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The relationship between phenotypic variation among offspring and mother body mass in wild boar: Evidence of coin-flipping?

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1 **The relationship between phenotypic variation among offspring and mother**
2 **body mass in wild boar: Evidence of coin-flipping?**

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5

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14 **Running headline:** Coin-flipping in wild boar

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21 **Summary**

22 **1.** In highly variable environments, the optimal reproductive tactics of iteroparous organisms
23 should minimize variance in yearly reproductive success to maximize the long-term average
24 reproductive success. To minimize among-year variation in reproductive success individuals
25 can either minimize the variance in the number of offspring produced at each reproductive
26 attempt (classical bet-hedging) or maximize the phenotypic diversity of offspring produced
27 within or among reproductive attempts (coin-flipping).

28 **2.** From a long-term detailed study of an intensively exploited population facing a highly
29 unpredictable environment, we identify a continuum of reproductive tactics in wild boar
30 females depending on their body mass.

31 **3.** At one end, light females adjusted litter size to their body mass and produced highly
32 similar-sized offspring within a litter. These females fitted the hypothesis of individual
33 optimization commonly reported in warm-blooded species, which involves both an optimal
34 mass and an optimal number of offspring for a given mother. At the other end of the
35 continuum, heavy females produced litters of variable size including a mixture of heavy and
36 light offspring within litters.

37 **4.** Prolific heavy wild boar females diversify the phenotype of their offspring, providing a first
38 evidence for coin-flipping in a warm-blooded species.

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41 **Key-words:** bet-hedging, phenotypic plasticity, repeatability, reproductive tactic, *Sus scrofa*

42 *scrofa*

43 Introduction

44 Bet-hedging (Murphy 1968, Slatkin 1974) refers to the way organisms increase their fitness
45 by decreasing the variance of annual reproductive success (Philippi & Seger 1989). In
46 unpredictable and variable environments, the life history tactic leading to the highest
47 individual fitness involves minimizing among-year variation in reproductive success rather
48 than consistently maximizing reproductive success each year (Slatkin 1974; Philippi & Seger
49 1989). Bet-hedging includes two non-exclusive mechanisms, risk spreading and risk-
50 minimizing (Seger & Brockman 1987). For instance, iteroparity corresponds to a risk-
51 spreading tactic, which has been interpreted as a response to environmental variation
52 (Charnov & Schaffer 1973, Schaffer 1974, Orzack & Tuljapurkar 1989, Gaillard & Yoccoz
53 2003). Likewise, producing each year the same limited number of offspring (Olofsson, Ripa
54 & Jonsén 2009) and adjusting reproductive effort to a low level relative to available resources
55 to avoid jeopardizing survival (Richard *et al.* 2002, Gaillard & Yoccoz 2003, Hamel *et al.*
56 2010, Nevoux *et al.* 2010, Jones 2011) correspond to a risk-minimizing life history tactic.
57 However, besides varying the number of offspring produced over breeding attempts during
58 their lifetime, mothers in long-lived iteroparous organisms may change the phenotype of these
59 offspring by allocating differentially among offspring within a given reproductive attempt
60 (see Köhl *et al.* 2007 for evidence of differential maternal allocation to male offspring
61 according to litter composition in saiga antelope *Saiga tatarica*). Such a mechanism involving
62 developmental plasticity among litter mates has been called coin-flipping by Kaplan &
63 Cooper (1984). Few studies have reported a phenotypic plasticity in offspring traits (Table 1).
64 Of 208 studies citing the Kaplan & Cooper's study on 12 January 2012, only 24 tested
65 developmental plasticity of offspring phenotypic traits or diversification of developmental
66 time. Most of them dealt with cold-blooded organisms as originally targeted by Kaplan &
67 Cooper (1984). Only two studies dealt with warm-blooded species (house wrens, *Troglodytes*

68 *aedon*, and yellow-bellied marmots, *Marmota flaviventris*) and provided support for the coin-
69 flipping hypothesis. In these cases, evidence for developmental plasticity of offspring was
70 reported among litters (Table 1), leaving open the question of the possible existence of
71 developmental plasticity within a litter.

72 In polytocous mammals, variation among females in phenotypic traits, genotype, and habitat
73 quality leads offspring produced by different mothers within a cohort to be more dissimilar
74 than litter mates, generating so-called family effects (*sensu* Gaillard *et al.* 1998, see Pettorelli
75 & Durant 2007 for a case study on carnivores). The dependence of offspring traits to maternal
76 condition (*i.e.*, condition-dependent state *sensu* McNamara & Houston 1996) has been
77 repeatedly reported in mammals (see Clutton-Brock 1991 for a review) and corresponds to an
78 individual optimization of the trade-off between size and number of offspring (Smith &
79 Fretwell 1974, Lloyd 1987). While a trade-off between number and size of offspring is
80 expected (e.g. Smith and Fretwell 1974, Stearns 1992; see Sæther & Heim 1993 in mammals),
81 it is rarely observed because of heterogeneity in individual quality (van Noordwijk & de Jong
82 1986). Thus, large females usually produce large litters of large offspring, whereas small
83 females produce small litters of small offspring, leading to strong family effects. This is in
84 apparent contradiction with the coin-flipping hypothesis involving a decoupling between
85 female attributes and early development of offspring so that females should produce a mixture
86 of large and small offspring. This discrepancy might explain why evidence for coin-flipping
87 has not been yet investigated in large mammals for which a tight link between mother and
88 offspring phenotypes is commonly reported (Clutton-Brock 1991).

89 In the present work we aim to fill the gap by using a long-term detailed study on a wild boar
90 (*Sus scrofa scrofa*) population. Wild boar is an especially relevant model to test for coin-
91 flipping because females produce large litter sizes (up to 14, see Servanty *et al.* 2007) at each
92 reproductive attempt and face highly variable and unpredictable environmental conditions as

93 they mostly feed on forest mast, the abundance of which fluctuates among years (Servanty *et*
94 *al.* 2007).

