime reproductive success (LRS) of dominant (a) male ($N = 52$) and (b) female ($N = 39$) Alpine marmots monitored in the Grande Sassière nature reserve between 1990 and 2010. The corrected LRS was obtained after accounting for the effect of the average number of other-sex subordinates and group instability on female and male LRS. Dots represent the observed data, their size being proportional to the sample size given in parentheses. Solid lines represent the model predictions; dashed lines show the associated standard errors.

FIG. 4. Effect of group characteristics on the components of the lifetime reproductive success of dominant male Alpine marmots ($N = 52$) monitored in the Grande Sassière nature reserve between 1990 and 2010. (a) Dominance tenure length as a function of the average number of same-sex subordinates in the group. The corrected tenure length was obtained after accounting for the effect of the average number of other-sex subordinates. (b) Breeding rate as a function of the number of female partner changes that a male faced during its tenure. Breeding rate is measured as the ratio of the number of years in which reproduction occurred to tenure length. Dots represent the observed data, their size being proportional to the sample size given in parentheses. Solid lines represent the model predictions; dashed lines show the associated standard errors. (c) Pup survival to one year of age as a function of the average number of subordinate males and females in the family group. The black and white circles, respectively, represent observed data greater and lower than predicted values represented by the surface.
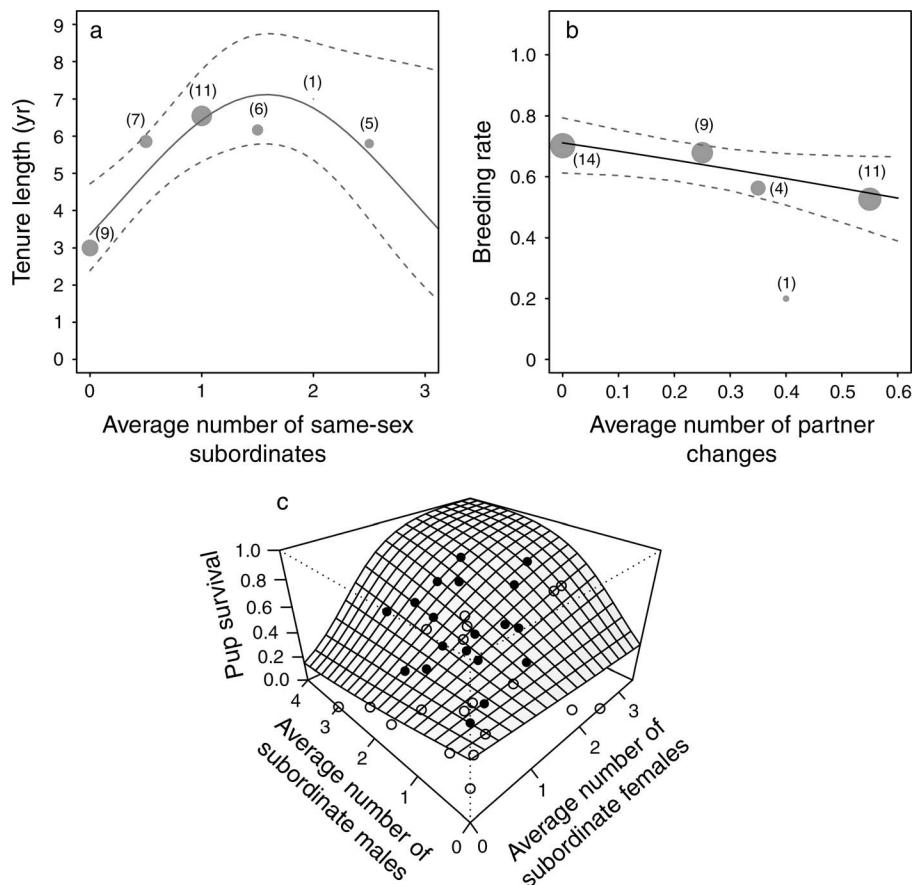
FIG. 5. Effect of group characteristics on the components of the lifetime reproductive success of dominant female Alpine marmots ($N = 39$) monitored in the Grande Sassière nature reserve between 1990 and 2010. (a) Dominance tenure length as a function of the average number of same-sex subordinates in the group. (b) Breeding rate as a function of the number of male partner changes that a female faced during its tenure. Breeding rate is measured as the ratio of the number of years in which reproduction occurred to tenure length. Dots represent the observed data, their size being proportional to the sample size given in parentheses. Solid lines represent the model predictions; dashed lines show the associated standard errors. (c) Pup survival to one year of age as a function of the average number of subordinate males and females in the family group. The black and white circles, respectively, represent observed data greater and lower than predicted values represented by the surface.

