Oecologia (2015) 179:753–763
DOI 10.1007/s00442-015-3375-6

POPULATION ECOLOGY - ORIGINAL RESEARCH

Litter sex composition influences dominance status of Alpine marmots (*Marmota marmota*)

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Received: 12 January 2015 / Accepted: 15 June 2015 / Published online: 14 July 2015

Abstract In social species, the hierarchical status of an individual has important consequences for its fitness. While many studies have focused on individual condition to explain access to dominance, very few have investigated the influence of the social environment, especially during early life. Yet it is known that environmental conditions early in life may influence several traits at adulthood. Here, we examine the influence of early social environment on accession to dominance by investigating the influence of litter size and sex composition on survival and the probability of ascending to dominance later in life using a 20-year dataset from a wild population of Alpine marmots (*Marmota marmota*). Although litter size had no effect on the fate of individuals, litter sex composition affected male juvenile survival and both male and female probabilities of reaching dominant status when adult. Male juveniles incur lower survival when the number of male juveniles in the litter increases, and individuals of both sexes from male-biased litters are more likely to become dominant than individuals from female-biased litters. However, the absolute number of sisters in the litter, rather than the sex ratio, seems to be an important predictor of the probability of acquiring dominant status: pups having more sisters are less likely to become dominant. Several potential mechanisms to explain these results are discussed.

Keywords Delayed effects · Group composition · Multi-event models · Reproduction access · Rodent · Social context

Introduction

In animal societies, the hierarchical status an individual can reach has important implications. It may affect many aspects of its life, such as access to food (Baker et al. 1981), health and physiology (Sapolsky 2005) or reproductive success (Ellis 1995; Creel et al. 1997), therefore entailing serious fitness consequences.

Many factors have been proposed to favour access to dominance, e.g. body condition (Poisbleau et al. 2006), genetic factors (Dewsbury 1990) or experience (Hansen and Slagsvold 2004). In long-lived mammals, another potential factor affecting the ability to reach dominant status is the environmental conditions encountered early in life. However, few studies have evaluated the influence of early conditions on access to dominance. Most have investigated the effect of early conditions on other traits later in life (e.g. growth, survival, habitat selection, sexual attractiveness; reviewed in Lindström 1999), and focus has been mainly on early environmental conditions (Cam et al. 2003; Douhard et al. 2013; Lee et al. 2013), whereas social factors have been largely overlooked.

Communicated by Janne Sundell.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-015-3375-6) contains supplementary material, which is available to authorized users.

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Nevertheless, some laboratory studies have highlighted the impact of early social conditions on individual performances (Zielinski et al. 1992; Correa et al. 2013). Particularly, a negative link between litter size and body size/mass has been evidenced in mammals (Charnov and Ernest 2006). In litter-bearing mammals, Mendi (1988) has shown that offspring from small litters usually weigh more, have a higher growth rate and faster physical development, and that these differences may last beyond the end of the lactation period. Other studies have shown that larger and/or bigger animals have a higher survival probability and are more likely to become dominant (Clutton-Brock et al. 1986; Jonart et al. 2007). Litter size can thus impact future body size and/or mass and therefore future hierarchical status.

In addition, litter composition can potentially influence the future hierarchical status of an individual through different pre- or post-natal mechanisms. Before parturition, the composition of the litter may directly affect the development of individuals because androgens, secreted by male foetuses, and oestrogens, secreted by female foetuses, diffuse across the foetal membranes in utero (Vom Saal et al. 1999). These hormones, particularly testosterone, affect the differentiation of morphological, physiological and behavioural traits such as ano-genital distance, oestrous cycle length or aggressiveness (Clemens et al. 1978; Even et al. 1992). Thus, the sex ratio of the litter, which is often used as a proxy of prenatal exposure to testosterone (Uller et al. 2004; Hackländer and Arnold 2012; Monclus and Blumstein 2012), may have long-term consequences on access to dominance by impacting juvenile survival and/or competitive abilities (Monclus et al. 2014). After birth, the sex of surrounding siblings can also influence the fate of juveniles since the levels of competition and/or cooperation among same-sex siblings can differ between males and females. In spotted hyenas (*Crocuta crocuta*), for instance, intra-sexual competition is higher among young females than among young males. This higher level of competition among young females results in a higher rate of siblicide in all-female litters, and leads in turn to lower survival of young females (Golla et al. 1999). Conversely, in African lions (*Panthera leo*), kin-related males cooperate and coalitions between male siblings are frequently observed. This particular form of cooperation allows them to secure access to a group of females, therefore ensuring a dominant position and high reproductive success (Packer et al. 1991). Such sex-specific interactions can thus influence the probability to survive to adulthood and/or to hold a dominant position.

