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Environmental, social, morphological, and behavioral constraints on opportunistic multiple paternity

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Abstract Multiple mating and multiple paternity in polytocous species have been mostly studied from an adaptive (i.e., cost–benefit) perspective. Disease, time, energy, and the risk of injuries are well-known costs of multiple mating, yet from both male and female perspectives, a number of genetic and non-genetic benefits have also been identified. The effects of environmental conditions and individual-specific behavior, however, are much less well understood. Using a long-term study on yellow-bellied marmots (*Marmota flaviventris*), we evaluated the impacts of environmental variation, social structure, female body mass, and female docility (a personality trait) on the occurrence of multiple paternity. Multiple paternity was influenced by environmental constraints, social constraints, a female's personality, and her body mass at emergence from hibernation. Personality and mass effects were detected only when environmental or social conditions were favorable. Our results suggest that multiple paternity is mainly limited by the opportunity to have access to multiple mates and is influenced by costs or mate choice because heavier females were more likely to have litters with multiple sires than smaller ones. Future studies in other species might benefit from considering environmental constraints when studying multiple paternity.

Keywords *Marmota flaviventris* · Yellow-bellied marmot · Personality · Multiple paternity

Traditional sexual selection theory states that females receive few fitness benefits from multiple paternities within a brood (Trivers 1972). However, more recent genetic evidence suggests that multiple paternity, and thus mating with multiple males, is common in many mating systems, including socially monogamous ones (Griffith et al. 2002; Cohas and Allainé 2009). Multiple paternity is often explained using an adaptive (i.e., cost-benefit) approach from both male and female perspectives (Solomon and Keane 2007; Waterman 2007). Males may mate with an already mated female to increase their reproductive success (Emlen and Oring 1977). Females may mate with more than a single male to obtain material and/or genetic benefits to increase their reproductive success (Arnqvist and Nilsson 2000; Jennions and Petrie 2000; Hosken and Stockley 2003). However, costs of multiple mating include a lost opportunity for foraging (Rowe 1992), higher predation risks (Magnhagen 1991), higher risks of acquiring diseases (Sheldon 1993; White et al. 2011), and increased risks of getting injured (Rowe 1994; Réale et al. 1996).

Generally, a number of factors may influence the likelihood of engaging in multiple mating. Environmental, social, morphological, physiological, and behavioral hypotheses have been proposed to explain multiple mating in socially monogamous systems (Gowaty 1996; Kokko et al. 2006; Clutton-Brock 2007). However, most of them are dependent on paternal care or resource benefits to the females (Gowaty 1996) and thus could not be tested in many mating systems. The switch point theorem, a quantitative statement of the hypothesis that

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stochastic effects favored the evolution of individuals able to make adaptively flexible reproductive decisions, provides a more general framework that could be applied to any mating system (Gowaty and Hubbell 2009). The theorem predicts that any parameter that influences survival, the probability of mate encounter, or the time available to mate could affect a females' probability of mating with more than a single male (Gowaty and Hubbell 2009). These parameters include (but are not limited to) social constraints (Gowaty and Bridges 1991; Sih and Kruppa 1995), environmental constraints (Schmoll 2011; Bleu et al. 2012), morphological variation (Hoogland 1998), physiological variation (Mokkonen et al. 2012), and behavioral variation (Patrick et al. 2012). For instance, the social environment may influence the opportunity for mating with different mates. Male-biased sex ratios have been shown to increase the prevalence of extra-pair paternity (Gowaty and Bridges 1991; Kokko et al. 2006). Environmental conditions may also influence the likelihood of mating with more than one male. Harsh conditions that limit movement during the period of female fertility or conditions that may decrease the length of the mating period could reduce the opportunity for multiple mating (Bergeron et al. 2011). Multiple mating can also be influenced by a female's size (Travis et al. 1990; Hoogland 1998). For instance, larger female sailfin mollys (*Poecilia latipinna*) produce larger litters, and their litters are more likely to be multiply sired (Travis et al. 1990). This may not be surprising because larger females might be more attractive to males because their body size permits them to produce more eggs. Additionally, females in better condition might also be better able to bear any costs associated with multiple mating (Hosken and Stockley 2003). Females in good condition might better be able to search for mates or move between males who each may be associated with a set of females (Byers et al. 1994). Finally, personality, which is defined as consistent individual differences in behavior across time or context (Réale et al. 2007), may influence the probability of a female reproducing and producing litters with multiple paternity (van Oers et al. 2008; While et al. 2009; Patrick et al. 2012). A previous research has shown that exploration or aggression may influence mode of paternity (intra- versus extra-pair paternity; van Oers et al. 2008; Patrick et al. 2012) and mating behavior (While et al. 2009) in socially monogamous species. More aggressive and more exploratory females may either encounter more mates or might be harder for a given male to defend (Smuts and Smuts 1993). Despite the potentially variable causes of multiple mating, few studies have investigated environmental determinants of multiple mating (but see Johnsen and Lifjeld 2003). In addition, the effect of personality on multiple mating has not been studied in non-socially monogamous systems.

