1 **Environmental, social, morphological and behavioural constraints on opportunistic**

2 **multiple paternity**

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4 *Running title: Opportunistic multiple paternity*

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18   **Abstract:** Multiple mating and multiple paternity in polytocous species have been mostly

19   studied from an adaptive (i.e., cost-benefit) perspective. Disease, time, energy, and the risk of

20   injuries are well known costs of multiple mating, yet from both male and female perspectives, a

21   number of genetic and non-genetic benefits have also been identified. The effects of

22   environmental conditions and individual-specific behavior, however, are much less well

23   understood. Using a long-term study on yellow-bellied marmots (*Marmota flaviventris*), we

24   evaluated the impacts of environmental variation, social structure, female body mass, and female

25   docility (a personality trait) on the occurrence of multiple paternity. Multiple paternity was

26   influenced by environmental constraints, social constraints, a female's personality, and her body

27   mass at emergence from hibernation. Personality and mass effects were detected only when

28   environmental or social conditions were favorable. Our results suggest that multiple paternity is

29   mainly limited by the opportunity to have access to multiple mates and is influenced by costs or

30   mate choice because heavier females were more likely to have litters with multiple sires than

31   smaller ones. Future studies in other species might benefit from considering environmental

32   constraints when studying multiple paternity.

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34   **Key-words:** *Marmota flaviventris*, yellow bellied marmot, personality, multiple paternity

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37 Traditional sexual selection theory states that females receive few fitness benefits from multiple

38 paternities within a brood (Trivers 1972). However, more recent genetic evidence suggests that

39 multiple paternity, and thus mating with multiple males, is common in many mating systems,

40 including socially monogamous ones (Griffith et al. 2002; Cohas and Allainé 2009). Multiple

41 paternity is often explained using an adaptive (i.e., cost-benefit) approach from both male and

42 female perspectives (Solomon and Keane 2007; Waterman 2007). Males may mate with an

43 already mated female to increase their reproductive success (Emlen and Oring 1977). Females

44 may mate with more than a single male to obtain material and/or genetic benefits to increase

45 their reproductive success (Arnqvist and Nilsson 2000; Jennions and Petrie 2000; Hosken and

46 Stockley 2003). However, costs of multiple mating include a lost opportunity for foraging (Rowe

47 1992), higher predation risks (Magnhagen 1991), higher risks of acquiring diseases (Sheldon

48 1993; White et al. 2011), and increased risks of getting injured (Rowe 1994; Réale et al. 1996).

49

50 Generally, a number of factors may influence the likelihood of engaging in multiple mating.

51 Numerous hypotheses have been proposed to explain multiple mating in socially monogamous

52 system (Gowaty 1996). However most of them are dependent on paternal care or resources

53 benefits to the females (Gowaty 1996) and thus could not be tested in many mating systems. The

54 switch point theorem, a quantitative statement of the hypothesis that stochastic effects favored

55 the evolution of individuals able to make adaptively flexible reproductive decisions, is more

56 general and could be applied to any mating system (Gowaty and Hubbell 2009). The theorem

57 states that any parameter that influences survival, the probability of mate encounter, or the time

58 available to mate could affect a females' probability of mating with more than a single male

59 (Gowaty and Hubbell 2009). These parameters include (but are not limited to) social constraints

60 (Gowaty and Bridges 1991), environmental constraints (Schmoll 2011; Bleu et al. 2012),

61 morphological variation (Hoogland 1998), physiological variation (Mokkonen et al. 2012) and

62 behavioral variation (Patrick et al. 2012). For instance, the social environment may influence the

63 opportunity for mating with different mates. Male-biased sex ratios have been shown to increase

64 the prevalence of extra-pair paternity (Gowaty and Bridges 1991). Environmental conditions

65 may also influence the likelihood of mating with more than one male. Harsh conditions that limit

66 movement during the period of female fertility or conditions that may decrease the length of the

67 mating period could reduce the opportunity for multiple mating (Bergeron et al. 2011). Multiple

