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Yellow-bellied marmots do not compensate for a late start: the role of maternal allocation in shaping life-history trajectories

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Abstract Yellow-bellied marmots, *Marmota flaviventris*, are obligate hibernators with a relatively short active season. Animals born earlier in the season have higher chances of fulfilling the energetic requirements to survive the long winter. Therefore, the onset of breeding should have a profound impact on juvenile survival. However, there are different ways to compensate for a late start. Late breeders might allocate more resources to late born offspring, making up for the bad start, or juveniles might show compensatory growth. They are not exclusive hypotheses and both can lead to juveniles entering hibernation with a similar body condition. We used data from a long term study in and around the Rocky Mountain Biological Laboratory in Colorado to test these two hypotheses. Animals are individually marked and trapped regularly. We compared mass at weaning, mass at the end of the season, growth rates and survival between animals born earlier and later in the season. We found no evidence of increased maternal input: late breeders had lighter offspring at weaning than early breeders, and late born juveniles did not increase their growth rates. Therefore, late born individuals ended the season with lower body mass, and were thus, less likely to survive the winter. In conclusion, life-history trajectories of juvenile yellow-bellied marmots were determined by maternal allocation, whereas post-weaning decisions did not modify their fate.

Keywords Compensatory growth · Early conditions · Hibernation · *Marmota flaviventris* · Maternal effects · Onset of breeding

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Introduction

Conditions experienced by an animal in early life might have profound implications for life-history traits and fitness (Lindström 1999). Adverse conditions during early development affect growth and a range of related properties, including metabolism and immunocompetence, and the effects might be apparent in future generations. For instance, in humans, early adverse development including low birth weight, poor postnatal growth rate or exposure to famine in utero have transgenerational effects (Lummaa and Clutton-Brock 2002). Therefore, the pattern of growth and development might explain much of the variation found in life-history traits (Côté and Festa-Bianchet 2001; Bize et al. 2006; Beamonte-Barrientos et al. 2010).

During early development, animals could be limited in the quantity, the quality, or the amount of time they allocate to fulfil their energetic requirements (Festa-Bianchet et al. 2000; Côté and Festa-Bianchet 2001; Auer 2010). However, growth rates are phenotypically plastic, and animals might be able to compensate for a bad start (Metcalfe and Monaghan 2001; Dmitriew 2011). Animals can respond to internal cues about energy accumulation thresholds and shape their resource and time allocation accordingly (Dmitriew 2011; Moreau and Fleming 2012). In these cases, energetically stressed individuals might increase food acquisition even at the expense of increasing exposure to predators (Oksanen and Lundberg 1995; Preisser et al. 2005; Monclús and Rödel 2009). This might result in heightened growth rates after a period of food shortage, a phenomenon known as compensatory growth (Álvarez and Metcalfe 2007; Hector and Nakagawa 2012). For example, wild brown trout, *Salmo trutta*, increased growth rates after a period of food restriction (Johnsson and Bohlin 2005). Moreover, mothers may directly influence offspring size from conception to weaning, and in social species maternal care might indirectly affect offspring size through resource facilitation later in life (Mousseau and Fox 1998; Altmann and Alberts 2005). Both mechanisms, compensatory growth and maternal input, should not be mutually-exclusive, though they have never been examined simultaneously.

Animals such as marmots (*Marmota* spp.; large hibernating ground squirrels), are environmentally constrained both in the amount of time they have to gain mass and in food quality, because as the vegetative growing season progresses, food quality decreases (Côté and Festa-Bianchet 2001; Margraf et al. 2003). Body mass at the end of the vegetation period is a good predictor of overwinter survival. Animals below a certain threshold are less likely to survive the winter (Rödel et al. 2004; Schwartz and Armitage 2005). Therefore, an animal born early in the season might benefit from a longer period of time to grow and more time to increase its condition. However, being born late in the season might be compensated by higher maternal input, or by increased growth rates (Gagliano and McCormick 2007).