Due to cryptic female choice (Eberhard 1996) and sperm competition (Smith 1984), mating with multiple males is not directly equivalent to having multiple sires within a litter for polytocous species. Parameters affecting multiple mating, however, are expected to also affect observed multiple paternities within a litter. Following the prediction of the switch point theorem, we use parentage assignments from a long-term study of yellow-bellied marmots (*Marmota flaviventris*) to investigate the environmental, social, morphological, and behavioral determinants of multiple paternity from a female's perspective. We use a multivariate approach that permits us to identify the relative importance of the variables in explaining variation in multiple paternity. Marmot mating systems have been described as female-defense polygyny, with litters that may be sired by more than a single male and without paternal care (Armitage 1986). Marmots mate belowground shortly after emergence from hibernation and are under a time constraint to gain mass and reproduce before the next hibernation (Frase and Hoffmann 1980). In sciurid rodents, multiple paternity varied from 16 to 90 % of litters (Waterman 2007), but it has not been estimated in yellow-bellied marmots. Based on the switch point theorem (Gowaty and Hubbell 2009), we developed the following hypothesis: multiple paternity should be affected by multiple variables including environmental, social, morphological, and behavioral traits.

Instead of testing only one type of trait included in the hypothesis, as has been done in most previous studies, we developed four predictions based on previous knowledge of our system and tested them simultaneously in a single model. First, we expected that male-biased sex ratios would increase multiple paternity due to a higher male–male competition and higher probability of meeting multiple males (Sih and Kruppa 1995; Kokko et al. 2006; Clutton-Brock 2007). Second, since individuals could move between different colonies during the mating season, we predicted that as snow cover increased during the mating season and as the date of emergence from hibernation of the first individual was delayed, the occurrence of multiple paternity would decrease because individual movements are limited by snow and constrained by time (Svendsen 1974; Bergeron et al. 2011). Third, considering that females in good condition might be able to better manage costs associated with multiple mating or might be preferred by males, we predicted that heavier females would produce more litters with multiple paternity. Finally, using docility as an index of personality (Réale et al. 2007), we predicted that a female's docility would be related to multiple paternity. Individuals with low docility could be considered as "pugnacious" (Réale et al. 2007), but docility could negatively or positively affect multiple paternity because non-docile females might be harder to guard or because docile females might tolerate more males. Following Petrie et al. (1992) showing that more dominant and aggressive females were more likely to mate multiply, we thus predicted that less docile females would produce more multiply sired litters.

Methods

Study system

Yellow-bellied marmots are large (3–5 kg), semi-fossorial sciurid rodents (Armitage 2003). Marmots typically live in colonies that consist of 1–6 adult females, 1–4 adult males, and a number of yearlings (1-year old) and juveniles. Males typically emerge first from hibernation and mate with receptive females within the first 2 to 3 weeks post-emergence (Armitage 1965; Blumstein 2009). Litter size ranges from 1–10 offspring in our population.