68 mating can also be influenced by a female's size (Travis et al. 1990; Hoogland 1998). For

69 instance, larger female sailfin mollys (*Poecilia latipinna*) produce larger litters, and their litters

70 are more likely to be multiply sired (Travis et al. 1990). This may not be surprising because

71 larger females might be more attractive to males because their body size permits them to produce

72 more eggs. Additionally, females in better condition might also be better able to bear any costs

73 associated with multiple mating (Hosken and Stockley 2003). Females in good condition might

74 better be able to search for mates or move between males who each may be associated with a set

75 of females (Byers et al. 1994). Finally, personality, which is defined as consistent individual

76 differences in behavior across time or context (Réale et al. 2007), may influence the probability

77 of a female reproducing and producing litters with multiple paternity (While et al. 2009; Patrick

78 et al. 2012). Previous research has shown that aggression may influence mode of paternity (intra-

79 versus extra-pair paternity; Patrick et al. 2012) and mating behavior (While et al. 2009) in

80 socially monogamous species. More aggressive and more exploratory females may either

81 encounter more mates, or might be harder for a given male to defend (Smuts and Smuts 1993).

82 Despite the potentially variable causes of multiple mating, few studies have investigated

83 environmental determinants of multiple mating (but see Johnsen and Lifjeld 2003). In addition,

84 the effect of personality on multiple mating has not been studied in non-socially monogamous

85   systems.

86

87   We use parentage assignments from a long-term study of yellow-bellied marmots (*Marmota*

88   *flaviventris*) to investigate the environmental, social, morphological, and behavioral determinants

89   of multiple paternity from a female's perspective. We use a multivariate approach that permits us

90   to identify the relative importance of the variables in explaining variation in multiple paternity.

91   Marmot mating systems have been described as female-defense polygyny, with litters that may

92   be sired by more than a single male and without paternal care (Armitage 1986). Marmots mate

93   shortly after emergence from hibernation and are under a time constraint to gain mass and

94   reproduce before the next hibernation (Frase and Hoffmann 1980). Unfortunately, mating

95   behavior is rarely observed since most of it happens underground. Hence, we studied multiple

96   paternity using parentage assignments and were not able to evaluate multiple mating directly. It

97   should be noted that multiple paternity is a direct indication of multiple mating, however, single

98   paternity does not imply single mating since a single male could sire all the litter despite a

99   multiple mating by a female. In sciurid rodents, multiple paternity varied from 16% to 90% of

100   litters (Waterman 2007) but it has not been estimated in yellow-bellied marmots. Based on the

101   switch point theorem (Gowaty and Hubbell 2009), we developed the following hypothesis:

102   multiple paternity should be affected by multiple variables including environmental, social,

103   morphological and behavioral traits.

104

105   Instead of testing only one type of trait included in the hypothesis, as has been done in most

106   previous studies, we developed four predictions based on previous knowledge of our system and

107   tested them simultaneously in a single model. First, we expected that male-biased sex-ratios

108   would increase multiple paternity due to higher male-male competition and higher probability of

5

109 meeting multiple males (Clutton-Brock 2007). Second, since individuals could move between

110 different colonies during the mating season, we predicted that as snow cover increased during the

111 mating season and as the date of emergence from hibernation of the first marmot increased, the

112 occurrence of multiple paternity would decrease because marmot movements are limited by

113 snow and constrained by time (Svendsen 1974; Bergeron et al. 2011). Third, considering that

114 females in good condition might be able to better manage costs associated with multiple mating

115 or might be preferred by males, we predicted that heavier females would produce more litters

116 with multiple paternity. Finally, using docility as an index of personality (Réale et al. 2007), we

117 predicted that a female's docility would be related to multiple paternity. Individuals with low

118 docility could be considered as 'pugnacious' (or 'aggressive') (Réale et al. 2007) but docility

119 could negatively or positively affect multiple paternity because non-docile females might be

120 harder to guard or because docile females were less aggressive and might tolerate more males.