The aim of this study is to investigate whether early social conditions, i.e. litter size and composition, can influence individual probability of acquiring a dominant position later in life. For this purpose, data from a 20-year study on the Alpine marmot (*Marmota marmota*) in the French Alps was used. The Alpine marmot is well suited for such a study because reproduction is strongly constrained by social status as the dominant pair monopolizes reproduction in the social group (Goossens et al. 1998; Cohas et al. 2006), and litters exhibit high variability in size (from 1 to 7 pups) and sex composition (from exclusively male to exclusively female litters; Allainé et al. 2000). We investigated whether individuals from small litters, assumed to be in better condition than those from large litters, were more likely to survive and to become dominant. As for the effect of litter composition, we considered the following three possibilities. First, we investigated whether the sex ratio of the litter influenced the fate of individuals of both sexes, i.e. whether individuals born to male-biased litters were more prone to become dominant. Second, we examined the possibility that intrasexual competition between siblings decreases the probability of further access to dominance either by decreasing juvenile survival or the probability of reaching a dominant position. Thus, females with many sisters and males with many brothers should display lower overall probabilities to become dominant. Third, we considered the possibility that cooperation between siblings of the same sex (formation of coalitions, for instance) outweigh the effect of intrasexual competition within litters. In this case, individuals with numerous same-sex siblings should be more likely to become dominant.

Materials and methods

Study species

The Alpine marmot is a hibernating ground-dwelling squirrel. This territorial and social mammal lives in family groups composed of a dominant couple, sexually mature and immature subordinates of both sexes, and pups born that year (Allainé et al. 2000).

Pups stay together as subordinates in their natal group at least until they reach sexual maturity at 2 years old. From this age, both males and females can reach dominance either by replacing the dominant of their natal territory when he/she dies or by dispersing and displacing a dominant of a neighbouring territory. Dispersal is often limited in space since more than 80 % of the dominant individuals captured were born in the study area and dominant individuals coming from outside the study area settled in its periphery. Dispersal patterns differ between sexes. Females inherit their dominant position more often than males do with, respectively, 35 % of the dominant females and 15 % of the dominant males which occupy their natal territory (Lardy 2012). In addition, males seem to disperse further away than females. Since dispersing individuals never become subordinates in a new family group, they are at a high risk of death and very rarely survive overwinter if they do not reach dominance during the active season (winter mortality of 0.9; Grimm et al. 2003). Male subordinates that delay dispersal are considered as helpers since their presence greatly increases the survival probability of pups during their first hibernation (Arnold 1988; Allainé and Theuriau 2004). Within family groups, reproduction is monopolized by the dominant couple. After 35 days of gestation, the dominant female gives birth to a litter of 1–7 pups in the second half of May. Given the gestation and weaning length, only one litter can be produced each year. A few sexually mature males manage to partially escape the reproductive control of the dominant male. Hence, while dominant females generally monopolize all reproduction, dominant males may lose some paternities (Cohas et al. 2006). Individuals of both sexes may stay dominant for several years (up to 11 for males and 14 for females in the study population), until natural death or eviction by a challenger (Lardy et al. 2011). Eviction of one of the dominants further leads to the loss of the litter produced, either by infanticide or by abandonment of the pups, and to the death of the evicted individual in most cases (Hackländer et al. 2003; Lardy et al. 2011).

Study site and data collection

Individuals were captured in a wild population of Alpine marmots located in the Grande Sassière nature reserve (2340 m a.s.l., French Alps, 45°29′N, 6°59′E) from 1990 to 2010. Marmots from up to 24 territories (five territories were created while one disappeared during the study) were monitored, from mid-April to mid-July each year, using both capture–mark–recapture and observations. Marmots were captured using two-door live-capture traps baited with dandelion *Taraxacum densleonis*. Traps were placed near the entrances of the main burrows to easily assign each captured individual to its family group. Juveniles were counted and caught by hand within the 3 days following their first emergence from the burrows, (i.e. approximately 40 days after their birth). Captured animals were tranquillized with Zolétil 100 and marked with a transponder (Trovan™, Germany) and a numbered ear tag. At each capture, marmots were aged from their size in three age classes (pups, yearlings and adults), sexed and their social status was determined according to scrotal development for males and teats development for females (Hackländer and Arnold 1999; Hackländer et al. 2003). Thanks to daily observations, the number of individuals of each sex and age class was further assessed for each family and scent-marking behaviour was used to confirm the identity of the dominant pair (Bel et al. 1995).

Litter characteristics

The exact composition of every litter and the identity of individuals that reproduced each year was determined using microsatellite markers and kinship analyses (Online Resource 1).

Litter size was calculated as the total number of pups from the same mother emerging a given year. The litter sex ratio was calculated as the number of males in a litter divided by the litter size. The number of brothers was calculated as the number of male pups in a litter minus one when the focal individual was a male. The same procedure was used to determine the number of sisters for each individual.

Capture–recapture analysis

We considered 806 individuals first captured as pups between 1990 and 2010 for which the litter size, litter sex ratio, number of brothers and number of sisters were known.

Model structure

Multi-Event Capture–Recapture models (ME-CR; Pradel 2005) were used to investigate the influence of the litter size and composition on marmot survival (ϕ) and access to dominance (ψ) because recapture probability (p) of individuals was lower than 1 (recapture probability varying from 0.380 to 0.886; Cohas et al. 2007). We defined 3 states: subordinate (s), dominant (D), and dead or permanent emigrant from the study site (†). We further incorporated information about the reproductive status (E) of each individual to refine the estimation of the probability to access dominance. Since the probability to reproduce is strongly linked to the dominant status (only 20 of the 806 pups studied were produced by subordinates), there is a high probability that an individual that successfully reproduced a given year was dominant even when its dominance status could not be determined. Thus, the different observable events retained were: no information (event 0), individual with uncertain dominance status that successfully reproduced, i.e. with its pups captured (event 1), individual captured as dominant but no reproduction observed, i.e. no pups captured (event 2), individual captured as dominant that successfully reproduced (event 3), individual captured as subordinate without pups of its own observed (event 4), individual captured as subordinate that successfully reproduced (event 5). Based on these events, recapture histories were then constructed for each individual (Online Resource 2).

