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Influences of climatic and social environment on variable maternal allocation among offspring in Alpine marmots

Floriane Plard[1] | **Benoit Chamiot-clerc**[1,2] | **Aurélie Cohas**[1,3]

[1]UMR CNRS 5558 Biométrie et Biologie Evolutive, Univ Lyon, Université Claude Bernard (Lyon I), Villeurbanne, France

[2]Department of Aquaculture and Fish Biology, Hólar University, Sauðrkrókur, Iceland

[3]Institut Universitaire de France (IUF), Paris, France

Correspondence
Floriane Plard
Email: floriane.plard@ens-lyon.fr

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Abstract

1. In an environment with limited resources, parents may trade-off the number of offspring produced against offspring mass. To maximize fitness under unpredictable environments, females must not only maximize mean annual reproductive success but also minimize between-year variation in reproductive success. Thus, preferred strategies of maternal allocation might be to maximize the mass of their offspring or to produce a number of offspring of variable body masses.
2. Many social species have evolved in variable and unpredictable environments where only the social environment can be predicted. If mothers seem to alter their total reproductive allocation to offspring depending on their social environment, how the total expenditure is allocated between the different offspring is still unknown.
3. Here, we analysed how climatic and social environments influence strategies of maternal allocation and how these strategies impact pup first-year survival in a wild population of Alpine marmots monitored between 1990 and 2016.
4. We found that females acted as income breeders using resources immediately available for reproduction. Our results showed that the proportion of maternal mass allocated to offspring varied mainly with litter size. However, how maternal allocation is shared between pups depended on climatic and social environments. In general, mothers tended to have litters of greater average mass and small variability in favourable social environments or when resources are abundant and lighter average pup mass but high variability in unfavourable social environments or when resources are scarce.
5. This variable allocation could correspond to dynamic bet-hedging such that mothers influence the variance of pup mass within the litter in response to poor current environmental conditions. Our analysis of first-year survival showed that females should maximize the body mass of their young whatever the conditions will be because pups of higher mass have higher survival, regardless of environmental conditions. When resources are scarce, this strategy might not be achievable for all pups so that mothers produced variable pups. In large litters, this strategy increased first-year survival.
6. Because pup variability affects parental fitness, differential allocation between pups of the same litter could have large consequences on fitness and thus on reproductive strategies of social species.

KEYWORDS
litter size, *Marmota marmota*, maternal allocation, maternal condition, maternal investment, pup mass, size-number trade-off

1 | INTRODUCTION

Individual fitness is the end result of series of survival and reproduction events (Fisher, 1930; McGraw & Caswell, 1996). At each reproductive event, how fast the descendants will spread into the population depends on both the number and the quality of offspring produced (Roff, 2002). However, when resources are limited, the quantity and the quality of offspring cannot be maximized at the same time and parents may trade-off the number of offspring produced against offspring mass/size (Lack, 1947; Smith & Fretwell, 1974). Environmental conditions influence the availability of resources and thus total parental reproductive allocation and the choice between strategies favouring the number or the quality of offspring (Albon et al., 1987; Kirst, 2011). When the future environmental conditions in which offspring will grow cannot be predicted, a preferred strategy might be to maximize a number of offspring of variable masses to maximize fitness both in favourable and unfavourable environments (Slatkin, 1974).

In variable environments, the long-term fitness, measured by the geometric mean fitness, is maximized when the variance in reproductive success between years is reduced (strategies of bet-hedging; Slatkin, 1974). To lower the variance of annual reproductive success, parents may either adopt a conservative strategy or a diversified strategy (Seger & Brockmann, 1987). In the case of a conservative strategy, the available energy would be equally split between offspring. In the case of a diversified strategy, the energy available would be unequally split between offspring to ensure the survival of at least some of them under poor environmental conditions (Marshall et al., 2008). Nevertheless, strategies combining conservative and diversified strategies depending on the available resources and the predictability of the future environment can also evolve (Olofsson et al., 2009).

After mating, once the number of offspring is determined, environmental conditions during gestation and lactation influence the amount of resources available. They can affect both parental condition (Fisher et al., 2011) and the chosen strategy of parental reproductive allocation (Olofsson et al., 2009) that can in return have an effect on mean offspring quality and their variability. Selection should favour parents that adapt plastically their allocation to future environmental conditions if they can be predicted from current environmental conditions (Parker & Begon, 1986). In the seed beetle *Stator limbatus*, mothers adjust egg size according to the host plant where they lay eggs (Fox et al., 1997). Climatic conditions during early offspring development can also directly influence offspring mean quality. For instance, cold temperature directly lowers mean offspring body mass as newborns spend more energy thermoregulating (Hull, 1973). Environmental variations can thus influence mean and variability of offspring quality indirectly through maternal condition and reproductive allocation or directly. But, these indirect and direct effects are rarely disentangled.

In cooperatively breeding species, offspring survival is influenced by parental care, by the climatic conditions during the harsh season but also by the social environment (number of helpers). Helpers provide alloparental care and enhance reproductive success of dominant individuals through direct provisioning of the young, predator avoidance or social thermoregulation during hibernation (Arnold, 1988; Hatchwell, 2009; Moran, 1984; Salomon & Lubin, 2007). While climatic conditions during the harsh season cannot always be predicted, social environment is often predictable (even with errors) and can be used by mothers to alter their allocation to offspring, as a result. In a cooperatively breeding cichlid *Neolamprologus pulcher*, and in sociable weavers *Philetairus socius*, mothers reduce egg size when the number of helpers is relatively high (Paquet et al., 2013; Taborsky et al., 2007). This pattern seems to hold in many cooperatively breeding non-mammals (Dixit et al., 2017). In cooperative mammals, if gestation and lactation are left mainly to the biological mother, helpers can nevertheless assume part of the parental care (Arnold, 1988; Moran, 1984). Thus, maternal allocation may be adjusted according to the presence or the absence of helpers. In the absence of helpers and with limited resources, mothers could thus adopt a dynamic bet-hedging strategy and produce heterogeneous litters. Small offspring being more likely to stay in the family as helpers than large offspring, it should be beneficial for mothers to produce some smaller offspring when there are few helpers in the family (Koenig & Walters, 2015; Russell & Lummaa, 2009). Thus, depending on the resources available and the social environment at each reproductive event, strategies of reproductive allocation combining maximization of offspring quality and offspring diversification within litter are expected to occur (Russell & Lummaa, 2009). But, empirical studies on parental allocation strategies showing how maternal allocation is divided among offspring are lacking in cooperative mammals (but see Russell et al., 2003).

Here, we investigated how mothers alter reproductive allocation according to climatic and social environment in a cooperative breeder living in a variable and unpredictable mountainous environment, the Alpine marmot *Marmota marmota* (Allainé et al., 2000; Cohas et al., 2006). We focused on the influence of climatic and social environment on total maternal reproductive allocation and on how this allocation is shared among offspring while accounting for the offspring size number trade-off. Litter size is poorly predictable but tends to increase with maternal mass and to decrease with harsh winters (Tafani et al., 2013). In this unpredictable environment, we expected climatic conditions to influence resources available to mothers for reproduction. Climatic conditions should thus influence maternal mass (a) as well as maternal allocation. When resources are limited during reproduction, a strategy of maternal allocation favouring the diversification of offspring (dynamic bet-hedging) should occur (b). Total maternal allocation should also decrease in favorable social environment (c) because helpers can share part of the costs associated with offspring production (Paquet et al., 2013; Russell et al., 2003). In the absence of helpers, mothers should produce offspring with variable masses (d). Finally, we tested if females that followed these expected strategies obtained fitness benefits. To do this, we investigated the influence of the mean and the variability of pup masses on first-year survival of pups under different environments.

2 | MATERIALS AND METHODS

2.1 | Studied species and population

The Alpine marmot is a hibernating ground-dwelling rodent (see Appendix S3, Figure S2 for life cycle). Socially monogamous and cooperatively breeding, it lives on a territory in a family group of 2–20 individuals, composed of a dominant pair (≥3 years old), sexually mature adult (≥3 years old), subadult (age 2–3 years) and yearling (age 1–2 years) subordinates, and juveniles (age 0–1 year; Allainé et al., 2000). Subordinates are typically relatives of the dominant individuals.