121 Following Petrie et al. (1992) showing that more dominant and aggressive females were more

122 likely to mate multiply, we thus predicted that less docile females would produce more multiply

123 sired litters.

124

125 **Methods**

126 *Study system*

127 Yellow-bellied marmots are large (3-5 kg), semi-fossorial sciurid rodents (Armitage 2003).

128 Marmots typically live in colonies that consist of 1-6 adult females, 1-4 adult males and a

129 number of yearlings (one year old) and juveniles. Males typically emerge first from hibernation

130 and mate with receptive females within the first two to three weeks post-emergence (Armitage

131 1965; Blumstein 2009). Litter size ranges from 1-10 offspring in our population.

132

133   We studied yellow-bellied marmots at the Rocky Mountain Biological Laboratory (RMBL),

134   Gunnison County, Colorado, U.S.A, from to 2001 to 2010. We regularly trapped and

135   systematically observed marmots from mid-April to mid-September. Once trapped, marmots

136   were transferred to cloth handling bags where sex, reproductive status, and mass (accurate to

137   within 50g using a digital scale) were determined. Marmots were given permanent ear tags for

138   long-term identification, as well as unique fur marks (with Nyanzol fur dye) that allowed us to

139   observe and identify animals from a distance. A hair sample was taken on first capture of an

140   individual for genetic analysis. All individuals were marked and genotyped and 95% of animals

141   were of known age because they were first captured as pups or as yearlings. Marmots were

142   observed in eight geographically distinct colonies in two different areas (4 down valley and 4 up

143   valley). Within a summer animals could disperse between colonies within an area but movement

144   between areas has never been observed within a summer (Ozgul et al. 2009). In addition, during

145   one reproductive season, different males have been estimated to sire pups in multiple colonies in

146   the same area but never in different areas. Thus, we define the operational sex-ratio (OSR) for a

147   colony, for a given year, as the ratio of the number of adult (2 years and older) males in the area

148   by the number of adult females in the colony.

149

150   *Environmental variables*

151   For our study, emergence date was defined as the date at which the first marmot was seen at the

152   RMBL colony site based on daily observations. The date of first sighting at this site indicated the

153   beginning of marmot yearly activity in our population; most of the rest of the population

154   emerged soon after this first sighting. Date was recorded as days since 1st of January. We used

155   depth of snow in cm on 1 May as an index of snow cover during the reproductive period. Depth

156   of snow was recorded at the RMBL weather station (38°57'N, 106°59'W at 2900 m). Both

157   emergence date and depth of snow were estimated at the population level.

158

159   *Body mass*

160   Each individual was weighted 2 to 15 times each year. Between 2002-2010, we collected 2161

161   mass data for 270 females (512 female-years). Since trapping started most years in mid-May

162   after marmots began foraging normally, 1 June was the earliest date we could accurately adjust

163   body masses every year. Using repeated measurements of the same individual each summer, and

164   a linear mixed model with a restricted maximum likelihood (REML) method, we adjusted body

165   mass to 1 June by fitting a function that had a quadratic effect of day of the year (Ozgul et al.

166   2010; Martin and Pelletier 2011). We included female identity (as an intercept), day (as a slope

167   representing individual mass gain rate), year, and colony as random effects. We then estimated

168   the 1 June yearly body mass for each female conditional on the predicted random effects given

169   by the best linear unbiased predictors, BLUPs. Despite potential biases associated with BLUPs

170   (Hadfield et al. 2010), this mixed model approach provides adjusted body masses that are more

171   accurate for each individual than those predicted using simple linear regressions (Martin and

172   Pelletier 2011).

173

174   *Docility index*

175   From 2001-2010, we quantified the behavioral response of 111 adult females during 1179

176   trapping events (average 6 trapping events per year for an individual). At each trapping event, we

177   estimated a marmot's docility, defined as an individual's reaction to a trapping event (Réale et al.