We studied yellow-bellied marmots at the Rocky Mountain Biological Laboratory (RMBL), Gunnison County, CO, USA, from to 2001 to 2010. We regularly trapped and systematically observed marmots from mid-April to mid-September. Once trapped, marmots were transferred to cloth handling bags where sex, reproductive status, and mass (accurate to within 50 g using a digital scale) were determined. Marmots were given permanent ear tags for long-term identification as well as unique fur marks (with Nyanzol fur dye) that allowed us to observe and identify animals from a distance. A hair sample was taken on first capture of an individual for genetic analysis. All individuals were marked and genotyped, and 95 % of animals were of known age because they were first captured as pups or as yearlings. Marmots were observed in eight geographically distinct colonies in two different areas (four down valley and four up valley). Within a summer, animals could disperse between colonies within an area, but movement between areas has never been observed within a summer (Ozgul et al. 2009). In addition, during one reproductive season, different males have been estimated to sire pups in multiple colonies in the same area but never in different areas. Thus, we define the operational sex ratio (OSR) for a colony, for a given year, as the ratio of the number of adult (2 years and older) males in the area by the number of adult females in the colony.

Environmental variables

For our study, emergence date was defined as the date at which the first marmot was seen at the RMBL colony site based on daily observations. The date of first sighting at this site indicated the beginning of marmot yearly activity in our population; most of the rest of the population emerged soon after this first sighting. Date was recorded as days since 1st of January. We used depth of snow in centimeter on 1 May as an index of snow cover during the reproductive period. Depth of snow was recorded at the RMBL weather station (38° 57′ N, 106° 59′ W at 2,900 m). Both emergence date and depth of snow were estimated at the population level.

Body mass

Each individual was weighted 2 to 15 times each year. Between 2002–2010, we collected 2,161 mass data for 270 females (512 female-years). Since trapping started most years in mid-May after marmots began foraging normally, 1 June was the earliest date we could accurately adjust body masses every year. Using repeated measurements of the same individual each summer, and a linear mixed model with a restricted maximum likelihood (REML) method, we adjusted body mass to 1 June by fitting a function that had a quadratic effect of day of the year (Ozgul et al. 2010; Martin and Pelletier 2011). We included female identity (as an intercept), day (as a slope representing individual mass gain rate), year, and colony as random effects. We then estimated the 1 June yearly body mass for each female conditional on the predicted random effects given by the best linear unbiased predictors, BLUPs. Despite potential biases associated with BLUPs (Hadfield et al. 2010), this mixed model approach provides adjusted body masses that are more accurate for each individual than those predicted using simple linear regressions (Martin and Pelletier 2011).

Docility index

From 2001–2010, we quantified the behavioral response of 111 adult females during 1,179 trapping events (average of six trapping events per year for an individual). At each trapping event, we estimated a marmot's docility, defined as an individual's reaction to a trapping event (Réale et al. 2000). While in the trap, we scored marmots on a 0–1 (no/yes) scale on whether they alarm called, tooth chattered, struggled, bit the cage, and delayed entry into the handling bag (i.e., did not run immediately into the handling bag when the trap was opened). The docility index was then defined as 5 minus the sum of these scores at each trapping event. A score of 5 thus indicates a docile individual, and inversely a low score indicates a non-docile individual. To obtain a unique docility score for each individual, we fit a linear mixed effects model of docility including time of the day, body mass at capture, and date at capture as fixed effects and marmot identity as a random effect. Using a log-likelihood ratio test (Pinheiro and Bates 2000), we found significant inter-individual variation in docility (LRT=268.78, $df=1$, $p<0.001$) with a repeatability of 0.295 estimated as the variance associated with the animal's identity divided by the phenotypic variance. We then extracted BLUPs for each individual and used these as a docility index.

Pedigree reconstruction

Parentage assignments were based on hair samples collected in the field from 2001–2010. DNA was extracted from samples and genotyped across 8–12 microsatellite loci. Alleles were visualized in GENEMAPPER, and parentage was assigned using CERVUS 3.0 (Kalinowski et al. 2007). We first assigned juveniles to their mother by trapping them as they emerged from their maternal burrows. When multiple lactating females used the same burrow, maternity was assigned only using genetic data. We then ran CERVUS to confirm behavioral assignment of mothers or assign mothers and assigned paternity for juveniles based on a likelihood approach set at 95 % trio confidence level. Further details on genotyping and parentage assignment are provided in Blumstein et al. (2010). Since 2002, 1,155 pups from 265 litters have been observed from which 1,141 were identified and trapped (i.e., only 14 pups from 10 litters were never trapped). Mothers were assigned to all pups, and fathers were assigned for 1,033 juveniles. Two hundred thirty-nine litters were polycotous (more than one juvenile). Paternity was not fully assigned for 29 litters (i.e., at least one juvenile was sired by an unknown male). See Table S1 in the appendix for details on trapping and genetic assignments of pups. A female with at least two different sires for a litter was defined as having multiple paternity. Litters without full paternity were considered multiply sired if at least one sire was assigned to a juvenile and that sire was not the most likely sire of other juveniles within the litter. Litters with not all juveniles captured, but with all juveniles assigned to a single male, were considered sired by a single male. Only polytocous litters were considered since monotocous litters could only have, by definition, one sire. Multiple paternity was then coded as 0 (only one sire) and 1 (multiple sires). Excluding litters without full paternity provided similar results.