Many studies have studied compensatory growth in changing environments characterized by acute food stress. However, only few have explored the decision making process when animals are time-limited in the completion of an ontogenetic phase (but see Festa-Bianchet et al. 2000; Margraf et al. 2003; Lee et al. 2012). More interestingly, and to our knowledge, no previous studies have explored different compensatory mechanisms in an animal in the field. Thus, we used yellow-bellied marmots (*Marmota flaviventris*) to investigate whether juveniles might be able to compensate for a bad start. Marmots are an ideal species in which to investigate compensation because they are obligate hibernators with a short active period. At our Colorado study site, marmots emerge from hibernation in April and May and begin hibernating as early as late September (Armitage 2003). We study marmots in a natural setting which provides both within- and between-year variation in the dates of conception and the length of the growing season. We used marmots from a long-term study, where animals are individually marked and we know the fate of the individuals from weaning to death (Armitage et al. 2011).

With our study we wanted to know whether compensation exists in yellow-bellied marmots. We followed a comprehensive approach looking for different and non-exclusive compensatory mechanisms. On the one hand, late born animals might compensate through a higher maternal input, and therefore, we would expect to find higher weaning mass in late born animals. On the other hand, juveniles might compensate through higher growth rates (compensatory growth), and therefore our expectation might be that later born animals should show higher growth rates.

Our second objective was to investigate the long-term effects of weaning mass and subsequent growth rate on overwinter survival. We focused on survival to the first hibernation. It is well known that mass at the end of the season is a good predictor of overwinter survival (Schwartz and Armitage 2005). Mass at the end of the season is the result of maternal genetic and non-genetic effects (McAdam et al. 2002), and depends on the offspring weaning mass plus the growth trajectory the individual has followed. Partitioning mass at the end of the season in its two main components (initial mass and growth rate), we wanted to know whether weaning mass or whether the combination of maternal input (weaning mass) and growth explain better the probability of an animal to survive the winter. If only weaning mass predicts better overwinter survival, it would indicate that maternal effects, and therefore, the very early environment, play an important role in shaping the offspring chances in life. By contrast, if the latter is true, juvenile marmots have some plasticity in their growth and are able to make up for a bad start. In addition to answering our questions, there might be important methodological implications of this result. If the former is true, one might want to direct all the effort to record mass at weaning, whereas if the addition of growth explains better overwinter survival, a continuous trapping effort during the whole season might be desirable to better predict overwinter survival.

Materials and methods

Study population and study area

We used data from our long-term study in yellow-bellied marmots in and around the Rocky Mountain Biological Laboratory, in the Upper East River Valley in Colorado (USA). Marmots have been studied there for the last 51 years (Armitage et al. 2011; Blumstein 2013). For this particular study we used data from 2002 to 2009 from 10 different colonies, 5 located up-valley and 5 located down-valley. These two different sets of colonies are separated by a maximum distance of 4.8 km (Van Vuren and Armitage 1991). Although the maximum difference in elevation is only 160 m (up-valley average = 3,043 m.a.s.l.; down-valley average = 2,883 m.a.s.l.), the phenology of both locations differs in about 2 weeks; emergence from hibernation, mating and emergence from the natal burrows occur, on average, 2 weeks earlier in the colonies down-valley (Blumstein 2009). There is no gene flow between up-valley and down-valley colonies, only within each location. Animals are individually marked, and sex, date of birth—and thus, age—social and family group affiliations are known.

Data collection

We performed daily observations of the different colonies with spotting scopes from mid-April to early September. Our regular observations allowed us to record the emergence date of each litter. Juvenile yellow-bellied marmots emerge above ground once they are weaned at the age of 30 days (Armitage 2003). Once emerged, we trapped the juveniles from the litter, sexed them, recorded their weight and marked them individually with eartags. Moreover we draw a unique symbol in the back of each animal with Nyanzol cattle dye, which could be easily read from the distance with a spotting scope. We collected hair samples for later DNA parentage assignment. Parentage assignment was assessed using 12 microsatellite loci and 95 % confidence assignments at the trio level using CERVUS 3.0 (Kalinowski et al. 2007). For further details on trapping and laboratory procedures, see Blumstein et al. (2010). For each year, we calculated the median cut of the emergence date of the pups. We considered that a juvenile was born late in the season if it emerged after the median date of the year.

