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1 **Does multiple paternity explain phenotypic variation among offspring in**
2 **wild boar?**

3

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15

16 **Running title:** Paternity and offspring diversification

17

18 **Abstract:** During pregnancy, littermates compete to extract maternal resources from the
19 placenta. Unequal extraction of resources leads to developmental differences among offspring
20 and thus within-litter variation in offspring mass. Because competition among littermates can
21 be stronger among half-sibs, multiple paternity may represent an adaptive strategy allowing

22 females to increase within-litter phenotypic variation among offspring when facing variable
23 environments. Wild boar (*Sus scrofa*) females produce large litters with diversified offspring
24 in terms of body mass. Additionally, multiple paternity within a litter has been observed in
25 this promiscuous species. One can hypothesize that multiple paternity represents the
26 mechanism by which females increase within-litter phenotypic variation. Combining long-
27 term monitoring data with paternity analyses in a wild boar population, we tested whether the
28 increase in the number of fathers within a litter explained the increase in within-litter variation
29 in offspring mass observed in large litters. We showed that heavy females mated earlier
30 during the rut, produced larger litters with a higher number of fathers and more variable fetus
31 mass than lighter females. Within-litter variation of offspring mass increased with gestation
32 stage and litter size, suggesting differential allocation of maternal resource among offspring *in*
33 *utero*. However, we found only a weak paternal effect on offspring mass and no direct effect
34 of the number of fathers on the within-litter variation in offspring mass. These results indicate
35 that differential maternal allocation to offspring during pregnancy is unlikely related to
36 paternal identity in this species.

37

38 **Keywords:** fetus mass, paternal identity, phenotypic polymorphism, sibling rivalry

39

40 **Introduction**

41 Natural selection on body size is generally positive (Kingsolver and Diamond 2011),
42 particularly during early life stages. For example, in mammals and birds, heavier offspring
43 often exhibit high survival (see Ronget et al. 2017 for meta-analyses). However, because of
44 trade-offs between the size and number of offspring (Smith and Fretwell 1974; Lloyd 1987;
45 Winkler and Wallin 1987), producing many large offspring within a single reproductive event
46 is not a sustainable reproductive tactic for polytocous species. Thus, maternal resources are
47 either equally allocated among offspring (favoring an optimal offspring size *sensu* Smith and
48 Fretwell 1974), or differentially allocated among them (Trivers 1974; see e.g. Kühl et al. 2007
49 in saiga antelope *Saiga tatarica*) leading to within-litter/clutch variation in offspring mass. In
50 variable and unpredictable environments, such a diversification of offspring phenotypes
51 through differential maternal allocation may contribute to minimizing variance in
52 reproductive success among years (Philippi and Seger 1989; Starrfelt and Kokko 2012;
53 Sæther and Engen 2015) and thus maximizing fitness (coin-flipping strategy *sensu* Kaplan
54 and Cooper 1984; see also Gamelon et al. 2013b for a review in a variety of taxa).

55 Within-litter variation in offspring mass can result from contrasting abilities for young
56 to acquire and/or use maternal resources. Indeed, in the uterine environment of polytocous
57 species, littermates compete to extract maternal resources from the placenta (Drake et al.
58 2008). Unequal extraction of resources ultimately leads to important developmental
59 differences among offspring (Mock and Parker 1997) and potential high within-litter variation
60 in offspring mass. In polyandrous species, where one female mates with multiple males in a
61 single breeding event, littermates sired by different fathers are genetically more diverse
62 (Williams 1975; Madsen et al. 1992). Hamilton's rule on kinship selection predicts that
63 competition among offspring should be stronger when genetic relationship is low (Hamilton,

64 1964; Trivers, 1974; Watson, 1991; Mock & Parker, 1997; Yasui, 2001). One can thus
65 hypothesize that multiple paternity represents an adaptive strategy allowing females to
66 increase within-litter phenotypic variation among offspring (Yasui 1998; Fox and Rauter
67 2003). Importantly, this hypothesis posits that the ability of offspring to acquire and/or use
68 maternal resources depends on paternally derived alleles.

69 In wild boar (*Sus scrofa*), litter size increases with mother body mass. Heavy females
70 produce large litters with a mixture of heavy and light offspring, whereas lighter females
71 produce litters with similar-sized offspring (Gamelon et al. 2013b). In this polytocous species,
72 contrary to other large mammalian species of herbivores (Gaillard et al. 2000), piglet body
73 mass has little influence on survival (Baubet et al. 1995) allowing females to produce a large
74 range of offspring phenotypes. Furthermore, by producing diversified offspring phenotypes at
75 birth, heavy females may match the mass of their offspring with teat productivity, thus
76 decreasing within-litter competition to get access to maternal milk, and thereby increasing the
77 chance of rearing many offspring at a given breeding event (Gamelon et al. 2013a). The
78 species has been classically described as polygynous with female monopolization by males,
79 but a recent study has reported multiple paternity suggesting a promiscuous mating system in
80 this species (Gayet et al. 2016). These observations open the possibility for polyandry in wild
81 boar to be an adaptive strategy that increases offspring diversity within a litter. If mating with
82 multiple males is the pathway by which females increase the phenotypic polymorphism of
83 their offspring, differences in piglet mass should be partly determined by paternally derived
84 alleles, and we expect a paternal genetic effect on offspring mass as well as more variable
85 offspring in litters sired by many fathers.

86 Taking advantage of a unique long-term monitoring of a wild boar population, we
87 tested the hypothesis that multiple paternity mediates within-litter diversification of offspring
88 phenotypes. We extended previous works linking female body mass with diversification of

89 offspring phenotypes (see Gamelon et al. 2013b) by including paternity analyses. We
90 identified fathers of fetuses from females killed during hunting and tested for a paternal effect
91 on fetus mass. Moreover, we explored the pathways through which female body mass
92 influences the diversification of offspring phenotypes by testing specifically a direct effect of
93 the number of fathers per litter on phenotypic variation among offspring.