178   2000). While in the trap, we scored marmots on a 0-1 (no/yes) scale on whether they alarm

179   called, tooth chattered, struggled, bit the cage, and delayed entry into the handling bag (i.e., did

180   not run immediately into the handling bag when the trap was opened). The docility index was

181 then defined as 5 minus the sum of these scores at each trapping event. A score of 5 thus

182 indicates a docile/non-aggressive individual, and inversely a low score indicates a non-

183 docile/aggressive individual. To obtain a unique docility score for each individual, we fit a linear

184 mixed-effects model of docility including time of the day, body mass at capture and date at

185 capture as fixed effects, and marmot identity as a random effect. We extracted best linear

186 unbiased predictors (BLUPs) for each individual and used these as a docility index. Using a log

187 likelihood ratio test (Pinheiro and Bates 2000), we found significant inter-individual variation in

188 docility (LRT = 268.78, df = 1, p < 0.001) with a repeatability of 0.295 estimated as the variance

189 associated with the animal's identity divided by the phenotypic variance.

190

191 *Pedigree reconstruction*

192 Parentage assignments were based on hair samples collected in the field from 2001-2010. DNA

193 was extracted from samples and genotyped across 8-12 microsatellite loci. Alleles were

194 visualized in GENEMAPPER and parentage was assigned using CERVUS 3.0 (Kalinowski et al.

195 2007). We first assigned juveniles to their mother by trapping them as they emerged from their

196 maternal burrows. When multiple lactating females used the same burrow, maternity was

197 assigned only using genetic data. We then ran CERVUS to confirm behavioral assignment of

198 mothers or assign mothers and assigned paternity for juveniles based on a likelihood approach

199 set at 95% trio confidence level. Further details on genotyping and parentage assignment are

200 provided in Blumstein et al. (2010). Since 2002, 1,155 pups from 265 litters have been observed

201 from which 1,141 were identified and trapped (i.e., only 14 pups from 10 litters were never

202 trapped). Mothers were assigned to all pups and fathers were assigned for 1,033 juveniles. 239

203 litters were polycotous (more than one juvenile). Paternity was not fully assigned for 29 litters

204 (i.e., at least one juvenile was sired by an unknown male). See Table S1 in the appendix for

205   details on trapping and genetic assignments of pups. A female with at least two different sires for

206   a litter was defined as having multiple paternity. Litters without full paternity were considered

207   multiply sired if at least one sire was assigned to a juvenile and that sire was not the most-likely

208   sire of other juveniles within the litter. Litters with not all juveniles captured, but with all

209   juveniles assigned to a single male, were considered sired by a single male. Only polytocous

210   litters were considered since monotocous litters could only have, by definition, one sire. Multiple

211   paternity was then coded as 0 (only 1 sire) and 1 (multiple sires). Excluding litters without full

212   paternity provided similar results.

213

214   *Statistical analysis*

215   We fitted a generalized linear mixed-effect model of the probability to have multiple sires in a

216   litter with a binomial error structure (logit link) as a function of the following fixed effects: litter

217   size, age, docility, mass in June, operational sex-ratio, emergence date, snow pack level on 1

218   May because these factors could restrict the ability for females to obtain additional mates. We

219   also tested different two-way interactions. First, we considered an interaction between snow

220   depth and emergence date because we suspected that their effects were cumulative rather than

221   simply being additive. Second, we considered that docility and body mass effects might be

222   dependent on adequate environmental conditions to be expressed. We thus tested two-way

223   interactions between environmental variables (snow depth, emergence date, and sex ratio) and

224   both docility and body mass. Following Whittingham et al. (2006), results were presented for full

225   models (i.e., including significant and non-significant effects) with the exception that non-

226   significant interactions were eliminated because of their potential to bias other estimates

227   (Engqvist 2005). All variables were standardized (mean of 0 and variance of 1) to facilitate

228   comparison of the effect of different variables. The mean and range of each variable is reported

229   in Table S2 in the appendix. To account for a non-linear change in the chance of detecting

230   multiple paternity as litter size increased, we fitted a quadratic effect of litter size. Fitting litter

231   size as a smoothed parameter in a generalized additive mixed model (gamm) provided a