Adult females were regularly trapped throughout their active season (goal: every other week). In each trapping session we recorded the identity, the weight and the reproductive status of the animal to further confirm maternities. We used female mass in June as a proxy of body condition during the lactation period.

Growth rates and body mass

We only used those individuals where we had at least four body mass measurements over a span of time of more than 20 days (number of measures 4–12; average = 6). We calculated individual growth rates, defined as the slope of the regression between age and mass, because juvenile marmots gain mass linearly during their first months and then they reach a plateau (Lenihan and Van Vuren 1996). With the estimates of the linear function, whenever significant ($p < 0.05$; $R^2 \geq 0.9$), we calculated mass at day 1 (weaning date), and mass on 1 September. The latter was used as a measure of late-season body mass.

Overwinter survival

Marmots hibernate between September and April/May. In April/May, adult males are normally the first animals spotted above ground, followed by adult females, and the last ones emerging are the juveniles of the previous season. The entire group emerges within a week and the entire colony site (some colony sites have more than one social group), emerges within 15 days. We considered that a juvenile had failed to survive the winter if (1) it was trapped and/or observed at the end of the previous season and (2) it was not observed nor trapped once the entire colony had emerged from hibernation.

Statistical analysis

We fitted linear mixed effects models (LMM) with the function lmer from the package *lme4* from the software package R, version 2.15.2 (R Development Core Team 2012). We ensured that the residuals of all models approximated to a normal distribution by visually checking normal probability plots and by the Shapiro–Wilk test, and that the distribution of the variances was homogeneous. Furthermore, we checked for the multicollinearity of the variables included in each model. In all cases the variance inflation factor was <1.5.

Our first objective was to know whether compensation exists in yellow-bellied marmots. To test whether late mothers increased their input we fitted a LMM with weaning mass as the dependent variable and we included the location where the animal was born (up-valley or down-valley), the sex of the animal and emergence time (early or late in the season) as fixed factors. Moreover we included a variable related to maternal quality. We considered maternal age and maternal body mass as proxies of maternal quality. However, both variables were highly correlated ($R^2 = 0.64$): older females are heavier, and therefore, we elected to not include simultaneously both variables in any model. We chose maternal mass as a proxy of maternal condition as many studies have found a positive relationship between maternal body mass and offspring body mass (Côté and Festa-Bianchet 2001). We included the interaction between emergence time and maternal body mass as fixed factors. We also included litter size as a fixed factor, because individuals from bigger litters tend to be smaller (Stearns 1992). We included litter identity and year as random factors to control for litter effects and between-year variation.

A further possibility that we explored is that marmots born later in the season grow at a higher rate to reach the end of the season at a similar size than animals born earlier. To test that, we fitted a model with growth as the dependent variable and mass at weaning, sex, litter size, location, emergence time and the interaction between location and emergence time as fixed factors, and litter identity and year as random factors. Whenever the interaction terms were not significant, they were removed from the final model (Engqvist 2005).

If compensation exists, juvenile marmots might reach the end of the season with similar body masses independently of the emergence time. For that we looked at the predictors that might explain body mass at the end of the season (dependent variable). We included mass at weaning, the sex of the animal, the emergence time, litter size and location as fixed factors. Once again, litter identity and year were included as random factors. For all the models, the significance of model parameters was obtained with the type III *Anova* function from package *car*.