The constructed multi-events model can be summarised by a transition matrix and associated vectors of survival, capture and successful reproduction probabilities (see Fig. 1 and Online Resource 3 for further details on the model construction). For pups, the model reduces to a single survival parameter because they cannot stay as pups more than 1 year and they are not able to reproduce or to

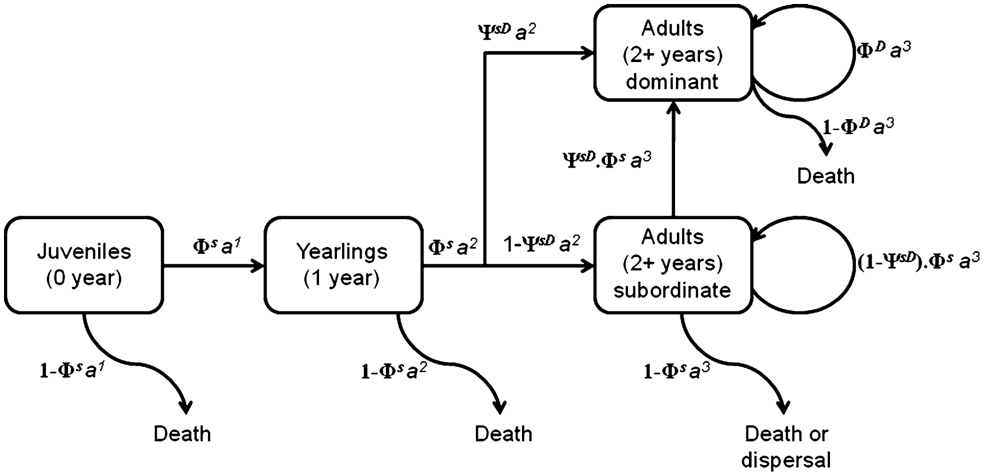

Fig. 1 Life cycle of Alpine marmots with three age classes (a^1 pup, a^2 yearling, a^3 adult) and two social status (*s* subordinate and *D* dominant); *arrows* represent the transition from one age class to the next with its associated probability: **Φ** represents survival probabilities and **ψ** represents transition from the subordinate to the dominant status. **ψ** is conditional on **Φ**

Table 1 Abbreviations used in models notations

Abbreviations	Meanings
p	Recapture probability
Φ	Survival probability
$1-\Phi$	Mortality probability (encompass both mortality and dispersal probabilities for individuals older than 2 years of age)
ψ	State transition probability (conditional on survival)
E	Event probability (probability of successful reproduction)
Subscript	
a	All age classes (1 to 3)
a^1	Age from 0 to 1 year
a^2	Age from 1 to 2 years
a^3	Age more than 2 years
$a^{x,y}$	Age classes x and y
sex ^{f,m}	Sex (f: female; m: male)
y	Time effect (year)
×	Interactive effect
+	Additive effect
Sex ratio	Litter sex ratio at emergence
Litter size	Litter size at emergence
Brothers	Number of male pups from the same mother in a litter
Sisters	Number of female pups from the same mother in a litter
Helpm	Number of male helpers present during the first hibernation
Superscript	
s	Subordinate status
D	Dominant status
†	Dead

become dominant. For yearlings, the model reduces to the estimation of probabilities of capture, survival, and access to dominance the following year. They are never captured as dominant and are not yet sexually mature. For older individuals, since dominant individuals never revert to the subordinate status (Farand et al. 2002; Stephens et al. 2002; Grimm et al. 2003), the model reduces for older individuals to two capture parameters, two survival parameters (one for subordinate and one for dominant individuals) and to the probability to access dominance when they are still subordinate.

Preliminary analysis

Data analyses were performed following three steps (Lebreton et al. 1992). We first tested whether a general model,

Table 2 Model selection for the effects of litter size, litter sex ratio, number of brothers and number of sisters in the litter on the juvenile survival probability of Alpine marmots marked from 1990 to 2010; all other parameters' constraint structure fixed as in the root model: $\boldsymbol{p}^{s}a \times y + \text{sex}\ \boldsymbol{\Phi}^{s}\ a^{2,3}\ \boldsymbol{E}^{s}a^{3}$, $\boldsymbol{p}^{D}a^{3} \times y + \text{sex}\ \boldsymbol{\Phi}^{D}a^{3}\ \boldsymbol{E}^{D}\ a^{3}\ \boldsymbol{\psi}^{sD}a^{2}$, $a^{3} \times \text{sisters}$