94

95 **Materials and methods**

96 **Study site and data collection**

97 The study was conducted in northeastern France in the 11,000 ha forest of Châteauvillain-
98 Arc-en-Barrois. In this area, wild boars are heavily hunted each year between October and
99 February and the annual survival is 0.48 [95% CI: 0.44; 0.51] and 0.23 [0.17; 0.30] for adult
100 females and adult males respectively (Toïgo et al. 2008). Between 2007 and 2014, we
101 recorded the dressed body mass (*BM*: body mass without digestive tract, heart, lungs, liver,
102 reproductive tract and blood) of 136 pregnant females shot and their sampling date. For each
103 female, we also recorded the litter size (*LS*) and each fetus (n=711) was weighed, measured
104 (crown-rump length, in millimeters) and sexed. From the average fetus length within a litter
105 (*Length*), we estimated gestation stage in days by applying the model of Henry (1968):
106 $\text{gestation stage (in days)} = 23.43 + 0.32 * \text{Length (in mm)}$ (see Gamelon et al. 2013b for a
107 similar approach). From this estimated gestation stage and the sampling date, we back-
108 calculated the timing of mating. In order to account for yearly variation in the timing of the
109 mating season, we expressed the timing of mating for each female as the number of days
110 elapsed since the first female has mated in each particular season (*Timing*). Thus, a *Timing* of
111 zero characterizes the most precocious female in each given year. The average fetus length at
112 sampling depends on both the timing of mating and the sampling date. Because both the
113 mating season (ranging between July and January, see Results) and the sampling period (from

114 October to February) are widely spread in the year, there is no correlation between the timing
115 of mating and the average fetus length within a litter when sampled.

116

117 **Paternity assessment**

118 Tissue samples were collected from 136 sows, their litters, and from sampled putative fathers.

119 As putative fathers we considered all the 762 males shot larger than 30 kilograms. The age

120 class of each putative father was recorded based on tooth eruption patterns (Matschke 1967).

121 Three age classes were considered: juvenile (less than one year of age), subadult (between one

122 and two years of age) and adult (two years of age or older). All tissue samples were

123 genotyped at 12 microsatellite loci (see Gayet et al. 2016 and Appendix S1 for details). The

124 genotypes of mothers, offspring and putative reproductive males, as well as the known

125 mother-offspring relationships were used in COLONY 2.0.6.1 (Jones and Wang 2010) to

126 assess, for each hunting season t , the father (whether sampled or not) of each sampled fetus.

127 We analyzed all the litters considering as putative fathers all males sampled at season t ,

128 subadult and adult males sampled at season $t+1$ and adult males sampled at season $t+2$.

129 Parentage among individuals was inferred by maximum likelihood with COLONY (Jones et al.

130 2010). As derived parameter from the paternity analysis, we calculated the number of fathers

131 per litter. To ensure that the number of fathers per litter was correctly estimated, the paternity

132 analysis has been performed four times as recommended (see for example Wang and Santure

133 2009; Todd et al. 2013). The estimated number of fathers per litter was effectively consistent

134 among paternity analyses (results not shown here).

135

136 **Effect of father identity on fetus mass**

137 For multiple paternity to translate into an increase in within-litter variation in offspring mass,

138 father identity should affect offspring mass *in utero*. We estimated this effect for fathers that

139 have produced more than one offspring by fitting a linear mixed-effect model using Markov
140 Chain Monte Carlo (MCMC) techniques (Hadfield 2010). Individual fetus mass was included
141 as response variable, fetus sex and mother identity as fixed factors and father identity as a
142 random factor and we assumed a Gaussian distribution. Including maternal identity and sex as
143 fixed effects allowed us correcting offspring mass for factors (female body mass and
144 condition, gestation stage, year and litter size) inducing among-litter variation in body mass as
145 well as the sex effect on offspring mass. The remaining part of the variance in offspring mass
146 thus only results from paternal effects and residual variation. We calculated the paternal effect
147 as the ratio of the variance in offspring mass due to father identity, divided by the total
148 variance: $\frac{\sigma_{\text{Father}}^2}{\sigma_{\text{Father}}^2 + \sigma_{\text{Residuals}}^2}$, where σ_{Father}^2 is the random variance associated with the father
149 identity, and $\sigma_{\text{Residuals}}^2$ is the residual variance. Half-sibs in different litters, i.e. from the same
150 father but different mothers, may have different body mass simply because they were sampled
151 at different gestation stages. Using mother identity as fixed factor does not entirely account
152 for this effect because mass and mass differences among fetuses do not increase linearly
153 during gestation. Neglecting such non-linear growth may artificially increase the residual
154 variance and thus decrease the estimate of the paternal effect. Therefore, the response variable
155 fetus mass was log-transformed in order to perform the analysis on a proportional scale.

156 We ran 260,000 MCMC iterations, with a burn-in of 10,000 iterations thinning every
157 250th observation, and non-informative priors were used (for the variance structures (R and
158 G), we used an expected variance of 1 and 0.002 degree of belief parameter for the inverse-
159 Wishart). We computed the posterior modes and the 95% credible intervals of this ratio, of
160 fetus sex and of the variance associated with the father identity with the “HPDinterval”
161 function of the package MCMCglmm (Hadfield 2010) in R 3.4.0 (R Development Core Team
162 2017). We assessed convergence with the functions “heidel.diag” (Heidelberger and Welch’s

163 convergence diagnostic) and “geweke.diag” (Geweke’s convergence diagnostic) in R and
164 from visual inspection. We checked normality and homoscedasticity of the residuals.

165

166 **Effect of the number of fathers on within-litter variation in fetus mass**

167 We estimated the within-litter variation in offspring mass by calculating the coefficient of
168 variation ($CV = SD/mean$) of fetus mass (on the natural scale) for each full litter, corrected for
169 small samples as suggested by Haldane (1955). To assess whether multiple paternity mediates
170 the increase of within-litter variation, we used confirmatory path analyses (Shibley 2009,
171 2013). We determined the causal pathways from mother body mass (BM) to within-litter
172 variation, through the number of fathers (F) within a litter and/or litter size (LS). We included
173 a correlation between F and LS (see Gayet et al. 2016). Because mating ranged between July
174 and January (see Results) and because females were killed from October to February, we
175 observed litters at different periods of the year and at different gestation stages. Therefore, we
176 included both the timing of mating ($Timing$) and the average fetus length ($Length$) (as a
177 measure of gestation stage) in our models.