Our second objective was to determine whether weaning mass alone might be a good predictor of overwinter survival or whether the growth trajectory should be included in those models. For the analysis of survival we followed an information-criterion approach. We used the second order AIC (AIC_c) because our sample size, in relation to the number of parameters explored was ≤40 (Burnham and Anderson 2002). We searched for the model that fitted our data with the lowest ΔAIC and the highest weight (w_i). Our set of candidate models consisted of a global model for mass and growth ($S \sim mass + growth + mass \times$ growth $+ sex + emergence + maternal\ age + emergence \times$ maternal age $+ location$), a global model for just mass ($S \sim mass + sex + emergence + maternal\ age + emergence \times$ maternal age $+ location$), and slight variations of those two, where we removed some of the variables which might not be as important explaining overwinter survival. We used maternal age as a proxy of maternal experience, as it may quantify the potential post-weaning maternal effects better than maternal body mass. We used a dichotomous variable, young females (≤3 years) and older females (>4 years). We also included a null model ($S \sim 1$) to control for the validity of the candidate models (Table 1). We calculated the relative weights of the variables, $w_+(j)$, as a measure of the relative importance of each variable, the model averaged estimates (Θ) and the unconditional standard errors (Burnham and Anderson 2002).

Results

We used a total of 161 juvenile yellow-bellied marmots stemming from 62 litters. 78 pups from 29 litters were born early in the season, whereas 83 pups from 33 litters were categorised as late born. The average lapse of time between early and late births was 9 days, but it varied from 1 to 30, depending on the year. 129 juveniles came from down-

Table 1 The table shows the set of candidate models that might explain overwinter survival in juvenile yellow-bellied marmots, including the null model (*S*·), the number of parameters (*K*), ΔAIC_c, the Akaike weights (w_i) and Nagelkerke´s pseudo R^2

Candidate models	K	ΔAIC_c	w_i	Pseudo R^2
$S_{m + l + e + ma + e \times ma}$	**8**	**0**	**0.254**	**0.152**
$S_{m + g + m \times g + l + e + ma + e \times ma}$	**10**	**0.484**	**0.200**	**0.185**
$S_{m + e + ma + e \times ma}$	**7**	**0.908**	**0.162**	**0.124**
$S_{m + s + l + e + ma + e \times ma}$	9	2.020	0.093	0.152
$S_{m + g + m \times g + s + l + e + ma + e \times ma}$	11	2.317	0.080	0.187
$S_{m + g + m \times g + e + ma + e \times ma}$	9	2.502	0.073	0.147
$S_{e + ma + e \times ma}$	6	3.287	0.0490	0.080
$S_{mass \times growth}$	6	4.227	0.030	0.071
S_m	4	4.435	0.028	0.028
S_s	4	6.575	0.009	0.006
$S\cdot$	3	5.105	0.019	0

In bold are the candidate models with good support from the data ($\Delta AIC_c \leq 2$)

S overwinter survival, *m* mass at weaning, *l* location, *e* emergence date, *ma* maternal age, *g* growth rate, *s* sex

valley colonies, and the rest from up-valley colonies. The average number of pups per litter was 4.2 ± 1.9 SD.

During the study period, the number of adult females per colony ranged between 1 and 21, and there were 1–14 adult females in each social group. We only trapped 57 out of the 62 mothers in June. Thus, in those analysis where maternal mass is included as a factor, sample sizes are reduced. We did not find significant differences in body mass between early and late breeders (early = 3,014.3 ± 416 g; late = 3,049.5 ± 545 g; Mann–Whitney U = 2,626; $p = 0.776$). Moreover, we did not find differences in the litter sex ratio between early litters and late litters ($\beta = -23.60 \pm 20.79$ SE, n = 153, $p = 0.256$), which could have biased the results.