Juvenile survival models		Deviance	k	AICc	ΔAICc	W_i
B1.3	$\boldsymbol{\Phi a^{1} \times \textbf{sex}^{m} \times (\textbf{log(helpm)} + \textbf{brothers}) + \textbf{sex}^{f} \times \textbf{log(helpm)}}$	**3617.04**	**72**	**3767.56**	**0.00**	**0.31**
B1.1	$\Phi a^{1} + \text{brothers} + \textit{sex} \times \log(\text{helpm})$	3618.74	72	3769.08	1.52	0.14
B1.2	$\Phi a^{1} \times \text{sex} \times (\log(\text{helpm}) + \text{brothers})$	3616.93	73	3769.63	2.07	0.11
R1	$\boldsymbol{\Phi a^{1} \times \textbf{sex} \times \textbf{log(helpm)}}$	**3621.41**	**71**	**3769.75**	**2.19**	**0.10**
L1.1	$\Phi a^{1} + \text{litter size} + \text{sex} \times \log(\text{helpm})$	3619.06	72	3769.85	2.29	0.10
SR1.1	$\Phi a^{1} + \text{sex ratio} + \textit{sex} \times \log(\text{helpm})$	3620.60	72	3770.93	3.37	0.06
L1.2	$\Phi\ a^{1} \times \text{sex} \times (\log(\text{helpm}) + \text{litter size})$	3618.48	73	3771.18	3.62	0.05
B1.4	$\Phi a^{1} \times \text{sex}^{m} \times \log(\text{helpm}) + \text{sex}^{f} \times (\log(\text{helpm}) + \text{brothers})$	3621.30	72	3771.63	4.07	0.04
S1.1	$\Phi a^{1} + \text{sisters} + \text{sex} \times \log(\text{helpm})$	3621.39	72	3771.73	4.17	0.04
SR1.2	$\Phi a^{1} \times \text{sex} \times (\log(\text{helpm}) + \text{sex ratio})$	3619.85	73	3772.55	4.99	0.03
S1.2	$\Phi a^{1} \times \text{sex} \times (\log(\text{helpm}) + \text{sisters})$	3620.32	73	3773.02	5.46	0.02

$n = 806$ individuals

Bold characters indicate the best model of the set and the root model for comparison

AICc Akaike Information Criterion corrected for small sample sizes, k number of identifiable parameters, Δ*AICc* difference in AICc with the best model of the set, W_i AICc weight

Table 3 Model selection for the effect of number of brothers in the litter on the yearling and subordinate adult survival probability of Alpine marmots marked from 1990 to 2010; all other parameters' constraint structure fixed as in the root model: $\boldsymbol{p}^{s}a \times y + \textit{sex}$ $\boldsymbol{\Phi}^{s}a^{1} \times \text{sex}^{m} \times (\log(\text{helpm}) + \text{brothers}) + \text{sex}^{f} \times \log(\text{helpm})\ \boldsymbol{E}^{s}a^{3}$, $\boldsymbol{p}^{D}a^{3} \times y + \text{sex}\ \boldsymbol{\Phi}^{D}a^{3}\ \boldsymbol{E}^{D}\ a^{3}\ \boldsymbol{\psi}^{sD}a^{2}$, $a^{3} \times \text{sisters}$

Yearling and adult survival models		Deviance	k	AICc	ΔAICc	W_i
R2	$\boldsymbol{\Phi^{s}\ a^{2,3}}$	**3617.04**	**72**	**3767.56**	**0.00**	**0.47**
B2.2	$\Phi^{s}\ a^{2}, a^{3} \times \text{sex}^{m} \times \text{brothers} + \text{sex}^{f}$	3615.64	73	3768.15	0.59	0.35
B2.1	$\Phi^{s}\ a^{2} \times \text{sex}^{m} \times \text{brothers} + \text{sex}^{f,}\ a^{3}$	3616.99	73	3769.5	1.94	0.18

$n = 806$ individuals

Bold characters indicate the best model of the set and the root model for comparison

AICc Akaike Information Criterion corrected for small sample sizes, k number of identifiable parameters, Δ*AICc* difference in AICc with the best model of the set, W_i AICc weight

namely the Cormack–Jolly–Seber model (Pollock et al. 1985), fitted our data. To this purpose, goodness-of-fit (GOF) tests were performed using the program U-CARE (Choquet et al. 2009a).

Following Burnham and Anderson (2002), the second step was to select the most parsimonious model, hereafter called the root model, among a set of models built by considering only a priori biological hypotheses based on our field experience and the literature (Arnold 1993; Farand et al. 2002; Stephens et al. 2002; Grimm et al. 2003; Allainé 2004). We thus considered age, year, sex effects and their interactions on all capture, survival, state transition and reproduction probabilities (Table 1). In addition, we considered an effect of the number of male helpers on juvenile survival during their first hibernation since it has been demonstrated to be an important factor (Arnold 1993; Allainé and Theuriau 2004). To do this, the logarithm of the number of male helpers [log(helpm)] was used as an individual covariate because the effect of male helpers was found to be non-linear (Allainé and Theuriau 2004).

Following a step-down approach, models were sequentially fitted with constrained parameterizations for recapture, survival, transitions and reproduction probabilities, in that order. We then checked that the root model could not be improved by exploring all neighbouring models. Model selection relied on the Akaike Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson 2002). Model selection and parameters' estimation were performed using the program E-SURGE 1.8.5 (Choquet et al. 2009b).