178 First, we fitted the global path model including all these possible effects (model 8 in
179 table 1 and Appendix S2). Therefore, the global path model consisted in five linear
180 relationships implemented with the `lm` function: one linking number of fathers F as a response
181 variable to mother body mass BM and timing of mating $Timing$, one linking litter size LS as a
182 response variable to BM , one linking $Timing$ as a response variable to BM , one linking
183 average fetus length $Length$ to $Timing$ and one linking CV of fetus mass within a litter as a
184 response variable to LS , $Length$ and F . Second, we fitted 12 competing models derived from
185 the global path model (see table 1 and Appendix S2). For the 13 competing path models, we
186 recovered the standardized regression coefficients of each linear relationships and their

187 associated SE. We used the Akaike Information Criterion corrected for small sample size
188 (AICc) to select the best path model among the ones presented in table 1 and Appendix S2.
189 We calculated the Fisher's C statistic of the path model retained as well as the chi-squared test
190 degrees of freedom. The C statistic should follow a chi-squared distribution if the data are
191 effectively generated following the cause-order effect modeled in the path model (Shipley
192 2009; 2013). The analyses were implemented using the package piecewiseSEM (Lefcheck
193 2016) in R version 3.4.0 (R Development Core Team 2017).

194

195 **Results**

196 **Effect of father identity on fetus mass**

197 This analysis has been restricted to fathers that have produced more than one offspring. The
198 sample consists in 148 fathers (42 sampled males and 106 unsampled males) and 624 fetuses,
199 with 178 offspring assigned to sampled fathers and 446 assigned to unsampled fathers. We
200 found no marked difference between sampled and unsampled fathers in terms of number of
201 offspring sired, with sampled fathers siring on average 4.24 ± 2.94 (mean \pm SD) offspring
202 while unsampled fathers sired 4.21 ± 2.37 offspring (figure 1). Remember that fathers siring
203 only one offspring have been excluded from the analysis. Errors in paternity assignment for
204 unsampled fathers would have led to lower average number of offspring sired by these
205 unknown males. The absence of marked difference in the number of offspring between
206 sampled and unsampled fathers confirms that the unsampled fathers have been correctly
207 assigned to their offspring. Overall, fathers sired offspring with one (61.5% of the cases), two
208 (29.1%), three (8.1%) or four (1.4%) partners.

209 The linear mixed-effect model evaluating paternal effect on fetus mass *in utero*
210 showed no lack of convergence (Appendix S3). After accounting for maternal effects, we
211 found that female fetuses were 5% [95% CRI: 0.04; 0.07] lighter than male fetuses, in
212 accordance with previous studies (Servanty et al. 2007). The variance associated with paternal
213 identity, σ_{Father}^2 , was low 0.0005 [95% CRI: 0.0002; 0.002]. The ratio $\frac{\sigma_{Father}^2}{\sigma_{Father}^2 + \sigma_{Residuals}^2}$ was
214 0.09 [95% CRI: 0.03; 0.21] indicating that paternal identity only explained 9% of the within-
215 litter variance in offspring mass, which is the variance remaining when sex and all maternal
216 effects were accounted for. Noticeably, the same analysis restricted to the 178 fetuses for
217 which fathers were known (i.e., sampled) also indicated a small contribution of father identity
218 to the within-litter variance (10% [95% CRI: 0.02; 0.37]).

219

220 **Effect of the number of fathers on within-litter variation in fetus mass**

221 Because this analysis required the estimation of within-litter coefficient of variation in fetus
222 mass (CV), it has been restricted to the 116 full litters; 15 had all fathers known (i.e.,
223 identified from sampled males), 30 had some fathers sampled while the others were
224 unsampled, and 71 litters had all fathers unsampled. The sample consists in 211 fathers (48
225 sampled and 163 unsampled males) and 617 fetuses, with 154 offspring assigned to sampled
226 fathers and 463 assigned to unsampled fathers. In this dataset, sampled fathers sired on
227 average 3.21 ± 2.88 offspring while unsampled fathers sired 2.84 ± 2.31 offspring (figure 2a).
228 Once again, this confirms that unsampled fathers have been correctly assigned to their
229 offspring. The average number of fathers within a litter was 2.28 ± 1.28 (figure 2b) and
230 multiple paternity was observed in 63.8% of the litters.

231 The best path model (model 1, table 1 and figure 3) satisfactorily fitted the data based
232 on comparison of the Fisher's C statistic to a chi-squared distribution ($C_{16}=21.53$, p-
233 value=0.159). It included indirect positive effects of mother body mass and number of fathers
234 per litter on the within-litter variation through an increase of litter size (figure 3). Indeed,
235 heavy females produced large litters sired by many fathers with diversified offspring mass,
236 but there was no direct link between the number of fathers per litter and the within-litter
237 variation in fetus mass. This was confirmed by the second best path model (model 2, table 1
238 and Appendix S2), close in terms of AICc value, that did not include direct effect of the
239 number of fathers per litter on CV of fetus mass either. In accordance with these results, the
240 global path model (model 8) confirmed the absence of effect of multiple paternity on within-
241 litter variation (effect size $\pm SE = 0.003 \pm 0.10$; table 1 and Appendix S2).

242 The earliest mating reported in our study occurred in mid-July (in 2014) and the latest
243 in mid-January (in 2011) suggesting a particularly long mating season. We found that *Timing*,
244 a metric indicating how precocious was the mating for a female in a given season, is
245 negatively associated with female mass (figure 3). Therefore, heavy females reproduced
246 earlier than lighter ones during the mating season. Moreover, within-litter variation increased
247 with gestation stage (defined as the average fetus length *Length*) (figure 3). Because within-
248 litter variation in offspring mass was estimated using the coefficient of variation (CV), this
249 effect indicates that variation in offspring mass increases more during gestation than the
250 expected proportional increase of the standard deviation with the mean. Although based on
251 cross-sectional data, this result suggests that offspring differ in their growth rate.