Statistical analysis

Multiple paternities within a litter could be analyzed using two different approaches: fitting the number of sires per litter using a Poisson distribution or fitting the probability to have multiple sires for a litter using a binomial distribution. Given the structure of our data, low proportion of litters with multiple sires (18 %, Table S1), and the small variation in the number of sires of multiply sired litters (2–3, Table S1), we did not have enough power to directly model the number of sires per litter. We thus fitted a generalized linear mixed effect model of the probability to have multiple sires in a litter with a binomial error structure (logit link) as a function of the following fixed effects: litter size, age, docility, mass in June, operational sex ratio, emergence date, and snow pack level on May 1st because these factors could restrict the ability of females to obtain additional mates. We also tested different two-way interactions. First, we considered an interaction between snow depth and emergence date because we suspected that their effects were cumulative rather than simply being additive. Second, we considered that docility and body mass effects might be dependent on adequate environmental conditions to be expressed. We thus tested two-way interactions between environmental variables (snow depth, emergence date, and sex ratio) and both docility and body mass. Following Whittingham et al. (2006), results were presented for full models (i.e., including significant and non-significant effects) with the exception that non-significant interactions were eliminated because of their potential to bias other estimates (Engqvist 2005). All variables were standardized (mean of 0 and variance of 1) to facilitate comparison of the effect of different variables. The mean and range of each variable is reported in Table S2 in the appendix. To account for a non-linear change in the chance of detecting multiple paternity as litter size increased, we fitted a quadratic effect of litter size. Fitting litter size as a smoothed parameter in a generalized additive mixed model (gamm) provided a functional form similar to a quadratic function; thus, only the results of the parametric estimation are presented. Fitting litter size as an ordinal variable was not possible due to sample size constraints. All of the necessary data were available for 153 litters including 708 pups produced by 72 females. Female identity, year, and colony were included as random effects to account for pseudo-replication problems. To test the significance of the random effects, we used a log-likelihood ratio test (Pinheiro and Bates 2000). To see the temporal trend of multiple paternity over the study period, we also fitted a logisitic regression of multiple paternity as a function of time. All analyses were run in R 2.14.0 (R Development Core Team 2012) using the lmer function in the lme4 package (Bates et al. 2011). All data are available at www.eeb.ucla.edu/Faculty/Blumstein/MarmotsOfRMBL/data.html.

Results

Multiple paternity was detected in 18 % of the litters with at least two pups (i.e., 28/153 litters) from 21 females in different colonies. For all 28 multiply sired litters, at least one male originated from another colony than the mother. Over the last decade, we observed an increase in the frequency of multiple paternity (0.464±0.125 se; $z=3.70$; $p=0.002$; $N=8$). The probability of being sired by more than one male was higher for litters of 5 to 7 pups (Table 1, Fig. 1a). The occurrence of multiple paternity was also influenced by the following interactions: operational sex ratio×mass in June, docility×emergence date, and emergence date×snow in May (Table 1, Fig 1b–d). When the operational sex ratio was male biased, heavier females were more likely to produce litters with multiple sires (Table 1, Fig. 1b). When emerging early, non-

Table 1 Generalized linear mixed model explaining variation in multiple paternity in yellow-bellied marmot females estimated with 153 observations from 72 females over 9 years at the RMBL, Colorado. Variables were standardized (mean of 0 and variance of 1) before fitting the model. For estimate on raw variable scales, see Table S3 in the appendix