Do mothers compensate for a late start? Factors affecting weaning mass

Mothers did not compensate for their offspring being born later in the season: weaning mass was smaller in later born offspring ($\beta = 396.15 \pm 166.11$ SE, n = 149, $p = 0.017$). Heavier mothers had heavier offspring ($\beta = 0.08 \pm 0.04$ SE, n = 149, $p = 0.046$), and as litter size increased, weaning mass of the offspring decreased ($\beta = -15.91 \pm 6.93$ SE, n = 149, $p = 0.021$). The interaction between maternal mass and the timing of breeding was statistically significant ($\beta = -0.13 \pm 0.05$ SE, n = 149, $p = 0.015$): offspring weaning mass was positively related to maternal mass, but only for those born early in the season ($\beta = 0.09 \pm 0.03$ SE, n = 73, $p = 0.011$; Fig. 1a). Later in the season we did not find that pattern any more ($\beta = -0.04 \pm 0.03$ SE, n = 76, $p = 0.247$; Fig. 1b).

We found sexual differences at weaning; males were heavier than females at weaning (males = 397.2 g ± 121 SD; females = 363.9 g ± 104 SD; $\beta = 31.89 \pm 15.25$ SE, n = 149, $p = 0.040$). The location where the animal was born (down-valley vs. up-valley) did not affect the weaning mass ($\beta = 65.55 \pm 34.65$ SE, n = 149, $p = 0.058$).

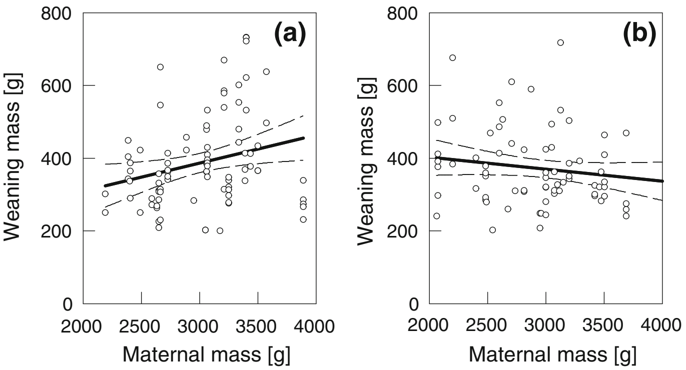


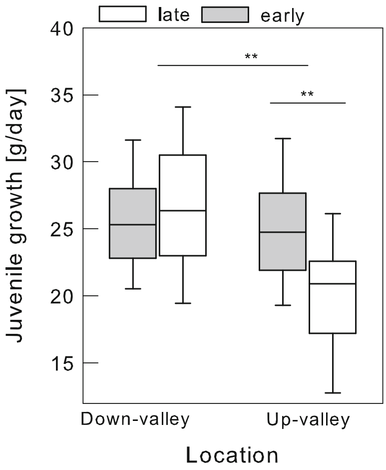
Fig. 1 Maternal body mass and offspring weaning mass are significantly correlated in **a** early but not in **b** late born animals. See text for statistics

Do pups compensate for a late start? Growth rates and final body mass

We did not find any sign of pup compensation. Growth rates were independent of the time of emergence above ground (β = 0.96 ± 1.08 SE, n = 161, $p = 0.376$) or the location where the animal was born (β = 0.84 ± 1.94 SE, n = 161, $p = 0.435$). However, the interaction between location and emergence time was significant (β = 7.28 ± 2.39 SE, n = 161, $p = 0.002$): the animals with significantly slower growth rates were the ones that were born up-valley later in the season (β = −6.05 ± 1.52 SE, n = 84, $p < 0.001$; Fig. 2). Males had higher growth rates than females (β = 2.98 ± 0.64 SE, n = 161, $p < 0.001$). Litter size did not affect growth rates (β = 0.07 ± 0.25 SE, n = 161, $p = 0.764$), and neither did weaning body mass (β = −0.01 ± 0.01 SE, n = 161, $p = 0.168$).