During the active period, from April to mid-October, all marmots of a given family spend part of the day and sleep during the night within the same burrow. From mid-October to the end of March, they hibernate together (Arnold, 1990b). Hibernation plays a central role in their life history. Fat accumulation during the active period and fat loss during hibernation (Körtner & Heldmaier, 1995) determine winter survival and subsequent reproductive success (Tafani et al., 2013). During hibernation, subordinate males increase first-year survival of pups through thermal benefits of synchronized arousal and active warming, whereas subordinate females do not participate in warming the burrow (Arnold, 1993; Ruf & Arnold, 2000). Only subordinate males are thus considered as helpers (Allainé et al., 2000; Arnold, 1993).

Shortly after the end of hibernation, dominant individuals monopolize reproduction and inhibit reproductive functions of sexually mature subordinates through aggressive behaviours (Arnold, 1990a, 1990b; Lardy et al., 2012). Dominant females give birth to a litter of 1–7 pups (median = 4) after a month of gestation and nurse them for another 40 days underground in the burrow. During this period, mothers make foraging trips outside the burrow to feed themselves and nurse the pups that do not leave the burrow until weaning. Due to suppression of reproductive functions, subordinate females cannot suckle the offspring of the dominant female. Pups first emerge above-ground at weaning (Psenner, 1957), which in our study population occurs between late June and mid-July (Allainé et al., 1998). A dominant pair can stay together for several years, the loss of dominance tenure being independent for the two sexes. When a new male or female dominant sets up in a territory, it kills the pups and mates with the remaining dominant in the following year.

The population of la Grande Sassière Nature Reserve in the French Alps (45°29′N, 6°59E, 2,300 m a.s.l.) was monitored from 1990 to 2016. Marmots were captured every year from May to mid-July using two-door live traps. Marmots were individually marked using ear tags and a transponder. Once captured, individuals were sexed and weighed. Social status (dominant or subordinate) was determined based on the development of the scrotal and teats for males and females, respectively. In addition, both hair samples and skin biopsies were collected on all trapped individuals for parentage analysis (Bichet et al., 2016). The annual number of helpers in each family was recorded by intensive observations of families (see Cohas et al. (2008) for details). The date of weaning and litter size at weaning (hereafter, litter size) in each family were determined from daily observations. Virtually, all emerging pups were either trapped with two-door live traps or caught by hand and weighed at weaning (within 3 days of emergence from the burrow).

2.2 | Relationship between pup mass, maternal allocation and maternal mass

According to Smith and Fretwell (1974), investment per offspring is proportional to the ratio of the total energy invested per parent over litter/clutch size. The total energy invested per parent is linked to the total reproductive allocation per female (R) and the investment per offspring can be approximated by offspring size or mass (Charnov & Morgan Ernest, 2006; Smith & Fretwell, 1974; Stearns, 1992). Thus, the offspring size number trade-off is often evaluated using the relationships between mean offspring individual mass ($\overline{M}_o$) and litter/clutch size (LS; Roff, 2002; Stearns, 1992).

$$\overline{M}_o \sim \frac{R}{LS}. \tag{1}$$

Some theoretical life-history models have predicted that R is proportional (β) to maternal mass (M_m) by an allometric coefficient ($b = 0.75$; Charnov, 2001).

$$\overline{M}_o \sim \frac{M_m^b \beta}{LS}, \tag{2}$$

Here, our first aim was to study the influence of environmental (climatic and social) conditions (E) on mean offspring mass. Because pups stay in the burrow during lactation, they are influenced mainly by maternal allocation but can also be influenced directly by environmental conditions such as ambient temperature. Thus, environmental conditions can directly influence offspring body mass (γ), the proportion of maternal mass allocated to offspring (β) and maternal mass (θ).

$$\begin{gathered} \overline{M}_o \sim \frac{M_m^b \beta_E}{LS} + \gamma_E, \\ M_m \sim \theta_E. \end{gathered} \tag{3}$$

In a litter, offspring can have variable individual body masses (M_o). Our second aim was to study how the maternal allocation was shared among the offspring of a litter. Thus, we studied the direct effects (η)

and indirect effects through maternal mass (θ) of environmental conditions on the variability of offspring masses within a litter. If we assumed that pup mass within a litter follow a normal distribution, the variability of individual masses can be measured by the standard deviation of pup mass within a litter (σ_o) and modelled as follows:

$$\begin{gathered} M_o \sim N\left(\overline{M}_o, \sigma_o\right), \\ \sigma_o = CV\overline{M}_o, \\ \log(CV) \sim \eta_{M_m} + \eta_E, \\ M_m \sim \theta_E. \end{gathered} \tag{4}$$

To avoid redundant effects of mean offspring mass on offspring mass variability, we directly modelled the coefficient of variation of offspring mass (CV) because contrary to the standard deviation, the coefficient of variation is not influenced by mean mass.

2.3 | Climatic and social variables

We tested the indirect influence of different climatic and social variables (see Figure S2) on pup mass through maternal body mass at parturition (θ). We also tested their effect on the proportion of maternal mass allocated to offspring (β) and how this allocation is shared among pups (η), and their direct effect on mean pup mass (γ). Finally, we analysed how environment influenced first-year survival.

Maternal body mass at a given reproductive event may depend on the environmental conditions at three independent periods of the year:

- Previous summer when marmots build fat reserves (July–August). Resource availability and quality in the previous summer were approached using the July to August Bagnouls–Gaussen aridity index (BGI, total daily rainfall minus twice the mean ambient temperature). BGI is an index of drought commonly used in Alpine ecosystems (Canale et al., 2016; Garel et al., 2004; Rézouki et al., 2016). Droughts often limit primary production during summer in these areas. Low BGI values indicate hot and dry summers with restricted food quality.
- Previous winter when marmots hibernate and live on their fat reserves (December–March). A higher investment in thermoregulation during hibernation when snow cover is thin and temperature is low may reduce maternal body mass (Tafani et al., 2013). Winter harshness has been estimated using the residuals of an orthogonal regression between annual winter (from December 1st to March 31st) temperature and snow precipitation and included 28 observation points from 1989 to 2016 (Rézouki et al., 2016).
- Early spring (last 2 weeks of April) determines the availability of resources during gestation and lactation. The availability of resources during gestation and lactation has been measured using the normalized difference vegetation index (NDVI). We used the measure of NDVI collected in the last 2 weeks of April and did not transform this measure. In spring, the NDVI informs about the green coloration of the landscape. High NDVI values indicate an early snow melt and early access to vegetation for mothers (Pettorelli et al., 2007).

Thus, we tested the effects of BGI, winter harshness and NDVI on maternal mass. The three climatic variables were not correlated (the largest correlation occurs between BGI and NDVI, $R = 0.19$, $p = 0.35$; Rézouki et al., 2016) and were included together in the complete model. Daily ambient temperature, precipitation and snow depth were recorded from Meteo France weather stations situated within 3 km from the study site, respectively: Val d'Isère (1,840 m), Tignes Brevières (1,560 m) and Tignes (2,080 m). The NDVI provided by the National Oceanic and Atmospheric Administration was obtained from the AVHRR dataset (1990–2000) within an 8 × 8 km pixel area and the MODIS dataset (2001–2016) with a resolution of 1 × 1 km pixel centered on the study site and one measure every 2 weeks (Rézouki et al., 2016).

Strategy of maternal reproductive allocation (proportion of maternal mass allocated to offspring and how this allocation is shared among offspring) should vary with maternal mass and available environmental resources. Environmental resources available during gestation and lactation were measured by the NDVI (same variable as presented above) since the onset of vegetation growth conditions the adequation between vegetation quality and quantity, and needs of mothers. We also included the effect of spring temperature (mean of daily temperature from March 1st to May 31st) that influences vegetation growth but also individual thermoregulation when temperature is low.

Mean pup mass should be influenced by total maternal reproductive allocation but also directly by the climatic environment pups face once born. Although altricial marmot pups stay in the burrow during early development, they have only little energy to invest in thermoregulation. Their thermal environment should then strongly condition their growth while vegetation should not directly affect mean pup mass. Indeed, pups were weighed at their first emergence from the burrow before foraging by themselves. We thus tested for the direct effect of spring temperature (as described above) on mean pup mass.