95 Using the long-term monitoring of the heavily hunted wild boar population at Châteauvillain-
96 Arc-en-Barrois, we first tested for individual optimization predicting that large females should
97 produce large litters while small females should produce small litters. We thus assessed the
98 relationship between fetus mass and female body mass as well as the relationship between
99 litter size and female body mass to check for the expected dependence between these two
100 variables and female phenotype (Clutton-Brock 1991). As mass at birth markedly influences
101 future survival (Stearns 1992, Roff 2002), especially in large mammals (Gaillard *et al.* 2000),
102 individual optimization should also lead to marked family effects to allow large females to
103 recruit more than small ones. To test explicitly the coin-flipping hypothesis, we investigated
104 developmental plasticity by both evaluating intra- and inter-litter variance of offspring mass.
105 Under the coin-flipping hypothesis, females should produce a mixture of heavy and light
106 offspring within a litter.

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115 **Materials and methods**

116 STUDY AREA AND DATA COLLECTION

117 We studied a wild boar population in northeastern France in the 11,000 ha forest of
118 Châteauvillain-Arc-en-Barrois. The territory is administratively divided into a core area that
119 covers 8,500 ha of national forest and a 2,500 ha surrounding area of private or communal
120 forest. These forests are mainly composed of oak (*Quercus petraea*), beechnut (*Fagus*
121 *sylvatica*) and hornbeam (*Carpinus betulus*). The climate is intermediate between continental
122 and oceanic types. Wild boars are hunted each year between October and February. Between
123 1995 and 2009, we recorded the dressed body mass (*i.e.*, body mass without digestive tract,
124 heart, lungs, liver, reproductive tract and blood) of each harvested female. Data on female
125 reproductive status were also collected based on the examination of uteri for the presence of
126 embryos or fetuses. Litter size was recorded and each fetus was weighed, measured (crown-
127 rump length, in millimeters), and sexed. This information was available for 319 females and
128 1,743 fetuses collected during 14 hunting seasons.

129

130 LINKING MASS OF FETUSES AND GESTATION STAGE

131 Offspring mass is expected to differ markedly among litters. In particular, not all litters were
132 at the same gestation stage because females were shot at different dates and also because
133 mating of wild boar occurs throughout most of the year in the study population, with a birth
134 peak in mid-April (Gamelon *et al.* 2011). We thus needed to standardize fetus mass by
135 gestation stage. To assess the gestation stage of a given litter, the mean length of fetuses in the
136 litter was first calculated. Then, we applied the model provided first by Henry (1968) to link
137 gestation stage to mean fetus length across litters (gestation stage (in days) = 23.43+0.32*
138 mean length (in mm)). The strength of this relationship was very high ($R^2 = 0.86$, $N = 20$,

139 Henry 1968). The gestation stage was thus estimated from Henry (1968)'s model for each
140 litter. We then regressed individual fetus mass of the entire dataset on the gestation stage and
141 used the best model to standardize fetus mass at a given gestation stage. Because the
142 relationship was quadratic (see Results), we corrected in all the following analyses the
143 individual fetus mass by gestation stage and gestation stage² by including them as fixed
144 effects.

145

146 LINKING LITTER SIZE AND FEMALE BODY MASS

147 Under the hypothesis of individual optimization, large females should produce large litters of
148 large offspring, whereas small females should produce small litters of small offspring. We
149 thus first assessed whether larger females produced larger litters than smaller females by
150 linking litter size to female body mass. We thus fitted three models (on a log-scale): a simple
151 linear regression model, a quadratic regression model, and a segmented regression model
152 (Toms & Lesperance 2003). AIC was used for model selection (Burnham & Anderson 2002).

153

154 LINKING MASS OF FETUSES WITH FEMALE BODY MASS

155 We assessed whether large females produced larger offspring than small females by assessing
156 possible effects of maternal mass on fetus mass. To do this, we used linear mixed models with
157 normal error terms. We included individual fetus mass as the response variable and mother
158 identity as a random effect. In addition, we accounted for differences in gestation stage among
159 litters (by including a quadratic regression as fixed effects) and for other potentially
160 confounding factors, namely hunting season, female body mass, litter size, and fetus sex. AIC
161 was used for model selection (Burnham & Anderson 2002).

162 WITHIN-LITTER VARIABILITY IN FETUS MASS

163 To provide a measure of within-litter variation in mass, we calculated the coefficient of
164 variation (CV) of fetus mass for each litter. To correct fetus mass by gestation stage, we used
165 the quadratic relationship linking fetus mass and gestation stage (see the section “Linking
166 mass of fetuses and gestation stage” for further details) and we standardized all fetuses at the
167 same gestation stage of 110 days (110 days corresponds to the latest gestation stage observed
168 in the dataset). To assess the effect of female body mass on the CV of fetus mass corrected for
169 gestation stage, we fitted a linear regression between CV of fetus mass and female body mass.
170 Moreover, we explicitly tested whether the variation in fetus body mass increased with female
171 body mass by including variance functions into the different models tested. We used the
172 “varPower” variance function (Pinheiro & Bates 2000) because of its flexibility. Models
173 including variance functions only differ from models without variance function in that the
174 within-group errors are allowed to be heteroscedastic. More precisely, the residual term of the
175 regression linking fetus mass and female body mass followed a Gaussian distribution with
176 mean zero and a variance that equals $\sigma^2 \cdot \text{female body mass}^{2\delta}$ where σ is the standard
177 residual standard deviation and δ a parameter to be estimated. Including variance functions
178 thus specifies that the variance in fetus mass changes with increasing female body mass
179 (Pinheiro & Bates (2000); see Cleasby & Nakagawa (2011) for an application of variance
180 functions). AIC was used for model selection (Burnham & Anderson 2002).

181 All these analyses were performed with R 2.12.2 (R Development Core Team 2011).

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185 Results

186 LINKING MASS OF FETUSES AND GESTATION STAGE

187 As expected, the mass of fetuses increased with the gestation stage, on a quadratic way
188 (gestation stage: slope = -17.175, SE = 0.371; p-value \ll 0.01; gestation stage²: slope =
189 0.209, SE = 0.003; p-value \ll 0.01; R² = 0.974; Appendix S1).