Because individuals born later were smaller and grew at a lower rate, they reached the end of the vegetative season with a smaller size relative to early born individuals (β = −224.70 ± 69.88 SE, n = 161, $p = 0.001$; Fig. 3). Mass at the end of the season was positively correlated with mass at the beginning of the season (β = 0.62 ± 0.22 SE, n = 161,

Fig. 2 Growth rate of juvenile yellow-bellied marmots in relation to the timing of emergence (early in *grey* and late in *white*) and location (down-valley and up-valley). *Asterisks* denote statistically significant differences in the post hoc analyses



$p = 0.005$). Males, as a consequence of their higher growth rates and their bigger weaning mass, remained heavier than females at the end of the season ($\beta = 205.47 \pm 42.77$ SE, $n = 161$, $p < 0.001$; males: 2,094.09 g ± 372 SD; females: 1,809.92 g ± 330). Whereas weaning mass did not depend on the location where the animal was born, juveniles' body mass at the end of the season did ($\beta = 194.67 \pm 84.36$ SE, $n = 161$, $p = 0.021$). Down-valley juveniles were significantly heavier. However, the interaction between location and emergence date was not statistically significant ($\beta = -339.44 \pm 174.90$ SE, $n = 161, p = 0.053$) and was removed from the final model. Litter size, which might represent a proxy of resource competition, was not related to the body mass at the end of the season ($\beta = 6.25 \pm 18.79$ SE, $n = 161, p = 0.748$).

Survival

Three models from our set of candidate models were equally supported by the data (Table 1). Mass at weaning and the interaction between emergence time and maternal age were present in all the models predicting overwinter survival. The model with those parameters plus growth was as likely to be the best of the candidate models as the others.

If we adopt the principles of simplicity and parsimony, the model with least number of parameters should be favoured, and thus, $S_{mass+location+emergence\ \times\ maternal\ age}$ could be considered the most plausible model. Mass at weaning and emergence time were the two variables with higher relative importance (see Table 2). Maternal age, growth, location and the interaction between weaning mass and growth had no effect on survival, because the 95 % confidence interval of the unbiased estimates included 0. Heavier animals were more likely to survive the winter (Fig. 4), and so did animals born earlier in the season. Whereas 90 % of the early born survived the winter, only 76 % of the late born were successful. These results were driven by the low overwinter survival of the offspring born late in the season from younger mothers (52 %), whereas the rest had significantly higher overwinter survival (73 % for juveniles from older females born early and late, and 79 % for juveniles from younger females born early in the season).

Discussion

In temperate climates, the onset of reproduction is of great importance because juveniles are energetically limited by the length of the vegetation period (Metcalfe and Monaghan

Fig. 3 Mass at the end of the season in juvenile yellow-bellied marmots in relation to the timing of emergence (early or late born animals)

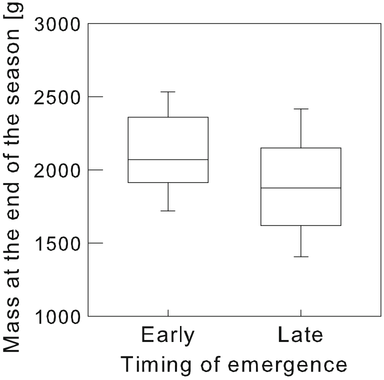


Table 2 Model-averaged parameter estimates $\hat{\theta}_a$; unconditional 95 % confidence intervals and the relative importance of the variables $w_+(j)$ for each parameter affecting overwinter survival in juvenile yellow-bellied marmots

Parameter	$\hat{\theta}_a$	Upper 95 % limit	Lower 95 % limit	$w_+(j)$
Weaning mass	**0.004**	**0.008**	**0.001**	**0.93**
Growth	0.066	0.168	−0.036	0.422
Weaning mass × growth	0.476	1.309	−0.567	0.387
$\text{Emergence}_{\text{early}}$	**2.065**	**3.888**	**0.242**	**0.905**
$\text{Location}_{\text{down-valley}}$	−1.25	0.312	−2.812	0.644
Maternal $\text{age}_{\text{young}}$	1.02	2.586	−0.546	0.905
Mat. $\text{age}_{\text{young}}$ × $\text{emergence}_{\text{early}}$	**2.835**	**4.777**	**0.893**	**0.905**
Sex_{male}	0.018	0.927	−0.892	0.185