First-year survival decreases with the harshness of the winter in the Alpine marmot (Rézouki et al., 2016). Thus, we included the influence of the winter harshness (same variable as presented above) but measured in the year following the production of the litter on pup first-year survival.

For the social environment, we tested the influence of the number of helpers present in the family at the end of hibernation preceding the litter production (number of helpers) on maternal mass, maternal reproductive allocation (total and among pup) and direct effect on pup mass. We tested the effect of the number of helpers in the family at the end of the hibernation following the litter production (number of helpers at $t + 1$) on first-year survival. The influence of helpers has been shown to be nonlinear on pup survival (Allainé et al., 2000; Allainé & Theuriau, 2004) and on dominant lifetime reproductive success (Lardy et al., 2015) with a threshold effect from two helpers. This variable was thus included as a continuous variable equal to 0, 1 and 2 helpers if 2 or more helpers were present in the family (Berger et al., 2018).

2.4 | Analysis

In this section, we present the four models that have been implemented (Table 1). We used three models to conduct a path analysis (Mysterud et al., 2008; Plard et al., 2015; Shipley, 2009) in a hierarchical Bayesian framework to investigate the direct effects and indirect effects of climate and social environment through maternal mass, on mean and variability of pup masses within a litter (see Appendix S4). We first tested for indirect effects given by the influence of environmental variables on adjusted maternal body mass at parturition. Then, to test for the direct influence of environmental variables on total maternal reproductive allocation, we used the mean pup mass at weaning corrected by litter size. Third, we tested for the direct effects of environmental variables on the variability in allocation among pups using the coefficient of variation of pup mass at weaning within each litter. For these analyses, we used annual data on families that had a litter, for which the mother had been captured and weighed during the reproductive season and for which all emerged pups were weighed within 3 days of emergence from the burrow. In total, we gathered complete data for 499 pups from 138 litters, 64 mothers and 22 territories. The data are available here: https://doi.org/10.5061/dryad.fqz612jr9. Finally, we used pup survival to 1-year old to test if the strategy of the mother can be rewarding in terms of maternal fitness. Code used for the four models can be found in the Supporting Information (Appendix S1).

2.4.1 | Effects of climate and number of helpers on adjusted maternal mass

We chose to use maternal body mass instead of an index of body condition as their use remains hotly debated (Green, 2001; Peig & Green, 2010). Body mass alone provides a better indicator of the total energy available than an unverified size-adjusted index (Schamber et al., 2009). Maternal body mass at the end of hibernation was not available because the study site is not accessible when marmots emerge in early April. Thus, we used adjusted maternal body masses to the date of parturition for the analyses. Maternal masses were adjusted for date of capture and reproductive status (Tafani et al., 2013). See Appendix S2 for details about maternal mass adjustment. Adjusted maternal mass was modelled using a Gaussian distribution and a linear mixed model. We used a larger dataset including also the mothers for which pups have been captured after the third day of emergence ($N = 205$ of 74 mothers). We investigated the influence of the BGI, the harshness of the winter, the NDVI and the number of helpers on adjusted maternal body mass. Maternal identity and territory (22 different territories) were included as random effects to correct for the repeated measurements of same mothers and the variable quality of territories, respectively. We simplified this model and selected the variables influencing adjusted maternal body mass by comparing information criteria between models including all possible combinations of variables (see model selection).

2.4.2 | Direct and indirect effects of climate and number of helpers on mean pup mass

Mean pup mass was estimated from raw data including individual pup mass at emergence from each litter (138 litters and 499 pups from 64 mothers). It was then modelled with a Gaussian distribution and a linear mixed model derived from Equation (3). In this model, we investigated the direct effect through the proportion of maternal mass allocated to offspring (β), as well as the direct effect (γ) of environmental variables on mean pup mass. As indirect effects through maternal mass (θ) on mean pup mass, we included the environmental variables that were selected in the model for adjusted maternal mass (NDVI and number of helpers, see results). We tested for the effect of NDVI, spring temperature and the number of helpers on the proportion of maternal mass allocated to offspring (β). Because NDVI and spring temperature were partially correlated ($R = 0.67$, $p < 0.001$), we did not include both variables in the same model but tested their effects in

TABLE 1 Description of the four models used. M_m, maternal mass; $\overline{M}_o$, mean pup mass; M_o, individual pup mass; CV_o, coefficient of variation of pup mass; *LS*, litter size; *b*, allometric coefficient; *NY*, number of pups per litter surviving to 1-year old; *p*, first-year survival probability; *BGI*, Bagnouls–Gaussen aridity Index; *Win*, the harshness of the winter; *Tspr*, spring temperature; *Help*, the number of helpers in the family; Win_{t+1}, the harshness of the winter following pup birth; $Help_{t+1}$, the number of helpers in the family during the winter following pup birth; *DOM*, change in dominance; ϵ_m and ϵ_t, random effects linked to maternal identity and territory; σ_{rm} and σ_{ro}, residual variance for maternal mass and mean pup mass, respectively

Variable analysed	Model	Explanatory variables to be selected	Correcting variables	Indirect effects through M_m	Sample size
Maternal mass	$M_m \sim N(\mu_m, \sigma_{rm})$	$\mu_m \sim BGI + Win + NDVI + Help$	$\epsilon_m + \epsilon_t$		205 maternal masses
Mean pup mass	$\overline{M}_o \sim N\left(\frac{M_m^b \beta}{LS} + \gamma, \sigma_{ro}\right)$	$\text{logit}(\beta) \sim (Tspr \mid NDVI) + Help + LS$ $\gamma \sim Tsp + Help$		$NDVI + Help + \epsilon_m + \epsilon_t$	138 litters
CV of pup mass	$M_o \sim N\left(\overline{M}_o, CV_o \overline{M}_o\right)$	$\log(CV) \sim M_m + (Tspr \mid NDVI) + Help$	*LS*	$NDVI + Help + \epsilon_m + \epsilon_t$	490 pups
Pup survival	$NY \sim B(p, LS)$	$\text{logit}(p) \sim \left(\overline{M}_o + CV_o\right) \times LS + \left(\overline{M}_o + CV_o\right) \times Win_{t+1} \times Help_{t+1}$	$Win_{t+1} \times Help_{t+1} + DOM + \epsilon_m + \epsilon_t$		129 litters

separate models (specified using | in Equations (5) and (6)) to keep only the variable with the largest effect on maternal allocation. We also included the effect of litter size (*LS*) on β to test whether the proportion of maternal mass allocated to offspring increased with the number of pups produced. We tested the direct effects (γ) of spring temperature and the number of helpers on mean pup mass. We selected the best model among variables influencing β and γ.

$$\begin{gathered}\overline{M}_o = \frac{R}{LS} + \gamma_T Tspr + \gamma_H Help + \epsilon_{ro},\\ R = M_m^b i\,\mathrm{logit}\left(\alpha_R + \left(\beta_N NDVI | \beta_T Tspr\right) + \beta_H Help + \beta_L LS\right),\\ M_m = \alpha_m + \theta_N \times NDVI + \theta_H \times Help + \epsilon_m + \epsilon_t + \epsilon_{rm},\end{gathered} \tag{5}$$

where α_R and α_m are parameters corresponding to intercepts, and ϵ_{ro} and ϵ_{rm} are the residual errors of the gaussian distribution of mean pup mass and adjusted maternal mass, respectively. ϵ_m and ϵ_t are random effects linked to maternal identity and territory.

2.4.3 | Direct and indirect effects of climate and number of helpers on pup mass variability

This analysis was done at the pup level ($N = 490$ pups from 129 litters and 63 females). We discarded litters of one pup ($N = 9$ litters) for this analysis. Following Equation (4), individual pup mass within each litter was modelled using a normal density probability function with a mean equal to the observed mean pup mass in each litter (directly estimated from raw data) and a standard deviation equal to the product of the coefficient of variation of pup mass and observed mean pup mass. With this model, we investigated the direct effect of climate and social environment (η) on the variability of pup mass. As indirect effects through maternal mass (θ) on the variability of pup mass, we included the environmental variables that were selected in the model for adjusted maternal mass (NDVI and number of helpers, see Section 3). We tested the effects (η) of maternal mass, NDVI, spring temperature and the number of helpers on pup mass variability. Because estimation of variability can vary in relation with litter size, we included litter size in this model but did not include it among the variables to be selected. We selected the best model among variables influencing η:

$$\begin{gathered}M_o \sim N\left(\overline{M}_o, CV\overline{M}_o\right),\\ \log(CV) = \alpha_{CV} + \eta_m M_m + \left(\eta_N NDVI | \eta_T Tspr\right) + \eta_H Help + b_L LS,\\ M_m = \alpha_m + \theta_N \times NDVI + \theta_H \times Help + \epsilon_m + \epsilon_t + \epsilon_{rm},\end{gathered} \tag{6}$$

where α_{CV} is a fixed parameter corresponding to an intercept and b_L is the slope correcting for litter size.