	Estimate (SE)	z	P
(Intercept)	−0.606 (0.345)	−1.757	0.079
Litter size	*1.229 (0.442)*	*2.777*	*0.005*
Litter size^2	*−0.685 (0.298)*	*−2.301*	*0.021*
Age (years)	−0.548 (0.363)	−1.507	0.132
Mass in June (g)	0.351 (0.366)	0.959	0.337
Docility	−0.273 (0.248)	−1.100	0.271
Operational sex ratio (OSR)	−0.077 (0.298)	−0.257	0.797
Emergence date (days)	*−1.192 (0.460)*	*−2.589*	*0.009*
Snow on 1 May (cm)	*−1.547 (0.522)*	*−2.963*	*0.003*
OSR × mass in June	*1.040 (0.526)*	*1.976*	*0.048*
Docility × emergence	*0.646 (0.329)*	*1.962*	*0.049*
Emergence × snow 1 May	*−3.289 (0.852)*	*−3.860*	*<0.0001*

Significant values are shown in italic

docile females had a higher probability of producing a multiply sired litter than more docile females, but docility had a weak effect on multiple paternity for individuals that emerged late (Table 1, Fig. 1c). During the 2 years of early emergence and with no (or limited) snow on 1 May, no multiple paternity was observed (Fig 1d). In years with later emergence date, a negative effect of emergence on multiple paternity was observed; there was an increasing effect with deeper snow on 1 May (Fig. 1d). The largest standardized effect sizes were estimated for emergence date and snow in May. Female identity, year, and colony explained no significant variation in the likelihood of producing a litter with more than one sire (all p values >0.90).

Discussion

Despite the fact that the reproductive strategy of yellow-bellied marmots is generally described as female-defense polygyny (Armitage 1986), we found that 18 % of their litters were sired by multiple fathers, a finding that suggests a