232   functional form really similar to a quadratic function, thus only the results of the parametric

233   estimation are presented. Fitting litter size as an ordinal variable was not possible due to sample

234   size constraints. All of the necessary data were available for 153 litters including 708 pups

235   produced by 72 females. Female identity, year, and colony were included as random effects to

236   account for pseudo-replication problems. To test the significance of the random effects, we used

237   a log-likelihood ratio test (Pinheiro and Bates 2000). To see the temporal trend of multiple

238   paternity over the study period, we also fitted a logisitic regression of multiple paternity as a

239   function of time. All analyses were run in R 2.14.0 (R Development Core Team 2012) using the

240   lmer function in the lme4 package (Bates et al. 2011). All data are available at

241   www.eeb.ucla.edu/Faculty/Blumstein/MarmotsOfRMBL/data.html.

242

243   **Results**

244   Multiple paternity was detected in 18% of the litters with at least two pups (i.e., 28/153 litters)

245   from 21 females in different colonies. For all 28 multiply sired litters, at least one male

246   originated from another colony than the mother. Over the last decade, we observed an increase in

247   the frequency of multiple paternity (0.464 ± 0.125; $z = 3.70$; $p = 0.002$; $N = 8$). The probability

248   of being sired by more than one male was higher for litters of 5 to 7 pups (Table 1, Fig. 1a). The

249   occurrence of multiple paternity was also influenced by the following interactions: operational

250   sex-ratio * mass in June, docility * emergence date, and emergence date * snow in May (Table 1,

251   Fig 1b,c,d). When the operational sex-ratio was large, heavier females were more likely to

252   produce litters with multiple sires (Table 1, Fig. 1b). When emerging early, non-docile females

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253   had a higher probability of producing a multiply sired litter than more docile females, but

254   docility had a weak effect on multiple paternity for individuals that emerged late (Table 1, Fig.

255   1c). During the 2 years of early emergence and with no (or limited) snow on 1 May, no multiple

256   paternity was observed (Fig 1d). In years with later emergence date, a negative effect of

257   emergence on multiple paternity was observed; there was an increasing effect with deeper snow

258   on 1 May (Fig. 1d). The largest standardized effect sizes were estimated for emergence date and

259   snow in May. Female identity, year, and colony explained no significant variation in the

260   likelihood of producing a litter with more than one sire (all p-values > 0.90).

261

262   **Discussion**

263   Despite the fact that the reproductive strategy of yellow-bellied marmots is generally described

264   as female-defense polygyny (Armitage 1986), we found that 18% of their litters were sired by

265   multiple fathers, a finding that suggests a polygynandrous mating system. The percentage of

266   litters with multiple sires was relatively low compared to other species of sciurid rodents where

267   multiple paternity varied from 16% to 90% of litters (Waterman 2007). Indeed, more social

268   species are expected to have higher rates of multiple paternity (Waterman 2007; Cohas and

269   Allainé 2009), and this relatively low level multiple paternity probably reflects the facultative

270   nature of yellow-bellied marmot sociality (Armitage and Downhower 1974; Frase and Hoffmann

271   1980).

272

273   Multiple paternity within a litter is related to environmental conditions, colony operational sex-

274   ratio, and by the female's body mass and docility. The standardized effect size of variables that

275   explained variation in multiple paternity were the largest for environmental variables (i.e.,

276   emergence date and snow in May; Table 1) suggesting that they were driving the main pattern of

277   multiple paternity. This result also supports previous work by Johnsen and Lifjeld (2003) that

278   show that multiple paternity is influenced by environmental variables. The effects of emergence

279   date, snow in May, and their interaction show that, for yellow-bellied marmots, multiple

280   paternity is environmentally constrained. During the relatively short growing season, marmots

281   must reproduce, lactate, wean pups, and gain sufficient mass before the next hibernation to

282   increase their odds of surviving the winter. Pups weaned earlier have a higher probability of

283   surviving their first winter (Armitage et al. 1976). Predation pressure during the mating season is