2.4.4 | Influence of mean pup mass and variability on first-year survival

Maternal fitness strongly depends on pup first-year survival as the survival to the second and third years is relatively high in this population (Lardy et al., 2015; Rézouki et al., 2016). We modelled pup survival using the number of surviving pups to 1-year old as the response variable and a binomial density probability function of parameters *n* equal to litter size and *p* equal to the probability of survival from emergence to 1-year old ($N = 129$ litters and 490 pups). To understand in which environments it is more rewarding to allocate in mean pup mass, in pup variability or in litter size, we tested the influence on survival probability (logit(*p*)) of two interactions of order 2 and two interactions of order 3. The two interactions of order 2 included the interactions between mean pup mass and litter size, and between coefficient of variation of pup mass and litter size. Mean pup mass and coefficient of variation of pup mass were estimated from raw data, being less precise for small litters. The two interactions of order 3 included the interaction between mean pup mass, winter harshness and number of helpers and the interaction between coefficient of variation of pup mass, winter harshness and the number of helpers. Winter harshness and the number of helpers were measured during the winter following birth. We further included an interaction between winter harshness and the number of helpers (Rézouki et al., 2016) and change of one of the dominant individual since when a dominant individual dies or is evicted by a competitor, the whole litter dies though infanticide. These last three variables were not included among the variables to be selected and were present in all models. Maternal identity and territory were included as random effects.

2.4.5 | Model parameterization and selection

All models were run in R (R Core Team, 2014) using a Bayesian framework and NIMBLE (NIMBLE Development Team, 2016). We defined normal distributions with mean 0 and variance 10^6 for the regression slopes and student distributions with parameters 0, 0.001 and 1 for the standard deviations as vague priors (Kéry & Schaub, 2012). We defined a uniform distribution over (0, 10) for the allometric coefficient *b*. We generated three chains of length 150,000 used the first 75,000 as burn-in and saved a value every 50 iterations. Combining all chains, we had 4,500 iterations in the posterior distributions. The convergence of chains was assessed using the Gelman and Rubin convergence diagnostic ($R < 1.01$, Gelman & Rubin, 1992). The autocorrelation of chains was assessed and inferior to 0.1 for all intercepts and slopes.

We selected the model that best explained each response variable using the Watanabe Akaike Information Criterion (wAIC, Hooten & Hobbs, 2015; Watanabe, 2013). Following the principle of parsimony, we selected the model with the smallest number of parameters among models with a wAIC smaller than the lowest wAIC + 2, and then compared the effect sizes of each of the selected explanatory variables.

When the response variable was modelled with a Gaussian distribution including a residual variance (maternal mass and mean pup mass), we estimated the proportion of variance explained by the model using $R^2 = 1 - \mathrm{var}(\epsilon_r)/\mathrm{var}(Y)$, where $\mathrm{var}(\epsilon_r)$ is the residual variance and var(*Y*) is the variance of the response variable (Gelman & Pardoe, 2006; Nakagawa & Schielzeth, 2013). We also estimated the R^2 associated with each explanatory variable by removing successively the different explanatory variables. The difference between two successive R^2 corresponded to the R^2 of the excluded explanatory variable. The order of exclusion had no influence. Finally, we estimated R^2 for models including only the random effects to estimate the proportion of the variance explained by random effects.

3 | RESULTS

3.1 | Maternal mass

The selected model of adjusted maternal mass (Tables S2 and S3) explained 61% of its variability. In accordance with our first prediction, the selected model included the effect of NDVI. It further included the number of helpers, but no variable linked to the previous summer and winter environment. The mass of the mothers increased from 3,539[3,452:3,625]g (here and below posterior mean values are given with 95% credible intervals in square brackets) in years when resources were accessible late (NDVI at the 10th percentile of its distribution) to 3,745[3,661:3,827]g in years when resources were accessible early (NDVI at the 90th percentile of its distribution) in the season (R^2 = 11%, ΔwAIC with the nested model excluding NDVI = 55.60, Figure 1a). Maternal mass also decreased with the number of helpers present in the family (R^2 = 0.8%, ΔwAIC with the nested model excluding the number of helpers = 8.73) from 3,686[3,602:3,767]g to 3,574[3,467:3,681] g when no helper versus more than one helper was present in the family (Figure 1b).

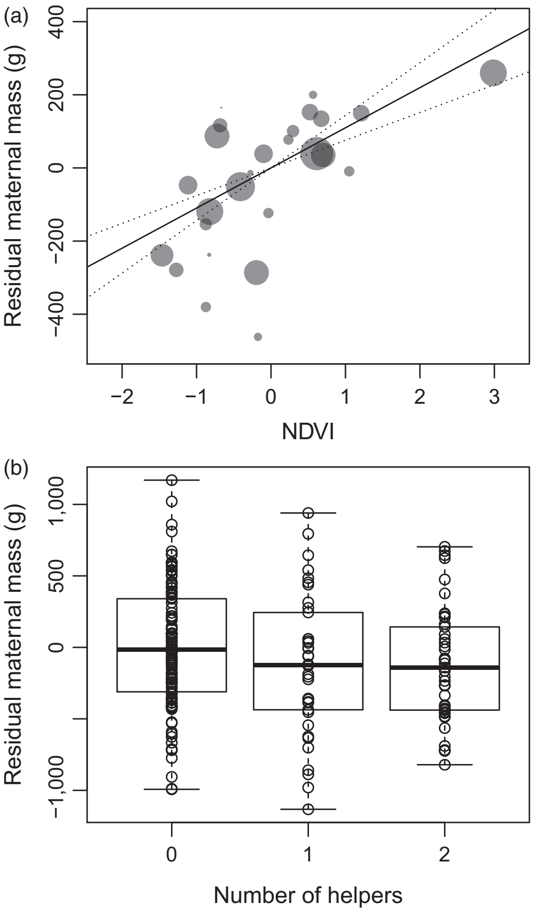

FIGURE 1 Influence of the normalized difference vegetation index (NDVI) and the number of helpers on adjusted maternal mass (g). (a) Mean (solid line) and 95% credible intervals (dotted lines) of the predicted relationship from the selected model are presented. Observed data are shown with points proportional to the number of females they represent. (b) Boxplots representing the distribution of maternal mass according to the number of helpers present in the family with points showing individual observed data. The number of helpers was included as a continuous variable in the model equalled to 0, 1 and 2 helpers if 2 or more helpers were present in the family. In this plot, we reported residual maternal mass controlling for the effect of the number of helpers (a) or NDVI (b)

3.2 | Mean pup mass at weaning

The selected model for mean pup mass explained 30% of its variation (Tables S4 and S5) and included the effect of litter size and spring temperature on the proportion of maternal mass allocated to offspring and the direct effect of spring temperature on pup mass. In addition, it included the indirect effect of NDVI and number of helpers through maternal mass. Contrary to our hypothesis (iii), the effect of social environment on the proportion of maternal mass allocated to offspring was not retained in the selected model. The proportion of maternal mass allocated to offspring varied with litter size which explained 19% of the variation in mean pup mass (ΔwAIC with the nested model excluding litter size = 61.52). Mothers allocated more in large than in small litters (total average litter mass of large [>4 pups] and median [3–4 pups] litters was 1,827[1,675:2,015]g and 1,394[1,335:1,450]g, respectively). Thus, the mean mass of the pups from large litters (305[279–336]g) decreased slightly compared to the mean mass of pups from litters of median size (398[382–414]g, Figure 2a). Spring temperature explained 11% of the variation in mean pup mass and influenced pup mass both directly and through the proportion of maternal mass allocated to offspring (ΔwAIC excluding the direct effect on pup mass of *Tspr* = 32.61 and excluding the effect through maternal allocation = 38.43), although these two effects were opposed. MCMC chains of these two effects were correlated (−0.77[−0.79:−0.75]). Nevertheless, the direct effect of spring temperature on pup mass was still positive when it was included without its effect on the proportion of maternal mass allocated to offspring (β_{Tspr} = 4.57[−10.07:18.45]). When including only the effect of spring temperature on the proportion of maternal mass allocated to offspring, its effect was still negative and its 95% credible interval excluded 0 (γ_{Tspr} = −0.09 [−0.18:−0.01]). The resulting effect of spring temperature on mean pup mass was positive (Figure 2b) as mean pup mass increased by 26[23:31]g, on average when spring temperature increased by 2°C (difference in temperature between cold and warm springs corresponding to spring temperature at the 10th and 90th percentiles of the distribution).