Effect of litter characteristics

Once the root model was obtained, we investigated in the final step whether the early social conditions affected both the survival rate and the probability to access dominance.

Table 4 Model selection for the effects of litter size, litter sex ratio, number of brothers and number of sisters in the litter on the probability to become dominant of Alpine marmots marked from 1990 to 2010; all other parameters' constraint structure fixed as in the root model: $\boldsymbol{p}^{s}a \times y + \text{sex } \boldsymbol{\Phi}^{s}a^{1} \times \text{sex}^{m} \times (\log(\text{helpm}) + \text{brothers}) + a^{1} \times \text{sex}^{f} \times \log(\text{helpm}); a^{2,3}\ \boldsymbol{E}^{s}a^{3}, \boldsymbol{p}^{D}a^{3} \times y + \text{sex } \boldsymbol{\Phi}^{D}a^{3}\ \boldsymbol{E}^{D}\ a^{3}$

Transition models		Deviance	k	AICc	ΔAICc	W_i
S3.2	$\boldsymbol{\psi^{sD}a^{2}, a^{3} \times}$ **sisters**	**3617.04**	**72**	**3767.56**	**0.00**	**0.23**
SR3.2	$\psi^{sD}a^{2}, a^{3} \times$ sex ratio	3617.41	72	3767.93	0.37	0.19
S3.1	$\psi^{sD}a^{2,3} \times$ sisters	3616.23	73	3768.93	1.37	0.12
R3	$\boldsymbol{\psi^{sD}a^{2,3}}$	**3620.90**	**71**	**3769.24**	**1.68**	**0.10**
SR3.1	$\psi^{sD}a^{2,3} \times$ sex ratio	3617.34	73	3770.04	2.48	0.07
B3.2	$\psi^{sD}a^{2}, a^{3} \times$ brothers	3619.80	72	3770.32	2.76	0.06
L3.2	$\psi^{sD}a^{2}, a^{3} \times$ litter size	3620.66	72	3771.18	3.62	0.04
B3.1	$\psi^{sD}a^{2,3} \times$ brothers	3618.58	73	3771.28	3.72	0.04
S3.3	$\psi^{sD}a^{2}, a^{3} \times$ sex × sisters	3616.64	74	3771.53	3.97	0.03
SR3.3	$\psi^{sD}a^{2}, a^{3} \times$ sex × sex ratio	3616.58	74	3771.47	3.91	0.03
L3.1	$\psi^{sD}a^{2,3} \times$ litter size	3620.50	73	3773.20	5.64	0.01
B3.3	$\psi^{sD}a^{2}, a^{3} \times$ sex × brothers	3619.03	74	3773.92	6.36	0.01

$n = 806$ individuals

Bold characters indicate the best model of the set and the root model for comparison)

AICc Akaike Information Criterion corrected for small sample sizes, *k* number of identifiable parameters, Δ*AICc* difference in AICc with the best model of the set, W_i AICc weight

Table 5 Correlation coefficients between the different covariates tested

	Sex ratio	Brothers	Sisters
Litter size	0.01	0.64	0.53
Sex ratio		0.62	−0.63
Brothers			−0.28

To test our hypotheses on juvenile survival, we built a model including every retained effect on probabilities to access dominance (model R1, Table 2) while the parameterization of all other parameters was set as in the root model. We then added an effect of the tested litter characteristic (i.e. litter size, litter sex ratio, number of brothers or number of sisters) as a logit linear relationship with the juvenile survival in a separate model. In addition, whenever a litter characteristic was found to influence juvenile survival, models with an effect of this covariate on yearling and adult subordinate survival were built to account for possible long-lasting effects. They were compared to a model with the effect of the litter characteristic considered on the juvenile survival only (model R2, Table 3). Because the main effects of the litter characteristics are likely to be on juvenile survival, we did not investigate the effect of the early conditions on yearling and adult survivals whenever no effect on juvenile survival was found.

Similarly, to test the same hypotheses on the probability to access dominance, we built model R3 (Table 4) that included all retained effects on survival, and compared it to models with a logit linear effect of the litter characteristic to test on the probability to access dominance for both yearlings and adults.

Finally, models with a sex-specific effect of the different covariates were constructed and compared to models without sex effects to test for a sex-specific competition or cooperation.

The importance of the tested litter characteristic was then assessed by comparing models using AICc weights (W_i; Burnham et al. 2011). Estimates and standard errors for the different regression slopes given in the results are on the logit scale. All other parameters are given on the natural scale.

Results

Mean litter size was 4.15 ± 0.05 pups in the population, ranging from 1 to 7. Mean sex-ratio was 0.53 ± 0.01 among all litters. Mean number of brothers was 1.66 ± 0.04 (from 0 to 5) while the mean number of sisters was 1.44 ± 0.04 (from 0 to 4). Correlation coefficients between the different litter characteristics are given in Table 5.