190

191 LINKING LITTER SIZE AND FEMALE BODY MASS

192 The segmented regression linking litter size with maternal mass provided the best fit to data
193 (AIC = 174.1; intercept = -1.29 (0.31); slope= 0.76 (SE: 0.08) before the threshold; R²=
194 0.219) when compared to the linear (AIC = 178.2; intercept= -0.67 (SE: 0.26); slope= 0.59
195 (SE: 0.06); R²= 0.204) and quadratic (AIC = 176.3; intercept= -6.23 (SE: 2.89); log(Female
196 Body Mass)= 3.53 (SE: 1.50); log(Female Body Mass)²= -0.38 (SE: 0.19); R²= 0.214) models.
197 The higher the female body mass is, the larger is the litter size until a threshold mass (Fig. 1).
198 Above this threshold mass, litter size did not increase with body mass. This threshold
199 corresponded to a female mass of 58.3 kg, at which litter size was about 6.2 fetuses.
200 Nevertheless, the AIC of the three tested models were very close and the differences among
201 models did not seem to be biological significant for most of the observed range in female
202 body mass. There was indeed a quite high variation in litter size both above and below the
203 threshold value. Moreover, there was a positive relationship between litter size and body
204 mass, but this relationship became weaker (quadratic model) or stopped to become constant
205 (piecewise model) as female body mass increases. The relationship between litter size and
206 female body mass thus appears positive but highly variable, and there is a limit on how many
207 offspring females can produce on average.

208 LINKING MASS OF FETUSES WITH FEMALE BODY MASS

209 The baseline model of variation in fetus mass only included the quadratic effects of gestation
210 stage and the random effect of mother identity. The best model retained (AIC=16962.28)
211 included in addition the fixed effects of hunting season, mother body mass (0.295 (SE:
212 0.117)) and fetus sex (-11.538 (SE: 1.394)) (Table 2A; see Appendix S2 for parameter
213 estimates). Fetus mass thus depended on maternal mass. The heavier the females are, the
214 heavier the fetuses are (Fig. 2). Nevertheless, from a biological viewpoint, this relationship
215 between fetus mass and female body mass was weak as shown by the small effect size
216 (maternal mass effect=0.2952 (SE: 0.1172)). Moreover, we found no effect of litter size on
217 fetus mass.

218

219 WITHIN-LITTER VARIABILITY IN FETUS MASS

220 The heavier the female body mass is, the higher is the CV of fetus mass (intercept: -3.276e-
221 03; slope = 3.545e-04; SE = 8.478e-05; p-value << 0.01; Fig. 3), meaning that the difference
222 in terms of fetus mass within a litter produced by a heavy female was higher than the
223 difference within a litter produced by a light female.

224 By including variance function into the different mixed models tested (Table 2B), we found
225 that the best model retained among all the models presented in Table 2 included effects of
226 hunting season, of mother body mass and of fetus mass as fixed effects, of mother identity as
227 random effect and included the variance function (AIC=16842.07; see Appendix S2 for
228 parameter estimates). We therefore found a marked increase in the log-likelihood associated
229 with the inclusion of the variance function. Consequently, in the best model retained the
230 variance in fetus mass increases with female body mass. More precisely, δ was estimated to

231 0.984 (with a 95% confidence interval of 0.812-1.156) meaning that the variance increases
232 with the square of female body mass.

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For Review Only

252 **Discussion**

253 We identified a continuum of reproductive tactics in wild boar females depending on their
254 body mass. At one end, light females adjusted the size of their litters to their body mass. This
255 was consistent with the individual optimization process involving a strong positive link
256 between litter size and mother's phenotypic attributes usually reported in mammals (see
257 Clutton-Brock 1991 and Gaillard *et al.* 2000 for reviews). However, while previous studies of
258 large mammals have reported that mothers in better than average condition produce heavier
259 offspring (e.g., Russell *et al.* 1981 and Holst, Killeen & Cullis 1986 for sheep *Ovis aries*;
260 Blaxter & Hamilton 1980, Moore, Littlejohn & Cowie 1988 for red deer *Cervus elaphus*),
261 body mass of female wild boar had a little influence on offspring mass. Fetus mass was
262 mainly influenced by gestation stage, sex, and year. The influence of gestation stage is trivial
263 and simply corresponds to fetal growth during gestation. Males were heavier than females, as
264 expected for a polygynous and dimorphic species like wild boar (Glucksmann 1974). The
265 marked among-year variation in fetus mass was also expected from the highly variable and
266 unpredictable food resources wild boars face with. Finally, we did not detect any effect of
267 litter size on fetus mass. This absence of any evidence for a trade-off between fetus mass and
268 litter size is especially noteworthy. This indicates that these females adjusted their
269 reproductive effort mainly through variation in litter size, and suggests that it pays more for
270 females acquiring an energy surplus to produce more offspring than to produce heavier
271 offspring. At this end of the continuum, we showed that light females produced fetuses that
272 have very similar mass. Indeed, the CV of fetus mass was lower in litters produced by light
273 females than in litters produced by heavy females, indicating little differences in fetus mass
274 within litters produced by light females.