of the variation in male and female dominance tenure length. In males, the average number of other-sex subordinates had a negative effect on tenure length. Whatever the sex, we found no effect of the average number of partner changes on tenure length (Table 3b).

Breeding rate.—The breeding rate was not influenced by group composition (Table 3b), but strongly decreased with group instability (Table 3b, Figs. 4b for males, and 5b for females) to the same extent in both sexes ($\chi^2 = 1.13$, df $= 1$, $P = 0.26$). The average number of partner changes accounted, respectively, for 92.78% and 89.50% of the explained variation in breeding rate of males and females (Table 3b).

Number of pups.—In both sexes, the average number of pups produced was not influenced by group composition or by group instability (Table 3b).

Pup survival.—We found a significant effect of the interaction between the average number of males and the average number of females in the group on pup survival for both sexes (Table 3b, Fig. 4c for males, and Fig. 5c for females). The average number of subordinate males and females and their interaction accounted for 99.21% of the explained variation in pup survival in males and 98.88% in females. In males, pup survival increased with the number of subordinates of a given sex, but decreased when the number of subordinates of the two sexes was very high or very low. In females, pup survival increased only when the average number of subordinates of both sexes increased, but not when the average number of subordinates of a given sex increased with the average number of the other sex remaining low. In males and females, pup survival was independent of the average number of partner changes (Table 3b).

Discussion

For a social species like the Alpine marmot, we expected an optimal group size (Giraldeau 1988) and sex-specific effects of social characteristics on fitness.
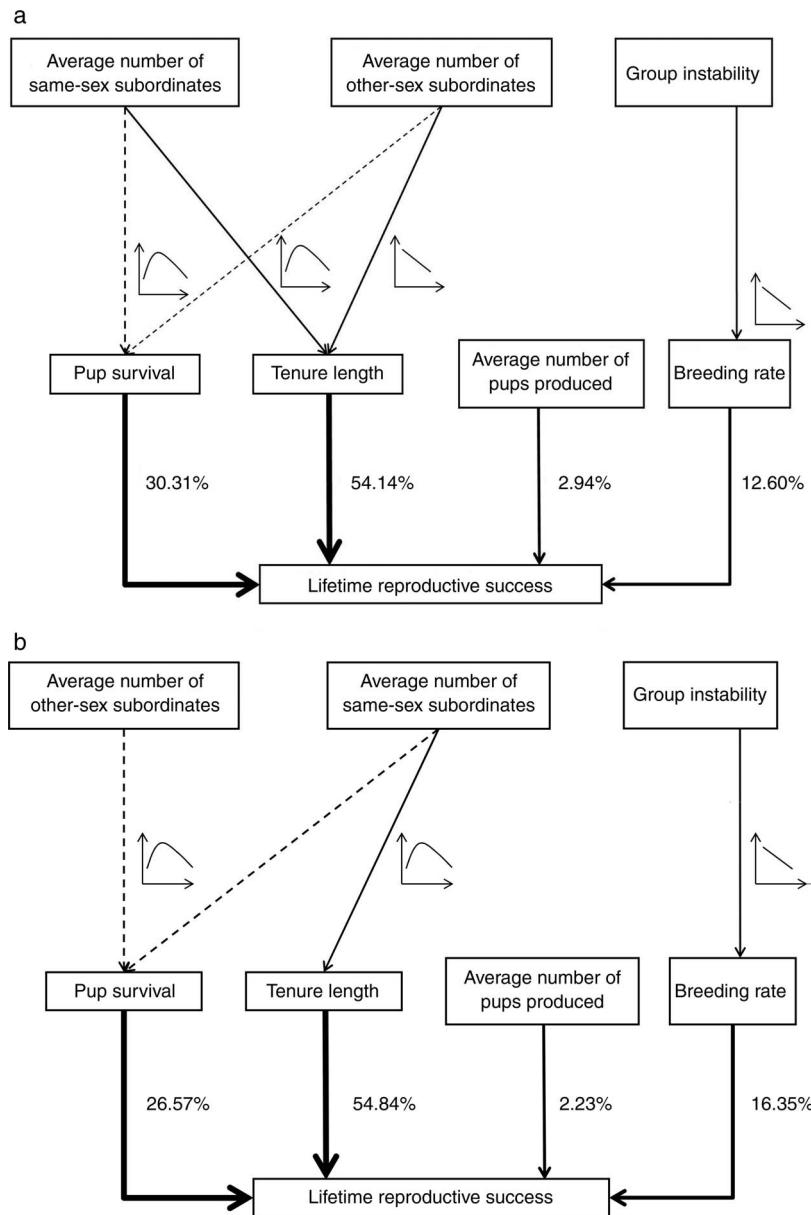
FIG. 6. Diagram of the pathways through which group characteristics affect the lifetime reproductive success of dominant (a) male and (b) female Alpine marmots monitored in the Grande Sassière nature reserve between 1990 and 2010. Lines between variables indicate a significant relationships ($P < 0.05$), dashed lines indicate a significant effect of interaction, and the insets show the shape of the relationship. The different thicknesses of the solid lines represent percentage contribution; the percentage values give the relative contributions of each fitness component to the explained variation in lifetime reproductive success.