284   high, and marmots are vulnerable to predation when crossing snow because they are conspicuous

285   and escape burrows are unavailable. Indeed, we have seen coyotes (*Canis latrans*) kill marmots

286   caught out from their burrows on snow-covered meadows. Not surprisingly, we found that

287   multiple paternity increased in years when marmots emerged earlier and with less snow on the

288   ground on 1 May. Ability to disperse and find mates during the reproductive season is a

289   necessary pre-condition for multiple paternity. In eastern chipmunks (*Tamias striatus*), the

290   percentage of litters with multiple paternity varied from 25% to 100% when mating happened

291   with and without snow respectively (Bergeron et al. 2011). In years with late snowmelt, a female

292   has two alternative strategies: she could come out and increase the risk of being killed while

293   searching for males, or she could mate as soon as possible (which may include mating below

294   ground if a male is present in the hibernaculum). In years when marmots emerged later, the time

295   to find a mate might be limited and higher synchronicity of females' estruses might decrease the

296   probability of multiple mating. We were not able, however, to evaluate the duration of

297   reproductive period or of breeding synchrony in our population. The interaction between

298   snowpack on 1 May and emergence date indicated that the two strategies are likely to reinforce

299   each other. Emerging late in a year with lot of snow was not associated with multiple paternity.

300   Thus, multiple paternity seems to be constrained by both time and mobility.

301

302   The time constrained on multiple paternity was not similar for all females. We found an

303   interaction between emergence date and a female's personality on multiple paternity. Late-

304   emerging females were not likely to produce multiply sired litters, but early-emerging, non-

305   docile females were more likely to have litters with more than one sire than docile females. Few

306   studies have investigated how personality influences multiple paternity, however, in the social

307   lizard (*Egernia whitii*), aggressive females were more likely to have litters with extra-pair

308   paternity than non-aggressive ones (While et al. 2009). From a male's perspective, it may be

309   more difficult to monopolize access to a non-docile mate, or non-docile females may be

310   generally more active and more likely to interact with males. From a female's perspective, if

311   females benefit from having more than one sire, non-docile females might not tolerate mate

312   guarding. Seeking a mate exposes individuals to enhanced predation risk compared to mating

313   with individuals from the same burrow. Given docility could be linked to risk taking behavior

314   (Careau et al. 2010), it might suggest that only non-docile females take the risks associated with

315   seeking mates. Quantifying detailed interactions between males and females during the

316   reproductive period would be required to study this but, unfortunately, we were not able to obtain

317   sufficient amounts of such data. In addition, better understanding how the behavior observed in a

318   trap (i.e., docility) is related to conspecifics interactions and more ecological traits would be

319   crucial for a better interpretation of that effect.

320

321   As expected by the intrasexual competition (Clutton-Brock 2007), we found a positive effect of

322   male-biased operational sex-ratio, however, the effect was modulated by female body mass.

323   Light females had a reduced probability of having multiple sires with a weak effect of the

324   operational sex ratio. Heavier females, however, had a higher rate of multiple paternity when the

325 OSR was male-biased. Those results could suggest a potential cost of multiple paternity that only

326 heavy females could bear. Potential costs associated with multiple paternity could be increased

327 predation risk (Magnhagen 1991), lost foraging time (Rowe 1992), increased risk of disease

328 (Sheldon 1993; White et al. 2011), or an enhanced risk of injury (Rowe 1994; Réale et al. 1996).

329 Alternatively, the observed relationship could be explained by the fact that heavier females were

330 more attractive (i.e., mate choice by males), or, as noted above, larger females could also be

331 harder to guard than smaller ones. Our data, however, did not allow us to discriminate among

332 these different possibilities.