275 At the other end of the continuum, heavy females produced a quite large variation in litter size
276 (from 3 to 11). Moreover, we showed that after a threshold body mass, additional body

277 reserves are not translated into additional offspring. This stabilization corresponds to 6 fetuses
278 on average. This could involve diminishing returns with increasing already large litters. Such
279 diminishing returns have been reported in several studies (e.g., Jordan & Brooks 2010 on
280 guppies *Poecilia reticulata*). Such a diminishing return can arise either because the marginal
281 benefits of continued effort decrease or because the marginal costs of further reproductive
282 effort increase (Jordan & Brooks 2010). In other words, when diminishing returns occur, a
283 doubling of reproduction provides less than a doubling of relative success (Frank & Slatkin
284 1990). In our case, the litter size per-unit female body mass decreases as body mass increases,
285 providing evidence for a marginal diminishing return. Therefore, heavy wild boar females did
286 not show any evidence for an individual optimization of their reproductive effort. Such a total
287 independence between female phenotypic attributes and size or number of offspring produced
288 despite a twofold variation in litter size has not been yet reported in any mammalian species
289 to our knowledge. Under the Lack model of optimal litter size (Lack 1948), selection should
290 act on parents to maximize the number of offspring recruited, leading a trade-off to occur
291 between number and size of offspring produced (Smith & Fretwell 1974, Lloyd 1987,
292 Winkler & Wallin 1987). Producing a lot of unviable offspring is obviously not a sustainable
293 reproductive tactic, and producing a lot of large fetuses was not possible. The reproductive
294 tactic displayed by most females of large mammals in response to these constraints involves
295 optimizing this number-size trade-off according to their condition (individual optimization,
296 Pettifor, Perrins & McCleery 1988, McNamara & Houston 1996). In addition, we showed that
297 CV of fetus mass was higher in litters produced by heavy females than in litters produced by
298 light females, indicating marked differences in fetus mass within litters produced by heavy
299 females. Such a pattern of variation in within-litter fetus mass variation according to female
300 body mass provides support for coin-flipping in litters produced by heavy females.

301

302 We could thus identify a continuum of reproductive tactics in wild boar females. At one end,
303 light females display an individual optimization tactic by producing a litter size depending on
304 their body mass with fetus of similar mass. At the opposite end of the continuum, heavy
305 females show a coin-flipping tactic by producing offspring with a highly diversified
306 phenotype. The mating system in this wild boar population could provide a pathway for such
307 a pattern related to coin-flipping. Indeed, recent works in the studied population have shown
308 that the number of fathers within a litter increased with litter size (Devillard *et al.* unpublished
309 data). Nevertheless, large litters are generally produced by heavy females (Fig. 1).
310 Consequently, the high phenotypic diversity of offspring observed in litters produced by
311 heavy females could thus result from multiple paternities.

312 Wild boar females, depending on their body mass, have thus different reproductive tactics,
313 maybe facilitated by the fact that wild boar piglets are not dependent on their size to survive
314 (Baubet *et al.* 1995) contrary to other large mammalian species of herbivores (Gaillard *et al.*
315 2000). In absence of survival costs in small-sized piglets, wild boar females can produce a
316 large range of offspring phenotypes. These females diversified the phenotype of their
317 offspring, likely to minimize variance in reproductive success among years in the highly
318 variable and unpredictable environment they faced with. Such a developmental plasticity
319 might indeed allow females to recruit successfully in both mast years and years without any
320 mast. Theoretical approaches have also shown that life cycle delays could increase fitness
321 when environments are sufficiently variable (Tuljapurkar 1990; Tuljapurkar & Wiener 2000).
322 Previous studies of coin-flipping (Table 1) have shown that a large range of organisms adjust
323 the number, the birth timing, and the phenotype of their offspring to maximize the number of
324 recruits in fluctuating environments. However, these empirical studies focusing on
325 development rate, asynchrony of hatchling, or dispersal capacities of offspring most often
326 dealt with cold-blooded invertebrates, fishes, amphibians and reptiles. Kaplan & Cooper

327 (1984) themselves, in their original paper, focused on cold-blooded organisms certainly
328 because developmental plasticity of offspring in warm-blooded species is expected to be
329 constrained by thermoregulation.

330 Wild boars are hunted in most European forests and have become short-lived animals despite
331 of their large body size. The generation time in heavily hunted wild boar populations is
332 around 2 years, which is closer to the turn-over of tit populations than to that of a 60 kg
333 mammal (Servanty *et al.* 2011). Such unusual demographic patterns have led wild boar
334 females to have only one or two breeding attempts during their lifetime, starting to breed at
335 one year of age (Gamelon *et al.* 2011) at a low threshold body mass (between 20 and 25 kg,
336 Servanty *et al.* 2009). Consequently, wild boar females could exhibit different reproductive
337 tactics during their life according to their body mass. An investigation of coin-flipping in an
338 un-hunted wild boar population in which individuals start to breed at a higher threshold body
339 mass would be required to test whether all heavy females display a coin-flipping tactic.

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621 **Table 1.** List of the 24 papers (out of 208 quoting Kaplan & Cooper (1984)'s paper on coin-
622 flipping on 12 January 2012) including tests of phenotypic polymorphism among offspring
623 produced by a given individual. The species considered in the study, the taxonomic order, the
624 offspring trait measured, the test outcome (coin-flipping (yes) or no (no)), and the reference of
625 the study are provided. The table is divided into two parts. Part **A** brings together studies
626 showing a developmental plasticity of offspring while part **B** brings together studies showing
627 diversification of developmental time. Warm-blooded organisms occur in bold.

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Order	Species	Traits	Coin-flipping validated	Reference
A				
Anura	Quacking frog (<i>Crinia georgiana</i>)	Eggs size within clutches	Yes	Dziminski, Vercoe & Roberts 2009
Anura	Quacking frog (<i>Crinia georgiana</i>)	Eggs size within clutches	Yes	Dziminski & Roberts 2006
Anura	15 Australian frog species	Offspring provisioning within clutch	Yes	Dziminski & Alford 2005
Anura	Red-crowned toadlet (<i>Pseudophryne australis</i>)	Offspring sizes	Yes	Thumm & Mahony 2005
Anura	Fire-bellied toad (<i>Bombina orientalis</i>)	Eggs size	Yes	Kaplan 1992
Araneae	Wolf spider (<i>Rabidosa punctulata</i> , <i>R. rabida</i>)	Offspring size among clutches	No	Reed & Nicholas 2008
Araneae	Web-building spider (<i>Agelena limbata</i>)	Offspring size within and among clutches	Yes	Tanaka 1995
Chelonia	Giant Asian pond turtle (<i>Heosemys grandis</i>)	Number and size of eggs among clutches	Yes	Goode & Ewert 2006
Cladocera	Freshwater zooplankter (<i>Daphnia magna</i>)	Offspring sizes within clutches	No	McKee 1997
Cyprinodontiformes	Poeciliid fish (<i>Heterandria formosa</i>)	Offspring size at birth	Yes	Henrich 1988
Cyprinodontiformes	Mosquitofish (<i>Gambusia affinis</i>)	Embryo size	Yes	Meffe 1987
Homoptera	Bird cherry-oat aphid (<i>Rhopalosiphum padi</i>)	Production of sexuals or parthenogenetic females	Yes	Halkett <i>et al.</i> 2004
Rodentia	Yellow-bellied marmot (<i>Marmota flaviventris</i>)	Social behavior	Yes	Armitage 1986