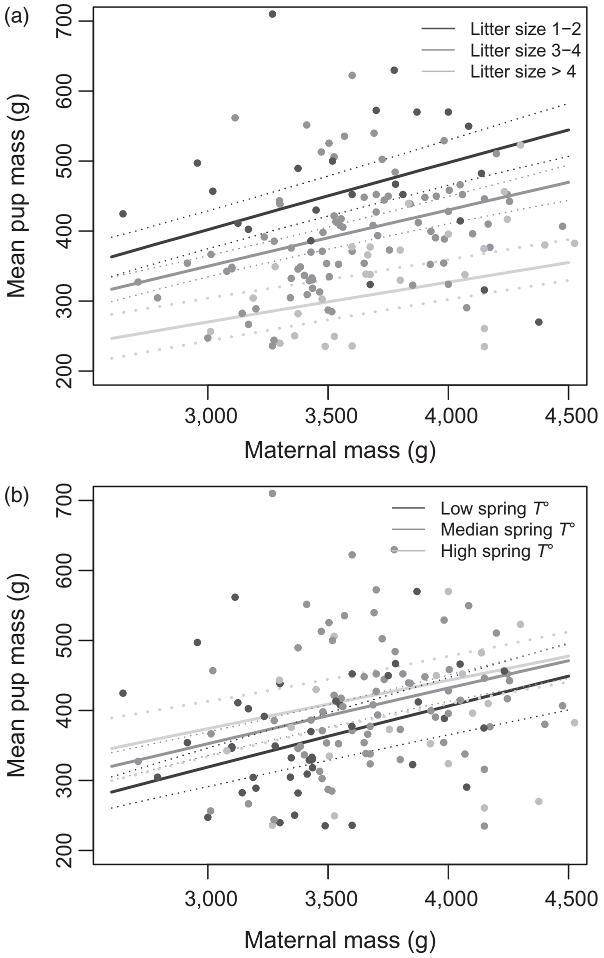

FIGURE 2 Influence of the proportion of maternal mass allocated to offspring on mean pup mass (g), in relation to (a) litter size and (b) spring temperature. Mean (solid line) and 95% credible intervals (dotted lines) of the predicted relationships from the selected model are presented. Points show observed data for each litter

3.3 | Coefficient of variation of pup mass at weaning

The selected model for the coefficient of variation of pup mass included maternal mass (ΔwAIC with the nested model excluding maternal body mass = 33.68), effects of spring temperature (ΔwAIC = 5.95) and number of helpers (ΔwAIC = 2.02, Tables S6 and S7, Figure 3). In addition, it included the indirect effect of NDVI and number of helpers through maternal mass. As expected with our hypothesis (ii), the variability of pup mass within a litter was higher in unfavourable environments where resources were scarce (Figure 3). It increased by 16.1[15.8:16.3]% (percentages here and below give the percent of increase in the coefficient of variation of pup mass) between mother of heavy and light masses (90th and 10th percentiles of the maternal mass distribution) and by 6.5[6.2:6.8]% between warm and cold springs (90th and 10th percentiles of the spring temperature distribution). As expected under our hypothesis (iv), the variability of pup masses increased in absence of helper in the family (by 5.8[3.1:8.1]% between families with more than one helper and no helper).

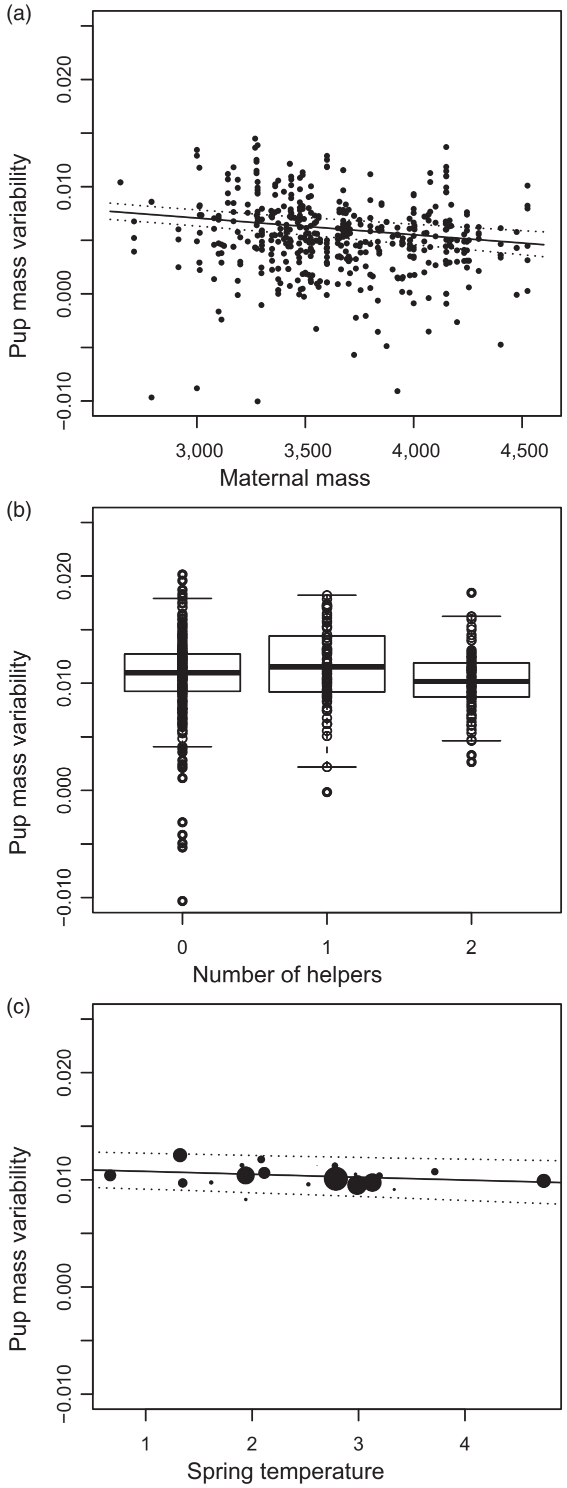

FIGURE 3 Influence of (a) maternal mass, (b) the number of helpers and (c) spring temperature on the coefficient of variation of pup mass in each litter. Mean (solid lines) and 95% credible intervals (dotted lines) of the predicted effects are presented. Points show the observed differences between pup individual mass (M_o) and mean litter mass ($\overline{M}_o$) divided by mean litter mass $\left(\frac{M_o-\overline{M}_o}{\overline{M}_o}\right)$. (a) Points show individual data for each pup. (b) Boxplots represent the distribution of pup mass variability according to the numbers of helpers present in the family with points showing individual observed data. (c) Observed data are shown with points proportional to the annual number of pups they represent

3.4 | First-year survival

The selected model for first-year survival included two interactions (Tables S8 and S9): between mean pup mass and the winter index (ΔwAIC with the nested model excluding the interaction = 21.25) and between the coefficient of variation of pup mass and litter size (ΔwAIC with the nested model excluding the interaction = 4.72). First-year survival increased with mean pup mass, particularly in mild winters (Figure 4a). If we separate the observed winter harshness values between two groups of same size, in the group corresponding to the harsher winters, first-year survival increased only from 0.33[0.18:0.51] to 0.51[0.31:0.69], on average between litters composed of light and heavy pups (10th and 90th percentiles of mean pup mass distribution), respectively. However, in mild winters, first-year survival increased from 0.37[0.20:0.57] to 0.87[0.73:0.95], on average between litters composed of light and heavy pups. First-year survival increased also with the coefficient of variation in large litters (>4 pups). In these large litters, first-year survival increased from 0.38[0.23:0.55] to 0.66[0.46:0.82] between pups of similar and variable masses (10th and 90th percentiles of the CV distribution), respectively (Figure 4b).