333

334 Multiple paternity in yellow-bellied marmots seemed to be an opportunistic strategy. Females

335 had multiple sires for their litters only in a rather narrow set of conditions: early snowmelt, early

336 emergence, male-biased operational sex-ratio, heavy and non-docile females. The precise costs

337 and benefits to females of having more than one sire, however, are still unclear. Females do not

338 obtain increased access to resources, obtain more care, or are more protected by mating multiply

339 in this system. Infanticide by males is extremely rare in yellow-bellied marmots, so paternity

340 confusion to avoid infanticide cannot explain multiple paternity in this species. We are not aware

341 of any obvious phenotypic benefits females obtained by mating with more than one male in this

342 species. However, from a genetic perspective, mating with more than one male could ensure

343 fertility (Hoogland 1998), increase mate quality (i.e., good genes) by promoting sperm

344 competition (Firman and Simmons 2008), enhance genetic compatibility (Ivy 2007), or increase

345 genetic variability of the litter (Hopper et al. 2003; for a review of genetic benefits see Jennions

346 and Petrie 2000). Multiple paternity in marmots should thus be influenced by indirect (i.e.,

347 genetic) but not by direct (i.e., material) benefits.

348

349   Post-copulatory inbreeding avoidance has been suggested as a potential benefit of multiple

350   mating, where the less related mate sired most of the offspring (Bergeron et al. 2011). Over the

351   last decade, we observed an increase in inbreeding but no pre-copulatory inbreeding avoidance

352   (based on mate choice) despite a survival cost of being inbreed (Olson et al. 2012). Over the

353   same period, we also observed an increase in the frequency of multiple paternity. Multiple

354   mating might then be associated with post-copulatory inbreeding avoidance tactics.

355   Unfortunately, the relatively limited number of litters sired by more than one male prevented us

356   from formally evaluating this hypothesis.

357

358   Females may gain genetic benefits by mating with more than one male because they can increase

359   their litter size or to avoid sperm depletion problems with a multiply mated male (Jennions and

360   Petrie 2000). Both hypotheses were supported by the strong positive relationship between litter

361   size and multiple paternity. Due to the low rate of multiple paternity observed, we cannot rule

362   out, however, that the increased probability in detection of multiple paternity with larger litter

363   sizes drives the observed relationship. It is important to note that not having multiple sires for a

364   litter does not necessarily mean the female did not mate multiply. We were unable to

365   systematically and repeatedly observe mating (most are inferred to happen below ground after a

366   brief bout of above ground courtship).

367

368   Based on long-term correlational data, we were not able to assess the causality pattern of

369   multiple mating. Taken together we have shown that environmental, social, morphological and

370   behavioral factors are related to breeding with multiple males, and that the environment has the

371   strongest effect. Future studies must identify the precise genetic benefits of multiple paternity

372   from the female's perspective and evaluate the causality of the relations in order to understand

373   the rather complex variation in multiple paternity in the wild.

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384

385   **Ethical standards**

386   The research was in compliance with ethical guidelines and the current laws of the USA.

387   Marmots were studied under protocols approved by the UCLA and the RMBL Animal Use and

388   Care Committees and under permits issued annually by the Colorado Division of Wildlife.

389

390   **Conflict of interest**

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

392

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Figure Captions

517 **Figure 1** Probability of a yellow-bellied marmot female siring offspring with more than one

518 male as a function of a) litter size, b) mass in June (g) and operational sex ratio, c) docility and

519 emergence date (Julian date) and d) snow on 1 May (cm) and emergence date. In a), each open

520 circle represent the proportion of litters with multiple sires in the raw data (with standard errors)

521 and sample size for non-multiply and multiply sired litters at 0 and 1 respectively. In contour

522 plots (b and c), full circles indicate litters with multiple paternity and open circles stand for

523 single paternity within a litter. Each line represents a given probability of multiple paternity.

524 Darker areas indicating higher probabilities of multiple paternity. Predictions were obtained from

525 the logistic regression summarized in Table 1 with data transformed back to their original scales.