Salmoniformes	Brook trout (<i>Salvelinus fontinalis</i>)	Eggs size	Yes	Koops, Hutchings & Adams 2003
Scleractinia	Scleractinian corals (<i>Pocillopora damicornis</i> , <i>Seriatopora hustrix</i> , <i>Stylophora pistillata</i>)	Dispersal capacities of larvae	Yes	Edmunds, Cumbo & Fan 2011
Scorpiones	4 species of scorpion	Offspring size within clutches	No	Brown 2004
Squamata	Black ratsnakes (<i>Elaphe obsoleta</i>)	Offspring size among and within clutches	No	Blouin-Demers & Weatherhead 2007
B				
Anura	Red-crowned toadlet (<i>Pseudophryne australis</i>)	Developmental rates	Yes	Thumm & Mahony 2006
Anura	Red crowned toadlet (<i>Pseudophryne australis</i>)	Embryonic development to the time of hatching	Yes	Thumm & Mahony 2002
Arguloidea	Parasitic crustacean (<i>Argulus coregoni</i>)	Intra-clutch variability in hatching among eggs	Yes	Hakalahti, Häkkinen & Valtonen 2004
Coleoptera	Chestnut weevil (<i>Curculio elephas</i>)	Duration of diapause	Yes	Menu & Debouzie 1993
Hemiptera	Triatominae (<i>Triatominae</i>)	Developmental delays	Yes	Menu <i>et al.</i> 2010
Hymenoptera	Pipe-Organ Mud-daubing Wasp (<i>Trypoxylon politum</i>)	Synchrony or asynchrony of emergence pattern	Yes	Brockmann 2004
Passeriformes	House wrens (<i>Troglodytes aedon</i>)	Synchrony or asynchrony in hatching eggs and weight	Yes	Bowers, Sakaluk & Thompson 2011

646 **Table 2.** Model selection of linear mixed models fitted with individual fetus mass (*mass*) as a response variable and mother identity (*mother*) as a
 647 random factor. The fixed effects correspond to gestation stage (*gestation*) and gestation stage² (*gestation*²), hunting season (*year*), fetus sex (*sex*),
 648 mother body mass (*mother body mass*) and litter size (*litter size*). Displayed are the AIC of each model and the difference in AIC between each
 649 candidate model and the best model (ΔAIC) for **(A)** all possible models presented in the column *Models* and for **(B)** the models presented in the
 650 column *Models* with a variance function specifying that fetus mass was allowed to differ in relation to female body mass. The selected models
 651 are in bold. Data come from wild boar females collected in the population of Châteauvillain-Arc-en-Barrois, France.

Models	A		B	
	AIC	ΔAIC	AIC	ΔAIC
mass~gestation+gestation ² +year+mother body mass+litter size+sex+mother	16963.60	1.32	16843.23	1.16
mass~gestation+gestation ² +year+mother body mass+litter size+mother	17028.32	66.04	16903.93	61.86
mass~gestation+gestation ² +year+mother body mass+mother	17027.01	64.73	16902.73	60.66
mass~gestation+gestation²+year+mother body mass+sex+mother	16962.28	0	16842.07	0
mass~gestation+gestation ² +year+sex+litter size+mother	16968.13	5.85	16847.06	4.99
mass~gestation+gestation ² +year+sex+mother	16966.20	3.92	16845.09	3.02
mass~gestation+gestation ² +year+ litter size+mother	17033.48	71.2	16908.19	66.12
mass~gestation+gestation ² +year+mother	17031.58	69.3	16906.25	64.18
mass~gestation+gestation ² +mother body mass+litter size+mother	17036.55	74.27	16910.19	68.12
mass~gestation+gestation ² +mother body mass+sex+mother	16972.24	9.96	16850.11	8.04
mass~gestation+gestation ² +mother body mass+litter size+sex+mother	16972.64	10.36	16850.33	8.26
mass~gestation+gestation ² +mother body mass+mother	17036.16	73.88	16909.95	67.88
mass~gestation+gestation ² +litter size+sex +mother	16974.56	12.28	16852.23	10.16
mass~gestation+gestation ² +litter size+mother	17039.04	76.76	16912.53	70.46
mass~gestation+gestation ² +sex+mother	16972.78	10.5	16850.47	8.4

mass~gestation+gestation²

17037.21

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16910.72

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For Review Only

652 **Figure legends**

653 **Figure 1.** Relationship between litter size and female body mass (on a log-scale) in the wild
654 boar population of Châteauvillain- Arc-en-Barrois, France. The best fitting model (segmented
655 regression, solid line) and the linear and quadratic relationships (dotted lines) are displayed.
656 The vertical solid lines correspond to the threshold body mass estimated from the segmented
657 regression and its associated confidence interval.

658 **Figure 2.** Relationship between standardized fetus mass (*i.e.*, corrected for gestation stage)
659 and female body mass. The solid line corresponds to the estimates provided by the linear
660 mixed model linking standardized fetus mass as a response variable, female body mass, fetus
661 sex and hunting season as fixed effects and mother identity as a random effect (intercept:
662 1005.166; slope: 0.295 (SE: 0.117)).

663 **Figure 3.** Relationship between the CV of fetus mass and female body mass from females
664 collected in the wild boar population of Châteauvillain-Arc-en-Barrois, France (intercept: -
665 3.276e-03; slope = 3.545e-04 (SE: 8.478e-05); p-value \ll 0.01).