Accordingly, an optimal group size maximizing male LRS and an optimal composition maximizing male and female LRS was evidenced. The consequences of social group characteristics on LRS differed for males and females, suggesting that group living affects individual fitness through sex-specific pathways (Figs. 6 and 7). Our results revealed the major role of intrasexual competition in shaping males' and females' fitness. In the two sexes, fitness strongly depended on the number of same-sex subordinates in the social unit, increasing

until an intermediate number of same-sex subordinates and decreasing thereafter.

The effects of group characteristics on fitness resulted in a bell-shaped relationship between group size and individual fitness. This pattern is in agreement with theoretical models predicting an increase of both the costs and the benefits of group living with group size, leading to a bell-shaped fitness function with the costs outweighing the benefits beyond an optimal group size (Giraldeau 1988). In the Alpine marmot, nonlinear
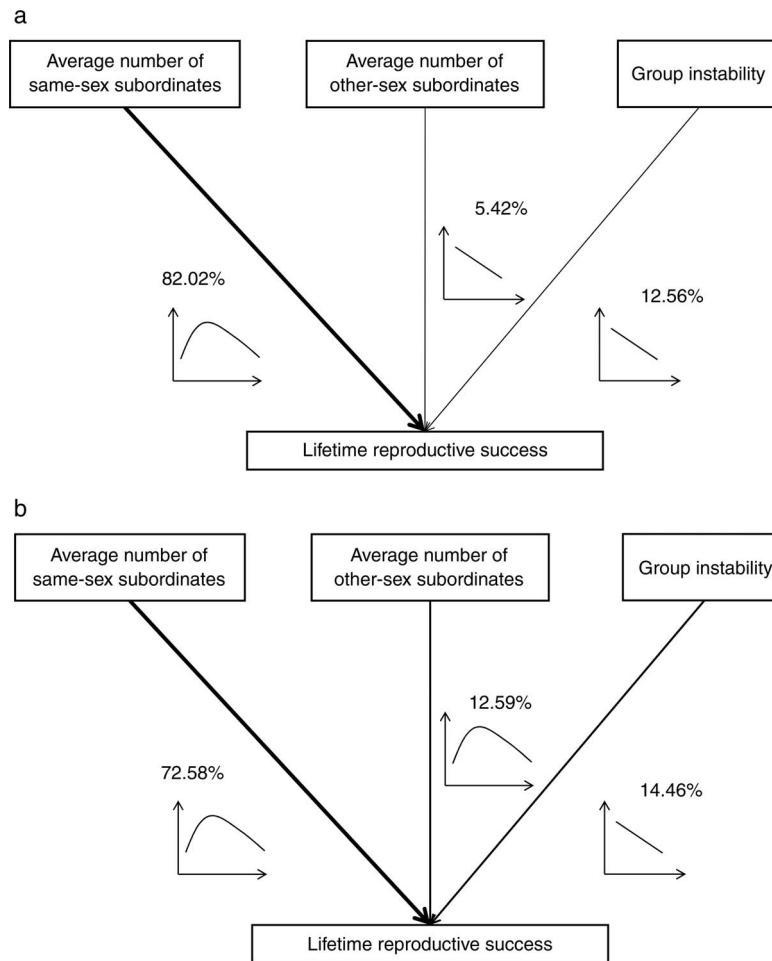
FIG. 7. Diagram of the direct effects of group characteristics on the lifetime reproductive success of (a) male and (b) female Alpine marmots monitored in the Grande Sassière nature reserve between 1990 and 2010. The lines between variables indicate a significant relationship ($P < 0.05$) and the insets show the shape of the relationship. The percentages give the relative contributions of each variable to the explained variation in lifetime reproductive success.