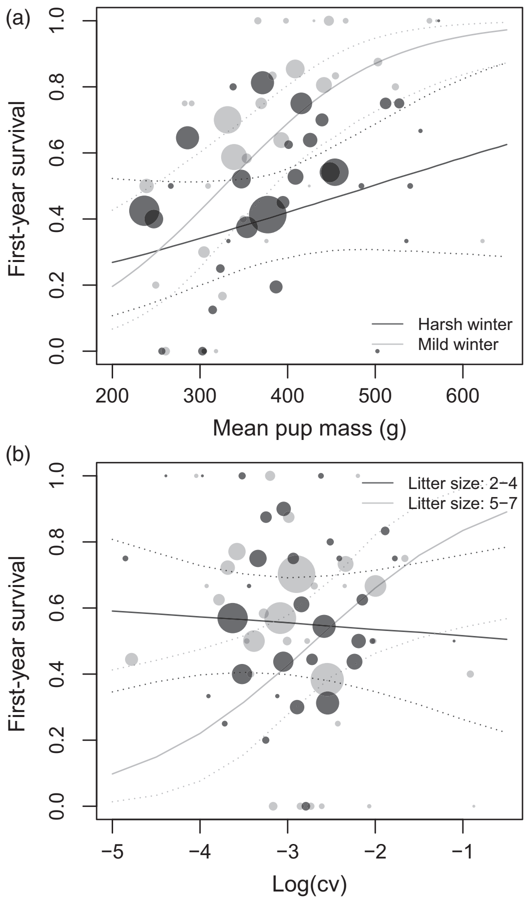

FIGURE 4 Influence of (a) the interaction between mean pup mass and the harshness of the winter, and of (b) the interaction between coefficient of variation of pup mass and litter size on first-year survival. Mean (solid lines) and 95% credible intervals (dotted lines) of the predicted relationships from the selected model are presented. Observed data are shown with points proportional to the number of litters they represent. Harsh and mild winters correspond to the average winter harshness values if we separate the observed winter harshness values between two groups of same size

4 | DISCUSSION

Maternal mass, and so the resources available for reproduction, was directly linked to the amount of resources accessible in spring measured by the NDVI. The previous summer and winter environment had no detectable effect on maternal mass. Thus, dominant females seem to act as income breeders and to use resources immediately available for reproduction. The proportion of maternal mass allocated to offspring increased with litter size such that difference in mean pup mass is buffered between median and large litters. Spring temperature influenced positively pup mass but negatively the proportion of maternal mass allocated to offspring. The social environment had no detectable effects on the proportion of maternal mass allocated to offspring. However, how this allocation is shared among the different pups of a litter depended on climatic and social environments. As predicted, pup masses were heterogeneous in the absence of helpers. Pups were also heterogeneous for mothers with low body mass or facing an adverse spring environment, characterized by cold temperature. First-year survival was directly correlated with mean pup mass, particularly in mild winters. First-year survival tended also to increase with pup mass variability in litters of more than four pups.

4.1 | Mothers seem to act as income breeders

The quantity and quality of resources available in the weeks following the end of hibernation were essential for dominant females to wean heavy pups. Adjusted maternal mass at parturition directly varied with resources available in spring. The match between quality food and lactation is crucial for fast early growth and weaning success in most seasonal iteroparous breeders. This is particularly true for species living in an environment where resources are unpredictable such as in mountains (Post et al., 2001; Visser & Both, 2005). Our results showed that in addition to being influenced by spring condition, adjusted maternal mass was negatively affected by the number of helpers in the family. In early spring, when resources are restricted, helpers may act as competitors for food (Koenig et al., 1998; Ulbrich & Henschel, 1999). Keeping helpers in family groups is known to be costly for males due to increase energy expenditures to secure dominance (Komdeur, 2001; Lardy et al., 2012; Mitchell et al., 2009) but our results showed that it can also be costly for dominant females in term of a decrease in maternal mass at parturition.

4.2 | Females increase allocation in large litters to buffer a quantity–quality trade-off

The proportion of maternal mass allocated to the pups mainly increased with litter size. Moreover, litter size is influenced by maternal mass, confirming that maternal condition constraints litter size

(Tafani et al., 2013). This suggests that although the number of pups produced does not perfectly fit to the maximum number of pups a mother is able to wean, mothers regulate their allocation (Lack, 1947). A first explanation could be that, rodents having evolved to raise large litters (Sibly & Brown, 2009), mothers do not allocate as much as they could in small litters because one or two pups may not be able to assimilate as much milk as their mother could produce. Another likely explanation is that mothers allocate more in large than in median litters to secure the survival of all pups that have been produced.

Our results showed that having a litter of greater average mass is advantageous because first-year survival was directly correlated with mean pup mass. While we expected the effect of pup mass on first-year survival to be higher in harsh than in mild winters, we observed the opposite. In these extreme environments, harsh winters may be too demanding even for large pups to reach high survival while they manage to do it in mild winters. Females that maximize the body mass of their young in large litters manage to reach a higher first-year survival than expected for large litters of average mass. As a result, the trade-off between pup first-year survival and litter size is reduced. Litter size should be canalized in long-lived species (Gaillard & Yoccoz, 2003) because its variability would greatly influence fitness in small mammals (Festa-Bianchet & King, 1991). In agreement with this hypothesis, parental fitness depends mainly on variability in first-year survival and to a lesser extent on litter size in Alpine marmots (Lardy et al., 2015).

4.3 | Influence of climatic environment on maternal reproductive allocation strategy

We found that the mean pup mass that was measured at the end of weaning varied directly with spring temperature. Before weaning, even if marmot pups are altricial and confined within the burrow, other factors than maternal allocation can nevertheless influence mass at weaning. During early development, warm temperatures influence metabolism and growth because pups have lower energy to invest in thermoregulation (Hull, 1973; Rödel et al., 2009). Our results suggested that mothers reduced partially their total reproductive allocation in warmer springs. This maternal strategy may allow producing large enough offspring in warm springs while allocating more energy to other costly activities such as territory defence.

In warm springs, mothers produce heavy litters while in cold spring mother produced light litters but with higher variability between pups. Spring condition may reflect both resource availability and thermal condition. In cold spring, few resources may be available and mothers have to spend more energy in thermoregulating. In these unfavourable environments where resources are limited, also measured by low female body mass, mothers seemed to favour the survival of at least some pups by having some larger and some smaller pups within a light litter. This variable allocation could result from the constraints linked to poor environmental conditions preventing mother to allocate equally in all pups. Alternatively, this variable allocation could correspond to a dynamic bet-hedging strategy (Crean & Marshall, 2009) such that mothers influence the variance of pup mass in response to poor current environmental conditions. At least some pups may attain a sufficient body mass to survive the following winter. In unpredictable climatic environments, the observed strategy is expected to reduce the variance of annual reproductive success and to increase maternal fitness (Slatkin, 1974). Our results on first-year survival showed that increasing the variability of pup mass seems to be rewarding in terms of fitness for large litters.

4.4 | Influence of social environment on maternal reproductive allocation strategy

Social environment had a weak indirect effect on mean pup mass through its negative effect on maternal mass. Our result suggested that the main effect of helpers, burrow thermoregulation during winter, did not hold in spring when they probably spend most of their time feeding themselves outside the burrow. In accordance with another mammal where only the dominant females feed their pups, weight at weaning was not influenced by the number of helpers in the meerkat *Suricata suricatta* (Russell et al., 2003). However, in other social species where subordinates help in provisioning food to offspring before weaning, maternal allocation decreased with the number of helpers (Dixit et al., 2017; Paquet et al., 2013).

However, our results suggested that how the total reproductive allocation was distributed among the pups of a litter depended on the social environment. The variability among pups is rarely studied in social mammals or birds (Russell & Lummaa, 2009). However, in a cooperative breeder such as the Alpine marmot, strategies increasing the variation of pup masses should have evolved to retain helpers in the family while decreasing the competition between them (Russell & Lummaa, 2009). The probability to become dominant varies with mass in Alpine marmot. Thus, light pups would stay helpers for a longer time than large pups. In accordance with our prediction (iv), our results showed that pups were more variable in families with no helper.