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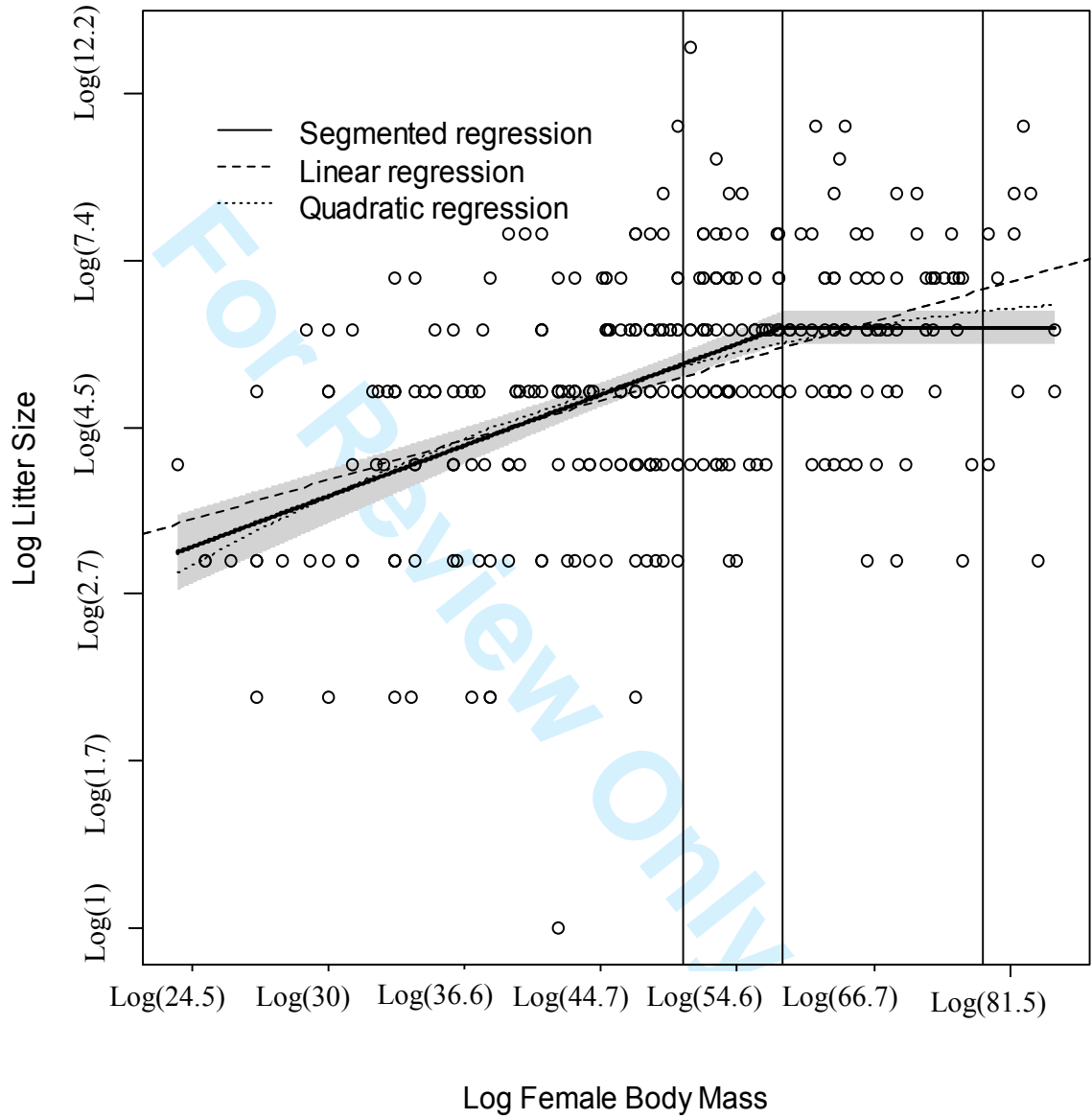
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673 Fig. 1.



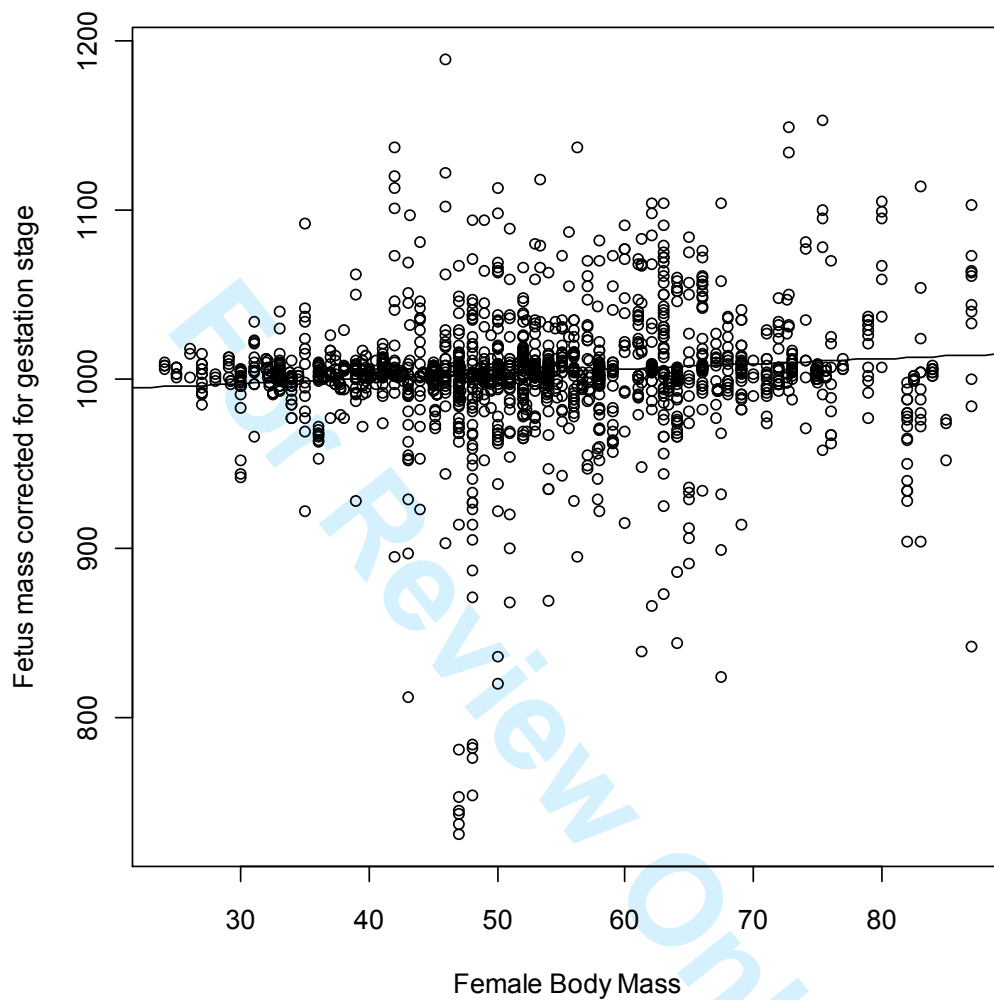
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678 **Fig. 2.**