effects of group characteristics on fitness arise from the fact that group characteristics affect the components contributing the most to the variation of fitness (tenure length and pup survival) and that they have positive or negative effects depending on the fitness component considered (Fig. 6). If there is compelling evidence of a quadratic relationship between annual fitness components and group size in other social species, e.g., *Papio cynocephalus anubis* (Hill et al. 2000); *Microtus ochrogaster* (Mcguire et al. 2002); *Panthera leo* (Mosser and Packer 2009); *Lemur catta* (Takahata et al. 2006), empirical evidence for an optimal group size for a lifetime proxy of fitness is scarce. Apart from this study, such a relationship has been evidenced in the yellow-bellied marmot (*Marmota flaviventris*), where the net reproductive rate peaks for intermediate group sizes, i.e., matriline sizes (Armitage and Schwartz 2000).

Beyond the similar effect of group size on fitness and its components in both sexes, males and females differed in which group characteristics were the most influential

on fitness. For instance, we found that the number of males in the group contributed the most to the variation in male fitness, whereas the number of females contributed the most to the variation in female fitness. Variation in fitness appears to be driven mainly by the number of same-sex subordinates present in the group for male and female Alpine marmots. More generally, intrasexual competition should be particularly acute in singular breeders where same-sex individuals strongly compete for social status and reproduction (Emlen 1982, Clutton-Brock et al. 2006, Stockley and Brø-Jorgensen 2011). In mandrills *Mandrillus sphinx* (Setchell et al. 2006) and meerkats (Hodge et al. 2008), the annual probability that individuals will lose dominance increases with the number of same-sex subordinates in the group. Because similar annual patterns were previously found in the Alpine marmot (Lardy et al. 2012, 2013), we expect long-term consequences of intrasexual competition on fitness of mandrills and meerkats, and more generally in social species.

Because intrasexual competition leads to different optimal group compositions for males and females, it should promote sexual conflicts. Theoretically, in groups where breeding females and dominant males have contrasting interests in terms of reproductive success, males and females should vary in their preferred social organization (Pradhan and van Schaik 2008). In the Alpine marmot, more subordinates of a given sex increases the risk for the dominant of the same sex to lose dominance (Lardy et al. 2012, 2013). Change of dominant in turn increases group instability and impacts negatively the breeding rate of the other dominant. Consequently, sexual conflict should be limited because the presence of too many subordinates of the opposite sex will be associated with fitness costs for the remaining dominant. In agreement with this expectation, in the Alpine marmot the optimal number of male subordinates for a dominant male was 2.4 individuals and for dominant females, 2.5 individuals. These values are close to those predicted by the models.