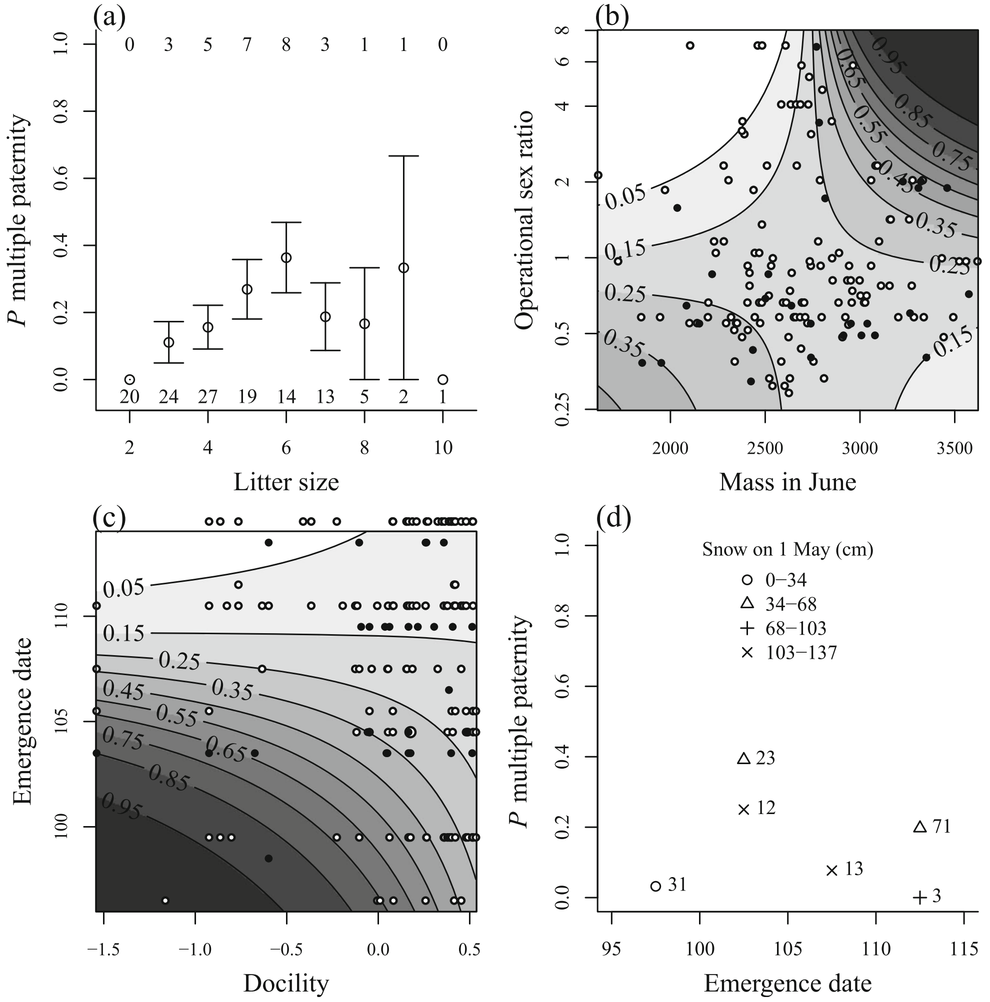

Fig. 1 Probability of a yellow-bellied marmot female siring offspring with more than one male as a function of **a** litter size, **b** mass in June (g) and operational sex ratio, **c** docility and emergence date (Julian date), and **d** snow on 1 May (cm) and emergence date. In **a**, each open circle represent the proportion of litters with multiple sires in the raw data (with standard errors) and sample size for non-multiply and multiply sired litters at 0 and 1, respectively. In contour plots (**b** and **c**), *full circles* indicate litters with multiple paternity, and *open circles* stand for single paternity within a litter. Each *line* represents a given probability of multiple paternity. *Darker areas* indicate higher probabilities of multiple paternity. Predictions were obtained from the logistic regression summarized in Table 1 with data transformed back to their original scales. In **d**, each point represents the proportion of litters with multiple sires in the raw data (with sample size) for different combinations of emergence date and snow on 1 May

polygynandrous mating system. The percentage of litters with multiple sires was relatively low compared to other species of sciurid rodents where multiple paternity varied from 16 to 90 % of litters (Waterman 2007). Indeed, more social species are expected to have higher rates of multiple paternity (Waterman 2007; Cohas and Allainé 2009), and this relatively low level multiple paternity probably reflects the facultative nature of yellow-bellied marmot sociality (Armitage and Downhower 1974; Frase and Hoffmann 1980).

Multiple paternity within a litter is related to environmental conditions, colony operational sex ratio, and by the female's body mass and docility. The standardized effect size of variables that explained variation in multiple paternity were the largest for environmental variables (i.e., emergence date and snow in May; Table 1) suggesting that they were driving the main pattern of multiple paternity. This result also supports previous work by Johnsen and Lifjeld (2003) that show that multiple paternity is influenced by environmental variables. The effects of emergence date, snow in May, and their interaction show that, for yellow-bellied marmots, multiple paternity is environmentally constrained. During the relatively short growing season, marmots must reproduce, lactate, wean pups, and gain sufficient mass before the next hibernation to increase their odds of surviving the winter. Pups weaned earlier have a higher probability of surviving their first winter (Armitage et al. 1976). Predation pressure during the mating season is high, and marmots are vulnerable to predation when crossing snow because they are conspicuous and escape burrows are unavailable. Indeed, we have seen coyotes (*Canis latrans*) kill marmots caught out from their burrows on snow-covered meadows. Not surprisingly, we found that multiple paternity increased in years when marmots emerged earlier and with less snow on the ground on 1 May. Ability to disperse and find mates during the reproductive season is a necessary pre-condition for multiple paternity. In eastern chipmunks (*Tamias striatus*), the percentage of litters with multiple paternity varied from 25 to 100 % when mating happened with and without snow, respectively (Bergeron et al. 2011). In years with late snowmelt, a female has two alternative strategies: she could come out and increase the risk of being killed while searching for males or she could mate as soon as possible (which may include mating below ground if a male is present in the hibernaculum). In years when marmots emerged later, the time to find a mate might be limited and higher synchronicity of females' estruses might decrease the probability of multiple mating. We were not able, however, to evaluate the duration of reproductive period or of breeding synchrony in our population. The interaction between snowpack on 1 May and emergence date indicated that the two strategies are likely to reinforce each other. Emerging late in a year with a lot of snow was not associated with multiple paternity. Thus, multiple paternity seems to be constrained by both time and mobility.