252

253

254 **Discussion**

255 Our findings showed that, contrary to expectations, the diversification of offspring phenotypes
256 within a litter did not directly result from multiple paternity and the genetic diversification of
257 the offspring. Indeed, our path analysis showed that although larger litters were sired by more
258 fathers as previously observed (Gayet et al. 2016) and contained fetuses of more variable
259 mass than smaller litters, within-litter variation in fetus mass did not directly result from an
260 increase in the number of fathers siring the litter. This result is further supported by the lack
261 of paternal effect on fetus mass *in utero*, as indicated by the small proportion of the within-
262 litter variance explained by paternal identity. Although expected for early-life stages (Wilson
263 et al. 2005), this weak paternal effect on offspring mass strongly limits the possibility for the
264 females to diversify the mass of their offspring by mating with several, genetically distinct,
265 fathers. It is noteworthy that, due to high genetic diversity among offspring belonging to
266 different fathers, other types of genetic effects such as dominance or epistatic interactions
267 may also affect within-litter variance in offspring mass (Neff and Pitcher 2005). Exploring
268 such effects would require repeated measurements of offspring produced by a given pair of
269 mother and father, which is unfortunately impossible in our study system.

270 The reliability of these results from the path analysis and the paternal effect analysis
271 depends on the correct assignment of fathers to their offspring. Correct assignment may be
272 problematic when the genotype of the father is not available (unsampled father). Error in
273 paternity assignment should lead to an underestimation of kinship among offspring by
274 assigning offspring from the same father to different fathers. This type of error would
275 underestimate the paternal (random) variance and would artificially increase the estimated
276 number of fathers per litter. However, we found similar contribution of paternal identity to the
277 within-litter mass variation when all offspring were included in the analysis and when the

278 analysis was restricted to offspring for which fathers were sampled. In addition, we showed
279 similar average number of offspring sired by sampled fathers and unsampled fathers. Finally,
280 the estimated number of fathers per litter was consistent among four paternity analyses.
281 Consequently, we are confident that potential errors in paternity assignment are unlikely to
282 affect our results.

283 Our path analysis identifies the most likely pathways through which female body mass
284 affects within-litter variation in fetus mass. Depending on their body mass, females mate at
285 different periods during the rut. Heavy/old females mate earlier during the rut and have larger
286 litters sired by a high number of fathers than lighter/younger ones. These findings suggest
287 inter-individual heterogeneity among females, with earlier mating and thus parturition dates in
288 old and heavy females compared to young and light ones (see Feder et al. 2008 for similar
289 pattern on bighorn sheep *Ovis canadensis*). Because wild boar females having reached 33–
290 41% of their full body mass are able to reproduce (Servanty et al. 2009), it is likely that
291 light/young females are primiparous, born in spring and reaching this threshold body mass to
292 reproduce only later during the mating season. In turn, large litters produced by heavy females
293 tended to have higher within-litter variation in offspring mass, this variation increasing during
294 gestation.

295 The increase in CV of fetus mass during gestation indicates that initial differences in
296 body mass among offspring are magnified during gestation most likely due to different
297 growth rates among offspring. This differential growth is not affected by the fathers' genotype
298 and the number of fathers in the litter. Indeed, if multiple paternity was involved in within-
299 litter variation in offspring mass, through different abilities among half-sibs to acquire and/or
300 use maternal resources, we should have detected a direct effect of the number of fathers on
301 within-litter diversification. This was not the case and we regard multiple paternity as an
302 unlikely mechanism to explain diversification of offspring mass in large litters. Differential

303 maternal allocation among offspring thus does not depend on father identity. Noticeably,
304 although polyandry does not affect offspring mass variation *in utero*, it may still lead to the
305 production of diversified offspring later in life and therefore might represent an adaptive
306 strategy for the females in variable environments.

307 Several mechanisms, not mutually exclusive, could explain differential maternal
308 allocation among offspring *in utero*. Competition among offspring to get access to maternal
309 resources might be particularly strong in the uterus (Drake et al. 2008), making sibling rivalry
310 one possible explanation for differential maternal allocation (Mock and Parker 1997; Hudson
311 and Trillmich 2007). For instance, some embryos may prevent the release of some uterine
312 secretions, thus affecting directly the growth of other littermates (Pope et al. 1990).
313 Development constraints can also favor differential maternal allocation among offspring.
314 Indeed, implantation sites along the uterine horns are heterogeneous in terms of space,
315 vascular supply and placental efficiency (Argente et al. 2006). Thus, the acquisition of
316 maternal resources clearly depends on the position of the offspring in the uterine environment.
317 This can ultimately lead to differences in offspring mass. In support of that, in domestic pig
318 (*Sus scrofa*) and rabbit (*Oryctolagus cuniculus*), there is evidence that offspring occupying
319 central positions in the uterine horns are generally lighter than the ones implanted at end
320 positions (Dziuk 1992; Bautista et al. 2015). Whether differential maternal allocation among
321 offspring *in utero* is a female strategy to produce diversified offspring and thus to minimize
322 variance in reproductive success among years (Philippi and Seger 1989; Starrfelt and Kokko
323 2012; Sæther and Engen 2015) or simply results from developmental constraints remains to
324 be carefully explored and offers promising avenues of research.