Intrasexual competition may further cause the discrepancy between the average group size of 4.6 individuals observed in the population and the optimal group size predicted from our models (5.6 and 6.7 individuals for dominant males and females, respectively). It is possible that there is a difference in the cost–benefit trade-off between a dominant and its subordinates in determining group size and characteristics. Theoretical models predict that dominants should prefer a larger group size than the group size conferring the highest per capita fitness (Vehrencamp 1983). In social systems with high reproductive skew, such as in the Alpine marmot, dominants may enjoy a greater fitness at group sizes that are detrimental to subordinates' fitness. In this situation, subordinates would gain more fitness benefits from dispersing and accessing dominance than staying in the group.

Tenure length and pup survival were the two fitness components contributing the most to the observed variation in fitness of male and female Alpine marmots. In this species, extra-dominance reproduction is rare and male and female reproduction is highly dependent on dominant status (Cohas et al. 2006). This strong constraint on access to reproduction may account for the large contribution of tenure length to fitness. In species where reproduction is contingent on social rank, a high contribution of tenure length was also found: Japanese macaque *Macaca fuscata* (Fedigan et al. 1986); savannah baboon *Papio cynocephalus* (Altmann et al. 1988); and meerkat (Hodge et al. 2008). The major influence of tenure length on fitness may have several evolutionary consequences. For instance, a high level of testosterone or a large body mass in dominant females of social species might have evolved because of their association with tenure length (Clutton-Brock et al. 2006). Although we could not test for an effect of individual condition on fitness, body mass is an important determinant in Alpine marmots' ability to

retain their status at an annual scale (Lardy et al. 2012, 2013). Similarly, in female meerkats, the tenure length decreases as the number of adult females in the group increases, and as the difference in body mass between the dominant female and its subordinates decreases (Hodge et al. 2008).

Group living also contributes to enhance offspring survival, the second most important fitness component in the two sexes. In the Alpine marmot, offspring annual survival increases with the number of male subordinates in the group, whereas it decreases with the number of female subordinates (Allainé and Theuriau 2004). Winter being a critical period for this mountain-dwelling species, social thermoregulation has been proposed to be the major evolutionary force shaping sociality in hibernating rodents (Armitage 2007). The role of male and female subordinates in offspring survival is less contrasted and more complex on the lifetime than on the annual basis. Although never quantified, male and female subordinates may improve offspring survival by play fighting and vigilance during the pup's first year of life. Alternatively, the competition between subordinates and dominants leads to group instability and to infanticide, hence lowering average offspring survival. Lifetime studies might not be appropriate for understanding fine-scale mechanisms, and fine-scale behavioral observations are needed to understand the role of subordinates during breeding.

Strategies maximizing reproductive success should differ between the sexes because reproductive costs are higher for females than for males (Trivers 1972, Parker 1979, Rice 2000). In polygynous species, the number of offspring sired is a critical component of male fitness, whereas female fitness depends mostly on offspring survival (Clutton-Brock 1988). In the polygynous red deer (*Cervus elaphus*), male mating success and offspring survival account for 30% and 20% of the variation in male LRS, whereas fecundity and offspring survival account for 7% and 57% of the variation in female LRS (Clutton-Brock et al. 1988). Comparisons of the contribution of fitness components to variation in fitness for each sex are limited in number for monogamous species. No sex difference in the contribution of fitness components to LRS was detected for House Sparrows *Passer domesticus* (Jensen et al. 2004) or humans *Homo sapiens* (Courtiol et al. 2012). In agreement with this pattern, the relative contributions of tenure length, fecundity, and offspring survival to the variation in fitness are similar in males and females of the socially monogamous Alpine marmot. In monogamous species in which the number of mates per breeding attempt is close to one, the reproductive success of a male is highly dependent on the reproductive success of its female. Consequently, similar relative contributions of fitness components to LRS should be observed in males and females (Rice 2000).

Our results suggest that multiple group characteristics are required to infer correctly the determinants of fitness

in social species. Such complex relationships could account for the apparent inconsistency between group characteristics and fitness that we observe in the literature (Silk 2007, Ebensperger et al. 2012). Group characteristics impact fitness differently in the two sexes, emphasizing the crucial role of intrasexual competition. Conducting similar integrative approaches across social and nonsocial species will undoubtedly offer great opportunities to decipher the major fitness determinants in social species and, ultimately, to understand the evolution of group living.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–G are available online: http://dx.doi.org/10.1890/15-0425.1.sm