526 In d), each point represents the proportion of litters with multiple sires in the raw data (with

527 sample size) for different combinations of emergence date and snow on 1 May.
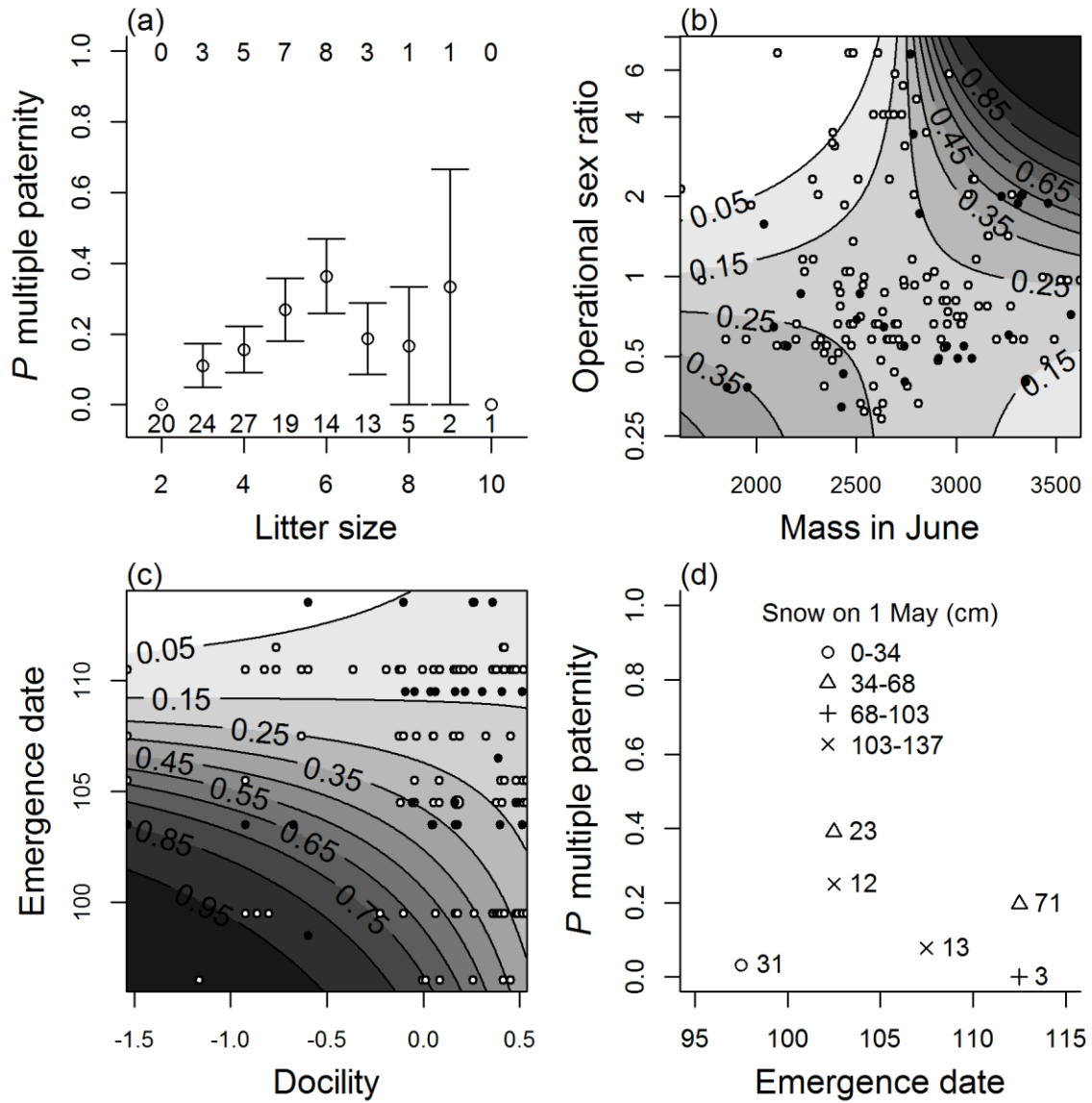
528 **Table 1:** Generalized linear mixed model explaining variation in multiple paternity in yellow

529 bellied marmot females estimated with 153 observations from 72 females over 9 years at the

530 RMBL, Colorado. Variables were standardized (mean of 0 and variance of 1) before fitting the

531 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 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**

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