Preliminary analysis

After checking for the goodness of fit of the model and AICc-based model selection (see Online Resource 4 for more details on the GOF tests and root model selection), the root model was $\boldsymbol{p}^{s}a \times y + \text{sex } \boldsymbol{\Phi}^{s}\ a^{1} \times \text{sex} \times \log(\text{helpm}); a^{2,3}\ \boldsymbol{E}^{s}a^{3}, \boldsymbol{p}^{D}a^{3} \times y + \text{sex } \boldsymbol{\Phi}^{D}a^{3}\ \boldsymbol{E}^{D}\ a^{3}\ \boldsymbol{\psi}^{sD}a^{2,3}$.

Recapture probabilities varied with year, sex, age and hierarchical status. The average recapture rate decreased with age, from yearlings (0.87 ± 0.06 for females; 0.83 ± 0.09 for males) to adults (subordinates 0.68 ± 0.11 for females; 0.60 ± 0.15 for males; dominants 0.64 ± 0.09 for females; 0.57 ± 0.10 for males).

Survival probabilities varied with age and status and male helpers had a strong sex-specific effect on juvenile survival. Juvenile survival varied from 0.38 ± 0.04 in the absence of helpers to over 0.80 ± 0.04 when five helpers or more were present for females and from 0.24 ± 0.05 to 0.93 ± 0.03 for males. Yearling survival rate was 0.77 ± 0.04, dominant adults survival rate was 0.81 ± 0.02. The apparent subordinate survival rate was much lower (0.53 ± 0.03) due to dispersal outside the study area that could not be distinguished from mortality. Access to dominance (0.04 ± 0.01 for yearlings and 0.49 ± 0.04 for adults) and annual reproduction probabilities (0.02 ± 0.01 for subordinates and 0.64 ± 0.03 for dominants) were found to be constant over time and sex.

Effect of litter size

No effect of the litter size was evidenced, neither on survival nor on the probability to become dominant. All models including an effect of litter size performed poorly compared to the corresponding root model (R1 vs. L1.1 and L1.2, Table 2; R3 vs. L3.1 and 3.2, Table 4).

Effect of litter composition

Sex ratio effect

The litter sex ratio did not affect the juvenile survival (models SR1.1 and SR1.2 vs. R1, Table 2). It was found to influence the probability to access dominance for adults but not for yearlings (models SR3.2 vs. SR3.1, Table 4). The probability for an adult to access dominance increased with the sex ratio from 0.35 ± 0.08 when no males were present to 0.63 ± 0.09 for an all-male litter (Model SR3.2, Table 4; $\beta_{\text{adults}} = 1.15 \pm 0.64$; Fig. 3a).

Sex specific effects

The number of brothers negatively affected male juvenile survival (model B1.3 vs. R1, Table 2). It decreased from 0.64 ± 0.07 to 0.28 ± 0.13 when the number of brothers in the litter increased from 0 to 5 ($\beta_{\text{males}} = -0.26 \pm 0.12$; Fig. 2) for an average number of helpers (3.6 in our population). This effect was no longer detected on the yearling or adult subordinate survival (R2 vs. B2.1 and B2.2, Table 3). The number of brothers did not influence male dominance access probability (models B3.3, B3.2 and B3.1 vs. R3, Table 4).

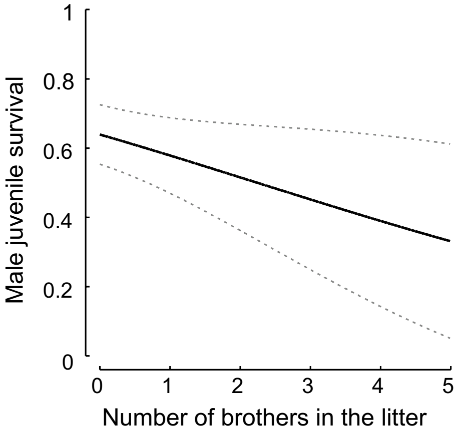

Fig. 2 Effect of the number of brothers in the litter at weaning on juvenile survival probability of males. *Solid line* indicates the estimated survival probabilities from the model $\boldsymbol{\Phi}^s$ $a^1 \times \text{sex}^m \times (\log(\text{helpm}) + \text{brothers}) + a^1 \times \text{sex}^f \times \log(\text{helpm})$ (B1.2); *dashed lines* 95 % confidence interval

The number of sisters had no effect on juvenile survival (models S1.1 and S1.2 vs; R1, Table 3) but negatively affected the probability that adult females (but not yearlings) accessed to dominance (model S3.1. vs. S3.2, Table 4). Interestingly, this effect was not sex-specific (S3.3 vs. S3.2, Table 4), and male dominance access probability was also found to be negatively related to the number of sisters in the litter. The dominance access probability decreased from 0.61 ± 0.08 to 0.30 ± 0.09 as the number of sisters increased from 0 to 4 (Model S3.2, Table 4; $\beta_{\text{adults}} = -0.32 \pm 0.17$; Fig. 3b).

Discussion

Our results confirm that the dominance status in Alpine marmots was influenced by the early social conditions encountered and more specifically by the composition of the litter in which an individual is born. The probability of becoming dominant was found not to be related to the litter size. Instead, our results indicate that the sex composition of the litter, in interaction with the sex of the focal individual, did impact future social status via an impact on both juvenile survival and dominance access probability.