325

326

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331

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338

339

340 **Data accessibility**

341 Analyses reported in this article can be reproduced using the data provided by Gamelon et al.
342 (2018).

343 **References**

- 344 Argente, M. J., M. A. Santacreu, A. Climent, and A. Blasco. 2006. Influence of available
345 uterine space per fetus on fetal development and prenatal survival in rabbits selected
346 for uterine capacity. *Livest. Sci.* 102:83–91.
- 347 Baubet, E., G. Van Laere, and J. M. Gaillard. 1995. Growth and survival in piglets. *J. Mt.*
348 *Ecol.* 3.
- 349 Bautista, A., H. G. Rödel, R. Monclús, M. Juárez-Romero, E. Cruz-Sánchez, M. Martínez-
350 Gómez, and R. Hudson. 2015. Intrauterine position as a predictor of postnatal growth
351 and survival in the rabbit. *Physiol. Behav.* 138:101–106.
- 352 Drake, A., D. Fraser, and D. M. Weary. 2008. Parent–offspring resource allocation in
353 domestic pigs. *Behav. Ecol. Sociobiol.* 62:309–319.
- 354 Dziuk, P. 1992. Survival of Peas, Peaches, and Prenatal Pigs. *Perspect. Biol. Med.* 35:357–
355 360.
- 356 Feder, C., J. G. A. Martin, M. Festa-Bianchet, C. Bérubé, and J. Jorgenson. 2008. Never too
357 late? Consequences of late birthdate for mass and survival of bighorn lambs.
358 *Oecologia* 156:773–781.
- 359 Fox, C. W., and C. M. Rauter. 2003. Bet-hedging and the evolution of multiple mating. *Evol.*
360 *Ecol. Res.* 5:273–286.
- 361 Gaillard, J. M., M. Festa-Bianchet, D. Delorme, and J. Jorgenson. 2000. Body mass and
362 individual fitness in female ungulates: bigger is not always better. *Proc. R. Soc. B*
363 *Biol. Sci.* 267:471–477.
- 364 Gamelon, M., M. Douhard, E. Baubet, O. Gimenez, S. Brandt, and J.-M. Gaillard. 2013a.
365 Fluctuating food resources influence developmental plasticity in wild boar. *Biol. Lett.*
366 9:20130419.

367 Gamelon, M., J.-M. Gaillard, E. Baubet, S. Devillard, L. Say, S. Brandt, and O. Gimenez.
368 2013b. The relationship between phenotypic variation among offspring and mother
369 body mass in wild boar: evidence of coin-flipping? *J. Anim. Ecol.* 82:937–945.

370 Gamelon, M., T. Gayet, E. Baubet, S. Devillard, L. Say, S. Brandt, C. Pélabon, and B.-E.
371 Sæther. 2018. Data from: Does multiple paternity explain phenotypic variation among
372 offspring in wild boar? *Behav. Ecol.* doi:10.5061/dryad.fn1q473.

373 Gayet, T., S. Devillard, M. Gamelon, S. Brandt, L. Say, and E. Baubet. 2016. On the
374 evolutionary consequences of increasing litter size with multiple paternity in wild boar
375 (*Sus scrofa scrofa*). *Evolution* 70:1386–1397.

376 Hadfield, J. D. 2010. MCMC Methods for Multi-Response Generalized Linear Mixed
377 Models: The **MCMCglmm** R Package. *J. Stat. Softw.* 33.

378 Haldane, J. B. S. 1955. The measurement of variation. *Evolution* 9:484–484.

379 Hamilton, W. D. 1964. The genetical evolution of social behaviour. I. *J. Theor. Biol.* 7:1–16.

380 Henry, V. G. 1968. Fetal development in european wild hogs. *J. Wildl. Manag.* 32:966–970.

381 Hudson, R., and F. Trillmich. 2007. Sibling competition and cooperation in mammals:
382 challenges, developments and prospects. *Behav. Ecol. Sociobiol.* 62:299–307.

383 Jones, A. G., C. M. Small, K. A. Paczolt, and N. L. Ratterman. 2010. A practical guide to
384 methods of parentage analysis. *Mol. Ecol. Resour.* 10:6–30.

385 Jones, O. R., and J. Wang. 2010. COLONY: a program for parentage and sibship inference
386 from multilocus genotype data. *Mol. Ecol. Resour.* 10:551–555.

387 Kaplan, R. H., and W. S. Cooper. 1984. The evolution of developmental plasticity in
388 reproductive characteristics: an application of the “adaptive coin-flipping” principle.
389 *Am. Nat.* 123:393–410.

390 Kingsolver, J. G., and S. E. Diamond. 2011. Phenotypic selection in natural populations: what
391 limits directional selection? *Am. Nat.* 177:346–357.

392 K hl, A., A. Mysterud, G. I. Erdnenov, A. A. Lushchekina, I. A. Grachev, A. B. Bekenov,
393 and E. J. Milner-Gulland. 2007. The ‘big spenders’ of the steppe: sex-specific
394 maternal allocation and twinning in the saiga antelope. *Proc. R. Soc. Lond. B Biol.*
395 *Sci.* 274:1293–1299.

396 Lefcheck, J. S. 2016. piecewiseSEM: Piecewise structural equation modelling in r for
397 ecology, evolution, and systematics. *Methods Ecol. Evol.* 7:573–579.

398 Lloyd, D. G. 1987. Selection of offspring size at independence and other size-versus-number
399 strategies. *Am. Nat.* 129:800–817.

400 Madsen, T., R. Shine, J. Loman, and T. H kansson. 1992. Why do female adders copulate so
401 frequently? *Nature* 355:440–441.

402 Matschke, G. H. 1967. Aging European wild hogs by dentition. *J. Wildl. Manag.* 31:109–113.

403 Mock, D. W., and G. A. Parker. 1997. *The Evolution of Sibling Rivalry*. Oxford University
404 Press.

405 Neff, B. D., and T. E. Pitcher. 2005. Genetic quality and sexual selection: an integrated
406 framework for good genes and compatible genes. *Mol. Ecol.* 14:19–38.

407 Philippi, T., and J. Seger. 1989. Hedging one’s evolutionary bets, revisited. *Trends Ecol.*
408 *Evol.* 4:41–44.

409 Pope, W. F., S. Xie, D. M. Broermann, and K. P. Nephew. 1990. Causes and consequences of
410 early embryonic diversity in pigs. *J. Reprod. Fertil. Suppl.* 40:251–260.