5 | CONCLUSIONS

To sum up, mothers tended to have litters with high average mass and small variability in favourable environments or low mean mass but high variability in unfavourable environments. Although we searched for effects on first-year survival, looking at the whole picture would involve investigating the influence of pup mass variability on the inclusive fitness of parents (Benton & Grant, 2000; Hamilton, 1964; Saether & Engen, 2015). Dominant individuals' inclusive fitness will depend on annual reproductive success but will also result from both direct fitness of subordinates that reach dominance and indirect fitness of subordinates that remain helpers. Since effects of pup variability on parental fitness may increase as pups get older, differential allocation between pups of the same litter may have large consequences on fitness and thus on reproductive strategies of social species. Because such strategies are strongly theoretically expected (Philippi & Seger, 1989; Russell & Lummaa, 2009) but few empirical tests had been conducted (but see in a social spider; Grinsted et al., 2014), we encourage detailed analysis of litter variability to improve our understanding of the evolution of parental reproductive strategies in social species.

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AUTHORS' CONTRIBUTIONS

F.P. and A.C. designed the study; A.C. supervised the study. A.C. and B.C.-c. collected the data; F.P. and B.C.-c. carried out the analysis; F.P. wrote the paper with contributions from all authors. All authors gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.fqz612jr9 (Plard et al., 2020).

ORCID

Floriane Plard https://orcid.org/0000-0002-8509-723X
Benoit Chamiot-clerc https://orcid.org/0000-0001-9619-5313

REFERENCES

Albon, S. D., Clutton-Brock, T. H., & Guinness, F. E. (1987). Early development and population dynamics in red deer. II. Density-independent effects and cohort variation. *Journal of Animal Ecology*, *56*, 69–81.

Allainé, D., Brondex, F., Graziani, L., Coulon, J., & Till-Bottraud, I. (2000). Male-biased sex ratio in litters of Alpine marmots supports the helper repayment hypothesis. *Behavioral Ecology*, *11*, 507–514.

Allainé, D., Graziani, L., & Coulon, J. (1998). Postweaning mass gain in juvenile Alpine marmots *Marmota marmota*. *Oecologia*, *113*, 370–376.

Allainé, D., & Theuriau, F. (2004). Is there an optimal number of helpers in Alpine marmot family groups? *Behavioral Ecology*, *15*, 916–924.

Arnold, W. (1988). Social thermoregulation during hibernation in Alpine marmots (*Marmota marmota*). *Journal of Comparative Physiology B*, *158*, 151–156.

Arnold, W. (1990a). The evolution of marmot sociality: I. Why disperse late? *Behavioral Ecology and Sociobiology*, *27*, 229–237.

Arnold, W. (1990b). The evolution of marmot sociality: II. Costs and benefits of joint hibernation. *Behavioral Ecology and Sociobiology*, *27*, 239–246.

Arnold, W. (1993). Social evolution in marmots and the adaptive value of joint hibernation. *Verhandlungen der Deutschen Zoologischen Gesellschaft*, *86*, 79–93.

Benton, T., & Grant, A. (2000). Evolutionary fitness in ecology: Comparing measures of fitness in stochastic, density-dependent environments. *Evolutionary Ecology Research*, *2*, 769–789. ISSN 1522–0613.

Berger, V., Lemaître, J. F., Allainé, D., Gaillard, J. M., & Cohas, A. (2018). Early and adult social environments shape sex-specific actuarial senescence patterns in acooperative breeder. *The American Naturalist*, *192*, 525–536.

Bichet, C., Allainé, D., Sauzet, S., & Cohas, A. (2016). Faithful or not: Direct and indirect effects of climate on extra-pair paternities in a population of Alpine marmots. *Proceedings of the Royal Society B: Biological Sciences*, *283*, 20162240.

Canale, C. I., Ozgul, A., Allainé, D., & Cohas, A. (2016). Differential plasticity of size and mass to environmental change in a hibernating mammal. *Global Change Biology*, *22*, 3286–3303.

Charnov, E. (2001). Evolution of mammal life histories. *Evolutionary Ecology Research*, *3*, 521–535.

Charnov, E. L., & Morgan Ernest, S. K. (2006). The offspring-size/clutch-size trade-off in mammals. *The American Naturalist*, *167*, 578–582.

Cohas, A., Yoccoz, N. G., Bonenfant, C., Goossens, B., Genton, C., Galan, M., Kempenaers, B., & Allainé, D. (2008). The genetic similarity between pair members influences the frequency of extrapair paternity in Alpine marmots. *Animal Behavior*, *76*, 87–95.

Cohas, A., Yoccoz, N. G., Da Silva, A., Goossens, B., & Allainé, D. (2006). Extra-pair paternity in the monogamous alpine marmot (*Marmota marmota*): The roles of social setting and female mate choice. *Behavioral Ecology and Sociobiology*, *55*, 597–605.

Crean, A. J., & Marshall, D. J. (2009). Coping with environmental uncertainty: Dynamic bet hedging as a maternal effect. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*, 1087–1096.

Dixit, T., English, S., & Lukas, D. (2017). The relationship between egg size and helper number in cooperative breeders: A meta-analysis across species. *PeerJ*, *5*, e4028.

Festa-Bianchet, M., & King, W. J. (1991). Effects of litter size and population dynamics on juvenile and maternal survival in Columbian ground squirrels. *Journal of Animal Ecology*, *60*, 1077–1090.

Fisher, J. T., Anholt, B., & Volpe, J. P. (2011). Body mass explains characteristic scales of habitat selection in terrestrial mammals. *Ecology and Evolution*, *1*, 517–528.

Fisher, R. A. (1930). *The genetical theory of natural selection*. The Clarendon Press.

Fox, C. W., Thakar, M. S., & Mousseau, T. A. (1997). Egg size plasticity in a seed beetle: An adaptive maternal effect. *The American Naturalist*, *149*, 149–163.

Gaillard, J. M., & Yoccoz, N. G. (2003). Temporal variation in survival of mammals: A case of environmental canalization? *Ecology*, *84*, 3294–3306.

Garel, M., Loison, A., Gaillard, J. M., Cugnasse, J. M., & Maillard, D. (2004). The effects of a severe drought on mouflon lamb survival. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *271*, S471–S473.

Gelman, A., & Pardoe, I. (2006). Bayesian measures of explained variance and pooling in multilevel (hierarchical) models. *Technometrics*, *48*, 241–251.

Gelman, A., & Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science*, *7*, 457–511.

Green, A. J. (2001). Mass/length residuals: Measures of body condition or generators of spurious results? *Ecology*, *82*, 1473–1483.

Grinsted, L., Breuker, C. J., & Bilde, T. (2014). Cooperative breeding favors maternal investment in size over number of eggs in spiders. *Evolution*, *68*, 1961–1973.

Hamilton, W. D. (1964). The genetical evolution of social behaviour. *Journal of Theoretical Biology*, *7*, 1–16.

Hatchwell, B. J. (2009). The evolution of cooperative breeding in birds: Kinship, dispersal and life history. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*, 3217–3227.

Hooten, M. B., & Hobbs, N. T. (2015). A guide to Bayesian model selection for ecologists. *Ecological Monographs*, *85*, 3–28. https://doi.org/10.1890/14-0661.1

Hull, D. (1973). *Comparative physiology of thermoregulation, chapter. Thermoregulation in young mammals* (pp. 167–200). Academic Press.

Kéry, M., & Schaub, M. (2012). *Bayesian population analysis using WinBUGS. A hierarchical perspective*. Academic Press.

Kirst, M. (2011). Egg size and offspring quality: A meta-analysis. *Biological Reviews*, *86*, 692–716.

Koenig, A., Beise, J., Chalise, M. K., & Ganzhorn, J. U. (1998). When females should contest for food-testing hypotheses about resource density, distribution, size, and quality with Hanuman langurs (*Presbytis entellus*). *Behavioral Ecology and Sociobiology*, *42*, 225–237.