In most litter-bearing mammals, single pups are usually heavier with a faster growth rate and development than pups born with littermates (Mendi 1988). These litter size effects on body mass can persist until adulthood and may largely determine the hierarchical status (Poisbleau et al. 2006; Hodge et al. 2008). In accordance in Alpine marmots, both mass at emergence and post-weaning growth rate decrease as the litter size increases (Allainé et al. 1998), but we did not find any effect of the litter size, either on the

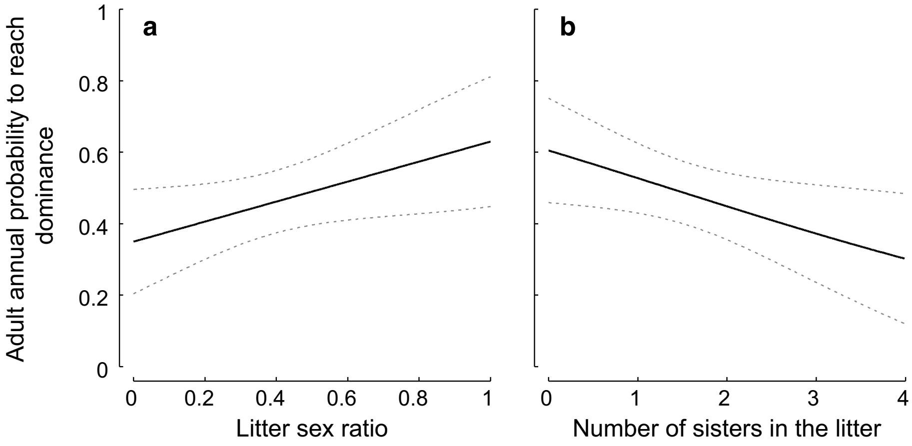

Fig. 3 Effect of **a** the litter sex ratio (model SR3.2) and **b** number of sisters in the litter (model S3.2) at weaning on annual transition probability from the subordinate to the dominant status for individuals of more than 2 years. *Solid line* indicates the estimated transition probabilities; *dashed lines* 95 % confidence interval

juvenile survival or on the probability to become dominant once sexually mature. Pups from large litters instead had as many chances as singletons to survive and to later become dominant. Several mechanisms may explain this result. First, the expected effect of litter size on juvenile survival may exist but may not be detected if it takes place before weaning (i.e. before emergence from the natal burrow), for example via a competition for teats access and/or maternal care. In this scenario, the pups captured at weaning are only those that survived to this early competition between siblings. Thus, the effect of litter size on survival may not be visible in our data. An alternative explanation is that juveniles growing with several littermates may profit from their presence, like in rabbits (*Oryctolagus cuniculus*), where pups have a higher body temperature and consequently a higher survival when experimentally raised with littermates compared to their siblings raised alone (Bautista et al. 2003). This thermoregulation effect can be of great importance, especially for a hibernating species like the Alpine marmot in which social thermoregulation has already been evidenced (Arnold 1988), and may explain why a single pup, even though heavier, does not survive better than pups raised with littermates. Although many studies have highlighted the negative consequences of a poor start on reproduction-related traits later in life (Metcalfe and Monaghan 2001; Yearsley et al. 2004), no effect of the litter size was found on the probability to reach dominance. Further studies are thus needed to investigate whether these early differences in mass and growth rate impact other traits related to fitness such as reproduction onset, number of offspring produced per litter or lifetime reproductive success.

Conversely, the litter composition had important effects on male juvenile survival and male and female probabilities to reach a dominant status. Neither the juvenile survival nor the probability to access dominance were positively affected by the number of same-sex littermates. Thus, our third hypothesis suggesting that cooperation between same-sex littermates may outweigh the possible cost of intra-sexual competition can be discarded. Our second hypothesis was partly supported. Indeed, only male pups had reduced chance to survive when raised with numerous brothers. However, this effect did not last after the first year of life. A higher level of competition among male than among female littermates may explain the negative effect of same-sex littermates on male juvenile survival. Alternatively, a higher requirement of male compared to female pups may also explain this pattern. In such a case, the mother of numerous males may not always fulfill their needs and male pups might reach hibernation in a poorer body condition, thus reducing their chances to survive overwinter. However, the reason for such a differential requirement in a monomorphic species remains unclear.

Once they reach adulthood, females had lower probabilities to reach dominance when raised with numerous sisters. A high proportion of females becomes dominant by inheriting their mother position (35 % of the dominant females). Consequently, the more sisters a female pup has, the higher the competition for a single dominant position. A high number of sisters is therefore a disadvantage for female pups. No such an acute intra-sexual competition is expected for males with numerous brothers since most of them reach dominance by dispersing and displacing another dominant in a neighboring territory (88 % of the dominant males). Accordingly, no effect of the number of brothers was detected on the probability to reach a dominant position.