411 R Development Core Team. 2017. *R: A language and environment for statistical computing*.

412 Ronget, V., J.-M. Gaillard, T. Coulson, M. Garratt, F. Gueyffier, J.-C. Lega, and J.-F.
413 Lema tre. 2017. Causes and consequences of variation in offspring body mass: meta-
414 analyses in birds and mammals. *Biol. Rev.*

415 S ther, B.-E., and S. Engen. 2015. The concept of fitness in fluctuating environments. *Trends*
416 *Ecol. Evol.* 30:273–281.

- 417 Servanty, S., J.-M. Gaillard, D. Allainé, S. Brandt, and E. Baubet. 2007. Litter size and fetal
418 sex ratio adjustment in a highly polytocous species: the wild boar. *Behav. Ecol.*
419 18:427–432.
- 420 Servanty, S., J.-M. Gaillard, C. Toïgo, S. Brandt, and E. Baubet. 2009. Pulsed resources and
421 climate-induced variation in the reproductive traits of wild boar under high hunting
422 pressure. *J. Anim. Ecol.* 78:1278–1290.
- 423 Shipley, B. 2009. Confirmatory path analysis in a generalized multilevel context. *Ecology*
424 90:363–368.
- 425 Shipley, B. 2013. The AIC model selection method applied to path analytic models compared
426 using a d-separation test. *Ecology* 94:560–564.
- 427 Smith, C. C., and S. D. Fretwell. 1974. The optimal balance between size and number of
428 offspring. *Am. Nat.* 108:499–506.
- 429 Starrfelt, J., and H. Kokko. 2012. Bet-hedging—a triple trade-off between means, variances
430 and correlations. *Biol. Rev.* 87:742–755.
- 431 Todd, E. V., D. Blair, C. J. Limpus, D. J. Limpus, and D. R. Jerry. 2013. High incidence of
432 multiple paternity in an Australian snapping turtle (*Elseya albagula*). *Aust. J. Zool.*
433 60:412–418.
- 434 Toïgo, C., S. Servanty, J.-M. Gaillard, S. Brandt, and E. Baubet. 2008. Disentangling natural
435 from hunting mortality in an intensively hunted wild boar population. *J. Wildl. Manag.*
436 72:1532–1539.
- 437 Trivers, R. L. 1974. Parent-Offspring Conflict. *Am. Zool.* 14:249–264.
- 438 Wang, J., and A. W. Santure. 2009. Parentage and Sibship Inference From Multilocus
439 Genotype Data Under Polygamy. *Genetics* 181:1579–1594.
- 440 Watson, P. J. 1991. Multiple paternity as genetic bet-hedging in female sierra dome spiders,
441 *Linyphia litigiosa* (*Linyphiidae*). *Anim. Behav.* 41:343–360.

- 442 Williams, G. C. 1975. *Sex and Evolution*. Princeton University Press.
- 443 Wilson, A. J., D. W. Coltman, J. M. Pemberton, A. D. J. Overall, K. A. Byrne, and L. E. B.
444 Kruuk. 2005. Maternal genetic effects set the potential for evolution in a free-living
445 vertebrate population. *J. Evol. Biol.* 18:405–414.
- 446 Winkler, D. W., and K. Wallin. 1987. Offspring size and number: a life history model linking
447 effort per offspring and total effort. *Am. Nat.* 129:708–720.
- 448 Yasui, Y. 2001. Female multiple mating as a genetic bet-hedging strategy when mate choice
449 criteria are unreliable. *Ecol. Res.* 16:605–616.
- 450 Yasui, Y. 1998. The 'genetic benefits' of female multiple mating reconsidered. *Trends Ecol.*
451 *Evol.* 13:246–250.
- 452

Figure 1. (a) Number of offspring per father for the 148 identified fathers (sampled in dark gray and unsampled in light gray) in the wild boar population of Châteauvillain-Arc-en-Barrois, France. Only males siring at least two offspring are included here.

Figure 2. (a) Number of offspring per father for the 211 identified fathers (sampled in dark gray and unsampled in light gray) in the wild boar population of Châteauvillain-Arc-en-Barrois, France; (b) Number of litters with 1 to 6 identified fathers, for the 116 litters included in the study. Only full litters are included here.

Figure 3. Path model with the best fit (see table 1) showing how mother body mass (*BM*) and number of fathers per litter (*F*) influence the within-litter variation in fetus mass (*CV*) through litter size (*LS*), timing of mating (*Timing*) and mean fetus length (*Length*). Numbers indicate standardized regression coefficients and their associated S

Table 1. Model fit of the 13 competing path models exploring the relationship between female body mass (*BM*), number of fathers within the litter (*F*), litter size (*LS*), timing of mating (*Timing*), mean fetus length (*Length*) and within-litter variation in fetus mass (*CV*) for each litter (n=116). Displayed are the likelihood degrees of freedom (N), the AICc of the tested models, and the difference between each model and the best one (Δ AICc).

Model notation	N	AICc	Δ AICc
1. F~BM / LS~ BM / Timing~BM / Length~Timing / CV~LS+Length	16	59.03	0
2. F~BM / LS~ BM / Timing~BM / Length~Timing / CV~Length	15	60.67	1.65
3. F~BM / LS~ BM / Timing~BM / Length~Timing / CV~ LS+Length+F	17	61.76	2.73
4. F~BM / LS~ BM / Timing~BM / Length~Timing / CV~LS	15	62.05	3.03
5. F~BM / LS~ BM / Timing~BM / Length~Timing / CV~Length+F	16	62.84	3.81
6. F~BM / LS~ BM / Timing~BM / Length~Timing / CV~Length	16	63.18	4.15
7. F~BM+Timing / LS~ BM / Timing~BM / Length~Timing / CV~LS+Length	16	64.20	5.17
8. F~BM+Timing / LS~ BM / Timing~BM / Length~Timing / CV~LS+Length+F	18	64.47	5.45
9. F~BM+Timing / LS~ BM / Timing~BM / Length~Timing / CV~LS	16	64.68	5.65
10. F~BM+Timing / LS~ BM / Timing~BM / Length~Timing / CV~Length+F	17	65.51	6.48
11. F~BM+Timing / LS~ BM / Timing~BM / Length~Timing / CV~LS+F	17	66.85	7.82
12. F~BM / LS~ BM / Timing~BM / Length~Timing / CV~F	15	67.50	8.48
13. F~BM+Timing / LS~ BM / Timing~BM / Length~Timing / CV~F	16	70.11	11.08