Koenig, W. D., & Walters, E. L. (2015). Temporal variability and cooperative breeding: Testing the bet-hedging hypothesis in the acorn woodpecker. *Proceedings of the Royal Society B: Biological Sciences*, *282*, 20151742. https://doi.org/10.1098/rspb.2015.1742

Komdeur, J. (2001). Mate guarding in the Seychelles warbler is energetically costly and adjusted to paternity risk. *Proceedings of the Royal Society B: Biological Sciences*, *268*, 2103–2111. https://doi.org/10.1098/rspb.2001.1750

Körtner, G., & Heldmaier, G. (1995). Body-weight cycles and energy-balance in the Alpine Marmot (*Marmota marmota*). *Physiological Zoology*, *68*, 149–163. https://doi.org/10.1086/physzool.68.1.30163923

Lack, D. (1947). The significance of clutch-size. *Ibis*, *89*, 302–352. https://doi.org/10.1111/j.1474-919X.1947.tb04155.x

Lardy, S., Allainé, D., Bonenfant, C., & Cohas, A. (2015). Sex-specific determinants of fitness in a social mammal. *Ecology*, *96*, 2947–2959. https://doi.org/10.1890/15-0425.1

Lardy, S., Cohas, A., Desouhant, E., Tafani, M., & Allainé, D. (2012). Paternity and dominance loss in male breeders: The cost of helpers in a cooperatively breeding mammal. *PLoS ONE*, *7*, e29508.

Marshall, D. J., Bonduriansky, R., & Bussière, L. F. (2008). Offspring size variation within broods as a bet-hedging strategy in unpredictable environments. *Ecology*, *89*, 2506–2517.

McGraw, J., & Caswell, H. (1996). Estimation of individual fitness from life-history data. *The American Naturalist*, *147*, 47–64.

Mitchell, J. S., Jutzeler, E., Heg, D., & Taborsky, M. (2009). Gender differences in the costs that subordinate group members impose on dominant males in a cooperative breeder. *Ethology*, *115*, 1162–1174.

Moran, G. (1984). Vigilance behaviour and alarm calls in a captive group of meerkats, *Suricata suricatta*. *Ethology*, *65*, 228–240.

Mysterud, A., Yoccoz, N. G., Langvatn, R., Pettorelli, N., & Stenseth, N. C. (2008). Hierarchical path analysis of deer responses to direct and indirect effects of climate in northern forest. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *363*, 2357–2366. Retrieved from http://rstb.royalsocietypublishing.org/content/363/1501/2357.abstract

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining r2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*, 133–142.

NIMBLE Development Team. (2016). *NIMBLE: An R package for programming with BUGS models*, Version 0.6-1. NIMBLE Development Team.

Olofsson, H., Ripa, J., & Jonzén, N. (2009). Bet-hedging as an evolutionary game: The trade-off between egg size and number. *Proceedings of the Royal Society B: Biological Sciences*, *276*, 2963–2969.

Paquet, M., Covas, R., Chastel, O., Parenteau, C., & Doutrelant, C. (2013). Maternal effects in relation to helper presence in the cooperatively breeding sociable weaver. *PLoS ONE*, *8*, e59336.

Parker, G. A., & Begon, M. (1986). Optimal egg size and clutch size-effects of environment and maternal phenotype. *The American Naturalist*, *128*, 573–592.

Peig, J., & Green, A. J. (2010). The paradigm of body condition: A critical reappraisal of current methods based on mass and length. *Functional Ecology*, *24*. 1323–1332.

Pettorelli, N., Pelletier, F., Hardenberg, A., Festa-Bianchet, M., & Côté, S. D. (2007). Early onset of vegetation growth vs. rapid green-up: Impacts on juvenile mountain ungulates. *Ecology*, *88*, 381–390. ISSN 0012–9658.

Philippi, T., & Seger, J. (1989). Hedging one's evolutionary bets, revisited. *Trends in Ecology & Evolution*, *4*, 41–44.

Plard, F., Yoccoz, N. G., Bonenfant, C., Klein, F., Warnant, C., & Gaillard, J. M. (2015). Disentangling direct and growth-mediated influences on early survival: A mechanistic approach. *Journal of Animal Ecology*, *84*, 1363–1372. https://doi.org/10.1111/1365-2656.12378

Plard, F., Chamiot-clerc, B., & Cohas, A. (2020). Data from: Influences of climatic and social environment on variable maternal allocation among offspring in Alpine marmots. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.fqz612jr9

Post, E., Levin, S. A., Iwasa, Y., & Stenseth, N. C. (2001). Reproductive asynchrony increases with environmental disturbance. *Evolution*, *55*, 830–834. https://doi.org/10.1111/j.0014-3820.2001.tb00818.x

Psenner, H. (1957). Neues vom murmeltier. *Säugetierkundliche Mitteilungen*, *5*, 4–10.

R Core Team. (2014). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Rézouki, C., Tafani, M., Cohas, A., Loison, A., Gaillard, J. M., Allainé, D., & Bonenfant, C. (2016). Socially-mediated effects of climate change decrease survival of hibernating Alpine marmots. *Journal of Animal Ecology*, *85*, 761–773.

Rödel, H. G., Starkloff, A., Seltmann, M. W., Prager, G., & Von Holst, D. (2009). Causes and predictors of nest mortality in a European rabbit population. *Mammalian Biology*, *74*, 198–209.

Roff, D. A. (2002). *Life history evolution*. Sinauer Associates.

Ruf, T., & Arnold, W. (2000). *Life in the Cold IV, chapter Mechanisms of social thermoregulation in hibernating Alpine marmots* (Marmota marmota*)* (pp. 81–94). Springer.

Russell, A. F., Brotherton, P. N. M., McIlrath, G. M., Sharpe, L. L., & Clutton-Brock, T. H. (2003). Breeding success in cooperative meerkats: Effects of helper number and maternal state. *Behavioral Ecology*, *14*, 486–492.

Russell, A. F., & Lummaa, V. (2009). Maternal effects in cooperative breeders: From hymenopterans to humans. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*, 1143–1167.

Saether, B. E., & Engen, S. (2015). The concept of fitness in fluctuating environments. *Trends in Ecology & Evolution*, *30*, 273–281.

Salomon, M., & Lubin, Y. (2007). Cooperative breeding increases reproductive success in the social spider *Stegodyphus dumicola* (Araneae Eresidae). *Behavioral Ecology and Sociobiology*, *61*, 1743–1750.

Schamber, J. L., Esler, D., & Flint, P. L. (2009). Evaluating the validity of using unverified indices of body condition. *Journal of Avian Biology*, *40*, 49–56.

Seger, J., & Brockmann, J. (1987). *Oxford surveys in evolutionary biology, volume 4, chapter What is bet-hedging?* (pp. 182–211). Oxford University Press.

Shipley, B. (2009). Confirmatory path analysis in a generalized multilevel context. *Ecology*, *90*, 363–368.

Sibly, R. M., & Brown, J. H. (2009). Mammal reproductive strategies driven by offspring mortality-size relationships. *The American Naturalist*, *173*, E185–E199.

Slatkin, M. (1974). Hedging ones evolutionary bets. *Nature*, *250*, 704–705.

Smith, C. C., & Fretwell, S. D. (1974). The optimal balance between size and number of offspring. *The American Naturalist*, *108*, 499–506.

Stearns, S. C. (1992). *The evolution of life histories*. Oxford University Press.

Taborsky, B., Skubic, E., & Bruintjes, R. (2007). Mothers adjust egg size to helper number in a cooperatively breeding cichlid. *Behavioral Ecology*, *18*, 652–657.

Tafani, M., Cohas, A., Bonenfant, C., Gaillard, J. M., & Allainé, D. (2013). Decreasing litter size of marmots over time: A life-history response to climate change? *Ecology*, *94*, 580–586.

Ulbrich, K., & Henschel, J. R. (1999). Intraspecific competition in a social spider. *Ecological Modelling*, *115*, 243–251.

Visser, M. E., & Both, C. (2005). Shifts in phenology due to global climate change: The need for a yardstick. *Proceedings of the Royal Society B: Biological Sciences*, *272*, 2561–2569. ISSN 0962–8452.

Watanabe, S. (2013). A widely applicable Bayesian information criterion. *Journal of Machine Learning Research*, *14*, 867–897.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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