The variables with a significant contribution are in bold

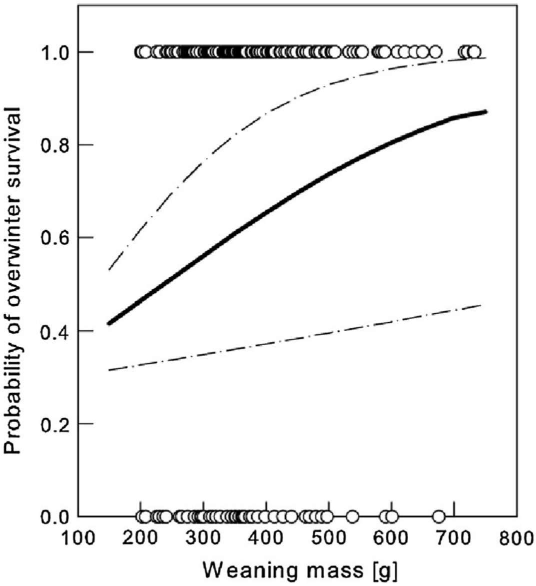


Fig. 4 Predicted (calculated from the unconditional parameter estimates of the best model of our set of candidate models: *thick line*) survival probabilities and observed survival (*open circles*) of juvenile yellow-bellied marmots in relation to weaning mass. The *dotted lines* represent the unbiased error estimates

2001). However, there are several mechanisms that might function to compensate for a shorter vegetation period, such as higher maternal input or higher growth rates. In this study we found no evidence of compensation. Juvenile yellow-bellied marmots born later in the season were lighter at weaning and reached hibernation with a lighter body mass than the animals born earlier in the season. Moreover, maternal input was higher in those animals born earlier in the season, apparent by the positive correlation between maternal mass and offspring mass. However, we cannot fully eliminate the hypothesis that late breeders did not compensate at all, because we had no access to their subterranean nests, and thus, birth mass was unknown. Taken together, our results suggest that the growth trajectory of juvenile yellow-bellied marmots is predetermined by maternal input, and juveniles do not compensate once they are weaned. Maternal decisions such as when or where to reproduce might be essential to understand an individual's trajectory in life.

Females that reproduced later might invest more in their offspring, and thus increase their chances of overwinter survival. However, we did not find strong support for this mechanism. Rather, we found the opposite: offspring from early breeders had higher body mass at weaning. Other studies have found similar results. For example in bison, *Bison bison*, calves born earlier were heavier and the effect persisted as long as 8 years after birth (Green and Rothstein 1993). Bighorn sheep, *Ovis canadensis*, born later in the season were lighter and less likely to survive the winter (Feder et al. 2008). Moreover, maternal input was significant for early born, but not for late born. Heavier female marmots are normally older females and thus, higher ranking (Huang et al. 2011). Other studies have found that the onset of breeding is a good proxy of maternal quality, and that older mothers, before the onset of senescence, have heavier offspring (Ericsson et al. 2001; Adams 2005; Hamel et al. 2012). These females might be able to hold more resources, and provide better opportunities for their offspring to grow (Stearns 1992; Rödel et al. 2005; Dearborn et al. 2008; Feder et al. 2008). Therefore, the behavior showed by early breeders provide support to the terminal allocation hypothesis (Wedadji et al. 2010). However, and interestingly, heavier females that delayed the onset of breeding followed a conservative strategy, reducing the actual reproductive input by decreasing their output in offspring.

A similar result could have been driven by sex-ratio skews between early and late litters. For instance, early broods of European shags (*Phalacrocorax aristotelis*) were male-biased, whereas later broods were female-biased (Velando et al. 2002). However, in yellow-bellied marmots we did not find such effect.