Fig. 1

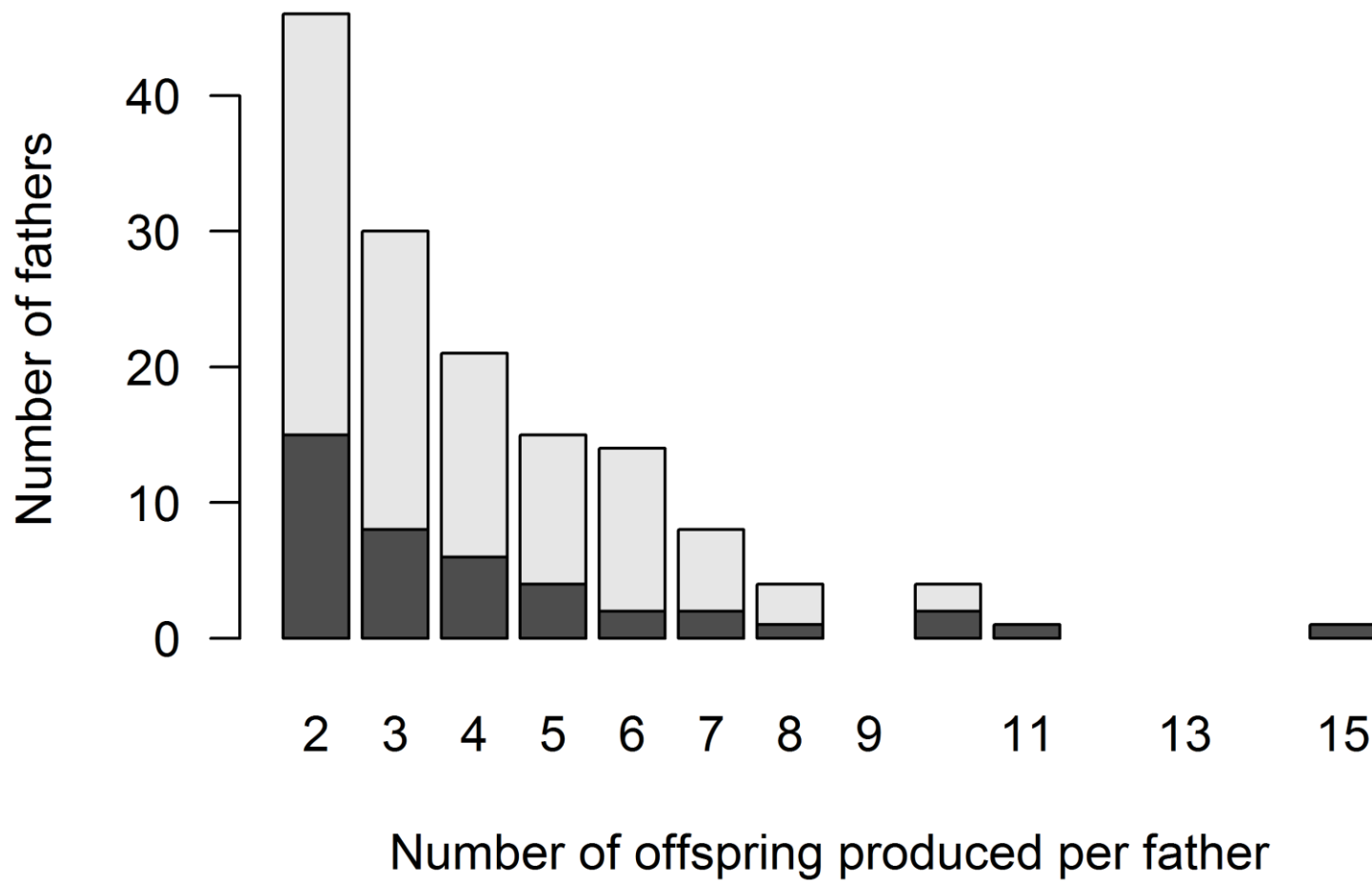


Fig. 2a

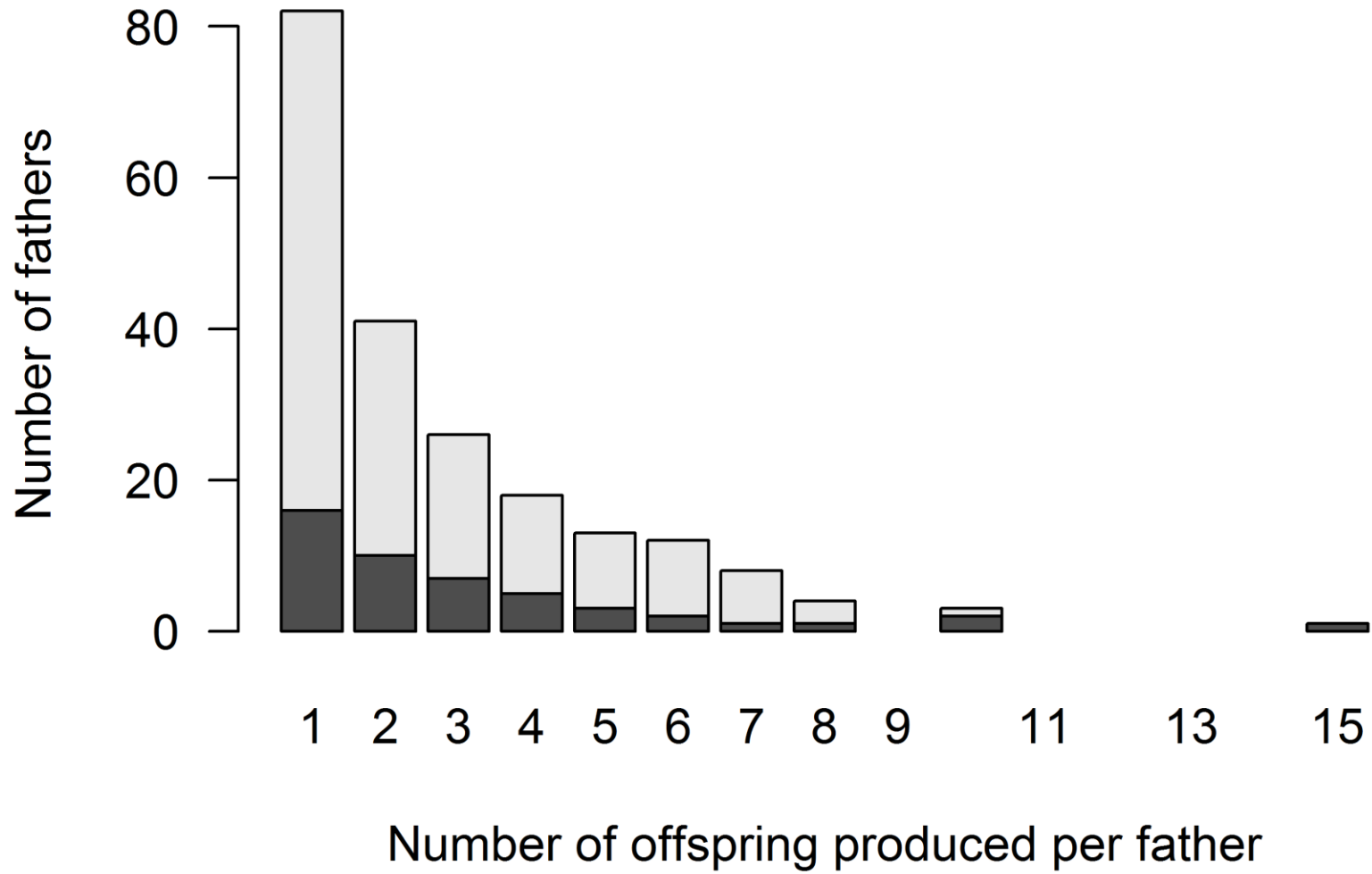