The time constrained on multiple paternity was not similar for all females. We found an interaction between emergence date and a female's personality on multiple paternity. Late-emerging females were not likely to produce multiply sired litters, but early emerging, non-docile females were more likely to have litters with more than one sire than docile females. Few studies have investigated how a female personality influences multiple paternity, however, in the social lizard (*Egernia whitii*), aggressive females were more likely to have litters with extra-pair paternity than non-aggressive ones (While et al. 2009). From a male's perspective, it may be more difficult to monopolize access to a non-docile mate, or non-docile females may be generally more active and more likely to interact with males. From a female's perspective, if females benefit from having more than one sire, non-docile females might not tolerate mate guarding. Seeking a mate exposes individuals to enhanced predation risk compared to mating with individuals from the same burrow. Given that docility could be linked to a risk-taking behavior (Careau et al. 2010), it might suggest that only non-docile females take the risks associated with seeking mates. Quantifying detailed interactions between males and females during the reproductive period would be required to study this, but, unfortunately, we were not able to obtain sufficient amounts of such data. In addition, better understanding how the behavior observed in a trap (i.e., docility) is related to conspecific interactions, and more ecological traits would be crucial for a better interpretation of that effect.

As expected by the intrasexual competition (Clutton-Brock 2007), we found a positive effect of male-biased operational sex ratio; however, the effect was modulated by female body mass. Light females had a reduced probability of having multiple sires with a weak effect of the operational sex ratio. Heavier females, however, had a higher rate of multiple paternity when the OSR was male-biased. Those results could suggest a potential cost of multiple paternity that only heavy females could bear such as increased predation risk (Magnhagen 1991), lost foraging time (Rowe 1992), or increased risk of disease (Sheldon 1993; White et al. 2011) Alternatively, the observed relationship could be explained by the fact that heavier females were more attractive (i.e., mate choice by males) or, as noted above, larger females could also be harder to guard than smaller ones. Our data, however, did not allow us to discriminate among these different possibilities.

Multiple paternity in yellow-bellied marmots seemed to be an opportunistic strategy. Females had multiple sires for their litters only in a rather narrow set of conditions: early snowmelt, early emergence, male-biased operational sex ratio, and heavy and non-docile females. The precise costs and benefits to females of having more than one sire, however, are still unclear. Females do not obtain increased access to resources, obtain more care, or are more protected by mating multiply in this system. Infanticide by males is extremely rare in yellow-bellied marmots, so paternity confusion to avoid infanticide cannot explain multiple paternity in this species. We are not aware of any obvious phenotypic benefits females obtained by mating with more than one male in this species. However, from a genetic perspective, mating with more than one male could ensure fertility (Hoogland 1998), increase mate quality (i.e., good genes) by promoting sperm competition (Firman and Simmons 2008), enhance genetic compatibility (Ivy 2007), or increase genetic variability of the litter (Hopper et al. 2003; for a review of genetic benefits, see Jennions and Petrie 2000). We suggest that multiple paternity in marmots should thus be influenced by indirect (i.e., genetic) but not by direct (i.e., material) benefits. It should be noted that multiple paternity is a direct indication of multiple mating; however, single paternity does not imply single mating since a single male could sire all the litter despite a multiple mating by a female.

Post-copulatory inbreeding avoidance has been suggested as a potential benefit of multiple mating, where the less related mate sired most of the offspring (Bergeron et al. 2011). Over the last decade, we observed an increase in inbreeding but no pre-copulatory inbreeding avoidance (based on mate choice) despite a survival cost of being inbreed (Olson et al. 2012). Over the same period, we also observed an increase in the frequency of multiple paternity. Multiple mating might then be associated with post-copulatory inbreeding avoidance tactics. Unfortunately, the relatively limited number of litters sired by more than one male prevented us from formally evaluating this hypothesis.

Based on long-term correlational data, we were not able to assess the causality pattern of multiple mating. Taken together, we have shown that environmental, social, morphological, and behavioral factors are related to breeding with multiple males and that the environment has the strongest effect. Future studies must identify the precise genetic benefits of multiple paternity from the female's perspective and evaluate the causality of the relations in order to understand the rather complex variation in multiple paternity in the wild.

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Ethical standards The research was in compliance with ethical guidelines and the current laws of the USA. Marmots were studied under protocols approved by the UCLA and the RMBL Animal Use and Care Committees and under permits issued annually by the Colorado Division of Wildlife.

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

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