Yellow-bellied marmot mothers allocated more resources to males. Males are likely under stronger pressures to attain a large body size. They are the allopatric sex and successful dispersal and settlement in a new colony might be related to their competitive ability (Nunes et al. 1998). High quality mothers could increase their fitness by investing in good sons, because those might generate more offspring than high-quality daughters (Trivers and Willard 1973).

The alternative, though non-exclusive, mechanism to compensate for a bad start might be compensatory growth. Compensatory growth has been described in many species after a temporal food shortage (Johnsson and Bohlin 2005; Bize et al. 2006; Auer 2010). However, other species do not compensate, or do not fully compensate (Hector and Nakagawa 2012). Even, compensation might depend on the life-history of the population, as it has been shown in some salmonids; for instance migratory brown trouts, *Salmo trutta*, where survival is size-dependent, showed compensatory growth (Johnsson and Bohlin 2005), whereas non-migratory fish did not fully compensate for food stress (Álvarez and Nicieza 2005).

Compensatory growth is thought to be costly (Lee et al. 2010; Dmitriew 2011; Lee et al. 2013). It is known to have short and long-term consequences for individual fitness, such as increased predation risk (Lima and Dill 1990; Stone 2007; Monclús and Rödel 2009), reproduction (Auer et al. 2010; Lee et al. 2012), resource allocation trade-offs (Lindström et al. 2005; Moreau and Fleming 2012), and/or oxidative stress (Metcalfe and Monaghan 2001; Álvarez and Metcalfe 2007). In some instances, the costs associated with compensatory growth might outweigh the potential benefits, and then, compensatory growth might not be apparent any more, or only partial compensation might occur. This might be the case in yellow-bellied marmots, where we found no evidence of compensatory growth. Young marmots are the common prey of numerous predators (Van Vuren 2001; Blumstein 2006; Monclús et al. 2011), and predation has a profound effect on meta-population persistence (Blumstein et al. 2006). Marmots have several anti-predator behaviours, which are known to compete with food acquisition (e.g., Bednekoff and Blumstein 2009;

Blumstein et al. 2010; Lea and Blumstein 2011) and might consequently limit growth rates (Careau et al. 2013). It could also be that marmots were food limited, and compensatory growth was just impossible. However, in our study populations food only becomes a limiting factor at the very end of the season after a dry summer (Armitage 1994), and at that point juveniles have already reached their hibernating mass (Lenihan and Van Vuren 1996). Whether yellow-bellied marmots do not show compensatory growth because the costs outweigh the benefits, or because they are indeed food limited constitutes an interesting question that deserves further work.

Most maternal input occurred before weaning, the effects were apparent at least until the beginning of the next season, although we cannot discard possible post-weaning maternal effects. This comes from the fact that weaning mass resulted a good predictor of overwinter survival, whereas the inclusion in the models of the growth trajectory the animal had followed from weaning to the end of the season did not improve the fit of the model. Animals born earlier in the season had higher survival probabilities; whether this was due to the longer growing season, the higher body mass attained at the end of the vegetation period or other maternal effects should be further explored in future studies.

Interestingly, in our analyses, we found no sex differences in overwinter survival. Whereas males were heavier and had faster growth rates, they were just as likely to survive the winter as females. A potential explanation is that both sexes are as likely to reach the critical mass necessary to survive the winter. Above that threshold marmots do not seem to increase the probability of overwinter survival (Woods and Armitage 2003). Moreover, offspring from older mothers that reproduced later were more likely to survive the winter than those from younger mothers that reproduced late. Again, older mothers might hold better resources such as better food patches or better hibernacula that might increase the chances of overwinter survival.

Taken together, our results suggest that maternal decisions such as when and where to reproduce could shape the offspring life-history trajectory and this initial maternal investment seems to override later offspring decisions. In similar systems, where animals do not compensate for a late start, special effort should be made to study animals at weaning, because such maternal effects may be essential to understand their fate.

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