Fig. 2b

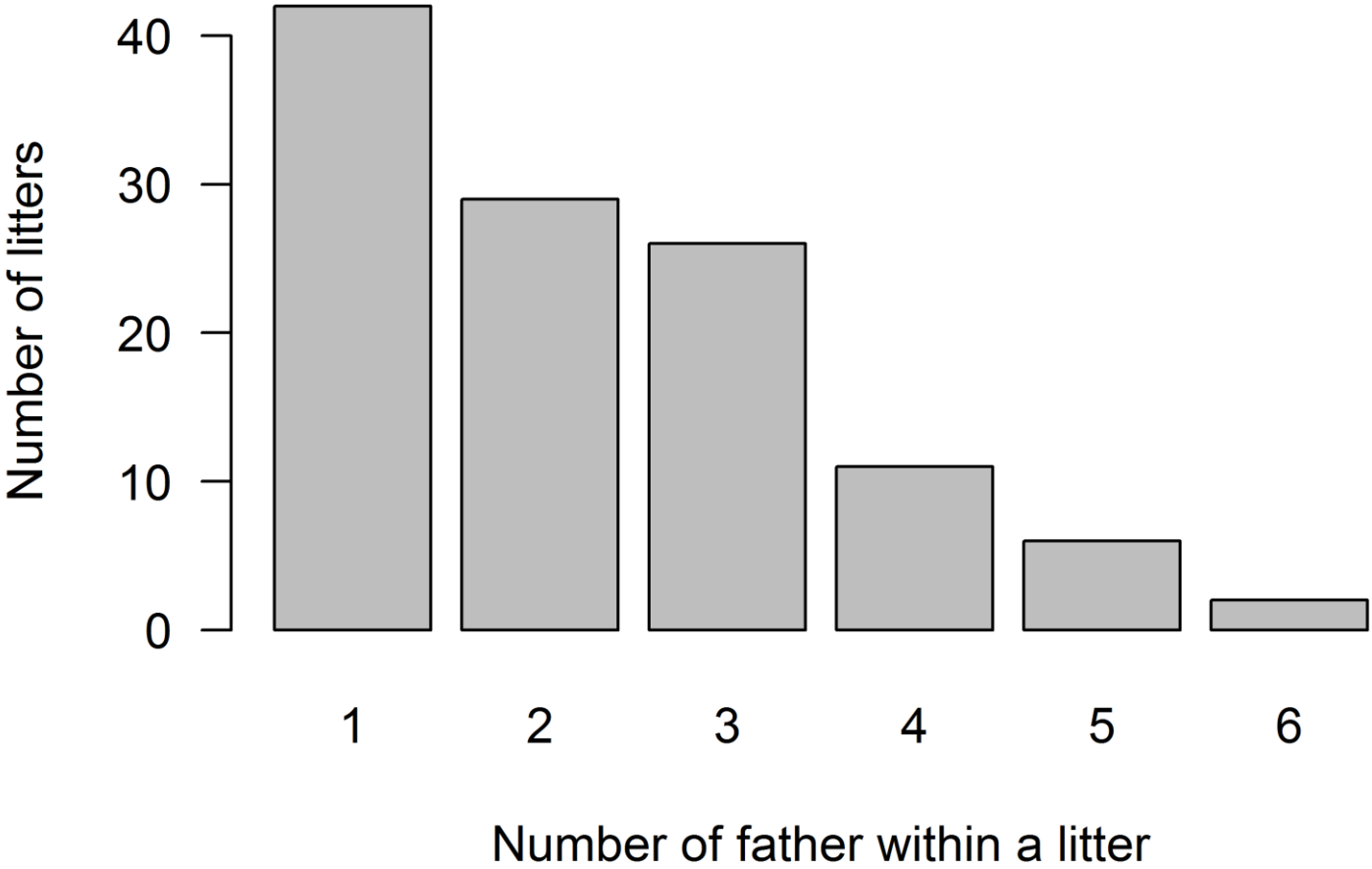


Fig. 3