However, males also had lower probabilities to reach dominance when raised with numerous sisters. Males as well as females can suffer from the presence of numerous sisters because of long-lasting effects of the exposition to in utero hormones. The fact that models including sex ratio were well ranked is in accordance with this hypothesis. Recently, Hackländer and Arnold (2012) reported that female Alpine marmots from male-biased litters were more likely to become dominant. In our study, this relationship was not limited to females, and males were also more likely to become dominant when born in a male-biased litter, thus supporting our first hypothesis. Such an effect of sex ratio is generally interpreted as a potential masculinisation due to pre-natal androgens exposure (Monclus et al. 2014). Being born in a male-biased litter results in a higher probability to develop adjacent to males in utero and thus coincides with higher levels of circulating testosterone and higher testosterone sensitivity, which in turn have several morphological, physiological and behavioural consequences (Ryan and Vandenbergh 2002). For instance, female Alpine marmots born in male-biased litters are more aggressive (Hackländer and Arnold 2012), while female yellow-bellied marmots (*Marmota flaviventris*) disperse more (Monclus and Blumstein 2012), two features favouring the access to dominance in Alpine marmots.

The number of brothers in the litter can also be considered as a proxy of the intrauterine exposition to androgens. Sex-ratio and the number of brothers within the litter are correlated but they do not match perfectly (see Table 5), and hence do not contain the exact same information. According to Even et al. (1992), the testosterone produced by a male foetus diffuses to the surrounding foetuses through the foetal membrane and the quantity of hormone approximately decreases by half when the distance to the secreting foetus increases by one foetus. Thus, an individual with a large number of brothers is thought to be generally exposed to a high amount of additional testosterone, whatever its position in utero. Interestingly, the absence of any effect of the number of brothers in the litter on access to dominance contradicts this general interpretation, and suggests that dominance status of Alpine marmots might not only be determined by the in utero exposure to testosterone and that other effects are likely to play a role.

Instead, our results highlighted the effect of the number of sisters on the probability of becoming dominant. Following the same reasoning as for the number of brothers and the quantity of androgens, we can suppose that the number of sisters increases the probability to develop between two female foetuses, and thus the quantity of oestrogens received in utero. Although poorly studied, examples of oestrogen-mediated long-lasting effects can be found in the literature. For example, Vom Saal et al. (1990) showed that female mice (*Mus musculus*) that developed between two other females had higher levels of circulating oestradiol and consequently affected reproductive traits, such as shorter oestrous cycle length, and Fadem and Tesoriero (1986) demonstrated that exposition to oestrogens during an early period of development could block testicular development in male gray opossum (*Monodelphis domestica*), while exposition to testosterone had no impact on both males and females. Thus, Alpine marmots born with many sisters may become dominant less often because they present more feminised characteristics due to higher levels of circulating oestrogens. However, our results do not allow us to disentangle the different mechanisms proposed here and further studies assessing the levels of circulating oestrogens and testosterone would be of great interest to understand the underlying mechanisms of such long-lasting effects of the early social environment.

Finally, even though our results do not take into account dispersal outside and into the study area, it seems rather unlikely that the impact of the litter composition (particularly the number of sisters and litter sex ratio) on the probability to access dominance would be different when doing so. We believe that, for several reasons, litter composition does not impact differently on the individuals permanently emigrating outside the study area. First, when dispersing, Alpine marmots settle in a vast majority in a neighbouring territory and only one individual dispersed further than four territories from its natal territory in 20 years. Thus, within the study area, all the range of dispersal distances usually encountered in this species is covered and successful longer distance dispersal seems at best to occur very rarely in the Alpine marmot. Second, if litter composition influenced the propensity of individuals to disperse outside the study area, a positive effect would have been detected on the apparent subordinate mortality since it includes both the actual mortality of subordinate individuals and the survival of individuals that left the study area and were never encountered again. Thus, if individuals with a certain litter composition dispersed more, they should have a lower apparent survival. No such effect was found in our data.

In summary, the survival and later hierarchical status of Alpine marmots are influenced by social conditions encountered during the early stages of life. More specifically, these results suggest that they are influenced by the sex composition of the litter. The number of female juveniles present during the development seems to have long-lasting effects on Alpine marmots' ability to reach a dominant position for both males and females despite potential differences in the underlying mechanisms. In addition, males seem to suffer from the presence of other males in the litter inducing a reduced survival when juveniles. It therefore appears that males' fitness expectancies are probably higher when raised alone while females seem to benefit from the presence of males siblings. These results provide new insights on the costs and benefits of a litter composition and should be taken into account when studying the pay offs parents can expect from their offspring.

Author contribution statement AC and DA conceived the study. RP and PD conceived the models and performed the analysis. PD wrote the manuscript. SL, AC, DA and PD contributed to the data collection. All authors provided editorial advice.

Acknowledgments We thank all students involved in the trapping of Alpine marmots at La Sassière. We warmly thank all Earthwatch volunteers for their help. Thanks are also extended to authorities of the Vanoise National Park for allowing us to work in the Grande Sassière Nature Reserve. Finally, we thank Earthwatch Institute for financial support. The experiments conducted comply with current French laws. All the handling and sampling were done by A.C. and S.L. who are authorized for experimentation with animals by the French Ministry of Agriculture and Fisheries (diploma nos 0ETRY20090520 and 433R45GRETAF110). The protocol was approved by the ethical committee of the University Claude Bernard Lyon 1 no. BH2012-92 V1.

Conflict of interest The authors declare that they have no conflict of interest.

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