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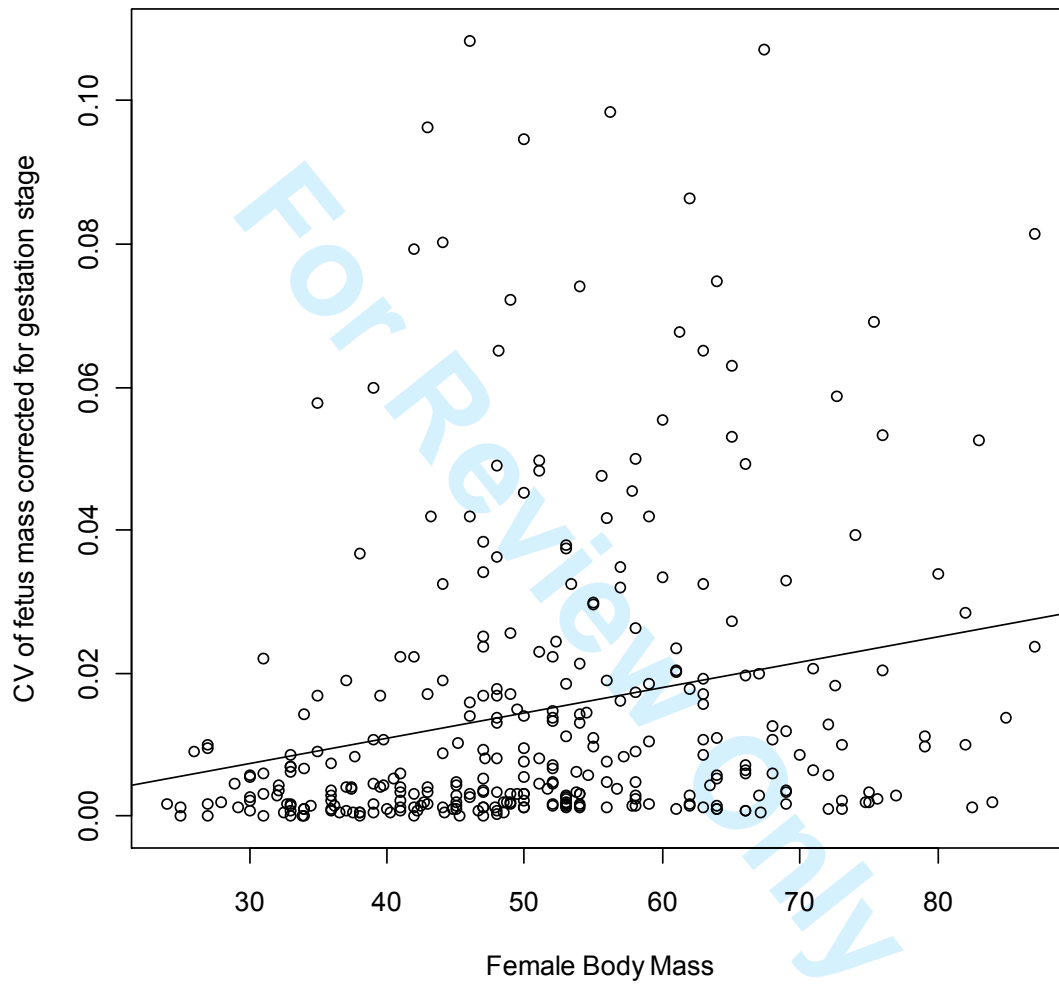
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685 **Fig. 3.**

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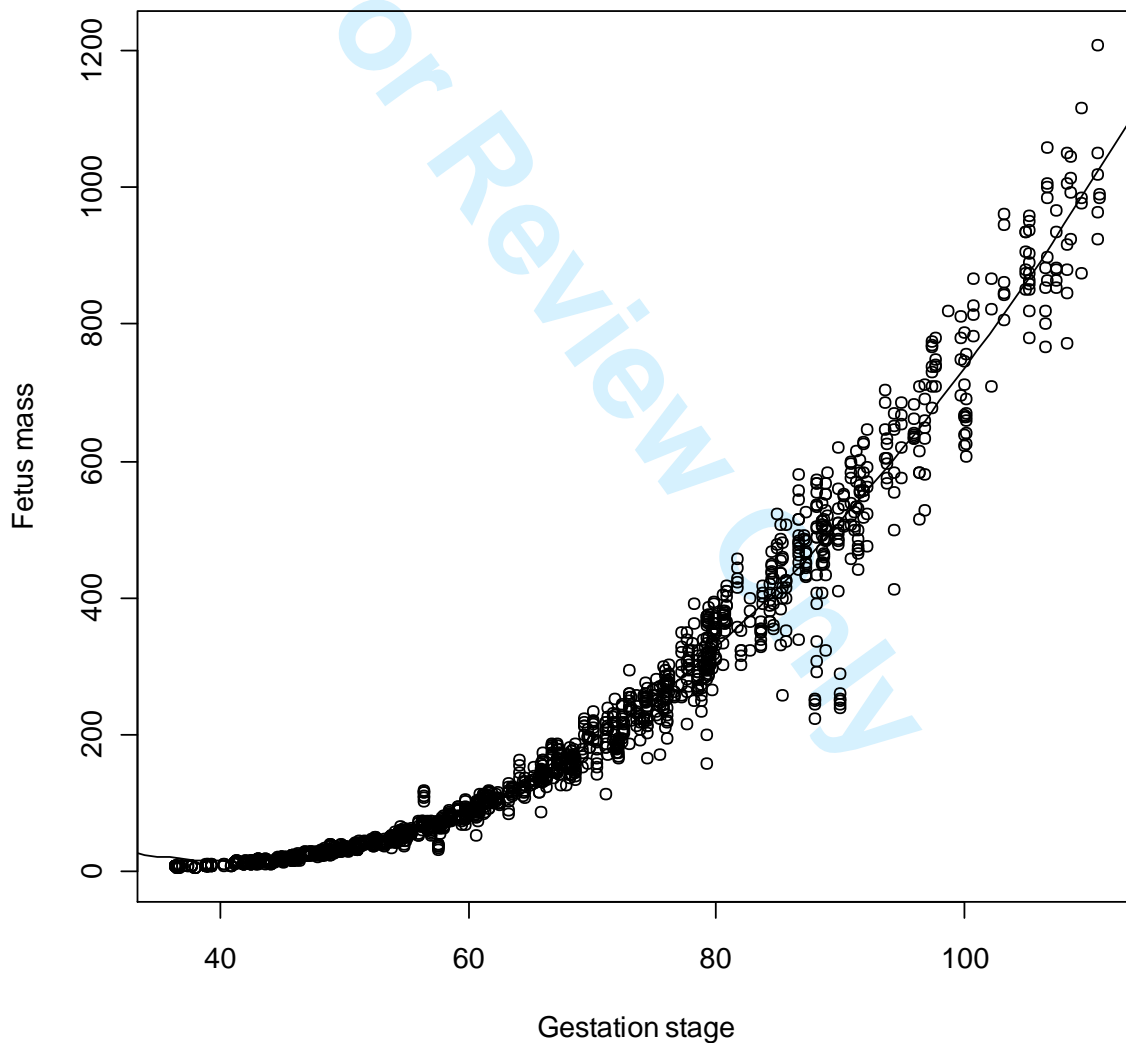
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1 **Supporting Information**

2 **Appendix S1**

3 Relationship between fetus mass and gestation stage in the wild boar population of
4 Châteauvillain-Arc-en-Barrois, France (gestation stage: slope = -17.175, SE = 0.371; p-value
5 $\ll 0.01$; gestation stage²: slope = 0.209, SE = 0.003; p-value $\ll 0.01$; $R^2 = 0.974$).



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Appendix S2: Model selection of linear mixed models fitted with individual fetus mass (mass) as a response

	Intercept
A)	
mass~gestation+gestation ² +year+mother body mass+litter size+sex+mother	380.634381
mass~gestation+gestation ² +year+mother body mass+litter size+mother	374.019765
mass~gestation+gestation ² +year+mother body mass+mother	372.598006
mass~gestation+gestation²+year+mother body mass+sex+mother	379.211825
mass~gestation+gestation ² +year+sex+litter size+mother	386.581145
mass~gestation+gestation ² +year+sex+mother	387.333558
mass~gestation+gestation ² +year+ litter size+mother	380.227457
mass~gestation+gestation ² +year+mother	381.145422
mass~gestation+gestation ² +mother body mass+litter size+mother	366.037266
mass~gestation+gestation ² +mother body mass+sex+mother	369.833861
mass~gestation+gestation ² +mother body mass+litter size+sex+mother	372.879994
mass~gestation+gestation ² +mother body mass+mother	362.987829
mass~gestation+gestation ² +litter size+sex +mother	377.763622
mass~gestation+gestation ² +litter size+mother	371.22766
mass~gestation+gestation ² +sex+mother	375.960021
mass~gestation+gestation ²	369.662583
B)	
mass~gestation+gestation ² +year+mother body mass+litter size+sex+mother	377.1696
mass~gestation+gestation ² +year+mother body mass+litter size+mother	371.4549
mass~gestation+gestation ² +year+mother body mass+mother	370.2911
mass~gestation+gestation²+year+mother body mass+sex+mother	375.9730
mass~gestation+gestation ² +year+sex+litter size+mother	382.5391
mass~gestation+gestation ² +year+sex+mother	382.9819
mass~gestation+gestation ² +year+ litter size+mother	376.9891
mass~gestation+gestation ² +year+mother	377.5949
mass~gestation+gestation ² +mother body mass+litter size+mother	364.3586
mass~gestation+gestation ² +mother body mass+sex+mother	367.4411
mass~gestation+gestation ² +mother body mass+litter size+sex+mother	370.1793
mass~gestation+gestation ² +mother body mass+mother	361.6615
mass~gestation+gestation ² +litter size+sex +mother	375.0776
mass~gestation+gestation ² +litter size+mother	369.4921
mass~gestation+gestation ² +sex+mother	373.2981
mass~gestation+gestation ²	367.9610

response variable and mother identity (mother) as a random factor. The fixed effects correspond to ge

SE	Gestation	SE	Gestation ²	SE	Year 1997	SE
24.298214	-17.460414	0.649493	0.210740	0.004557	1.667687	18.481280
24.203270	-17.449995	0.647200	0.210706	0.004541	1.360027	18.430091
24.121921	-17.458280	0.646658	0.210823	0.004535	1.575622	18.415428
24.217388	-17.468858	0.648948	0.210859	0.004551	1.883398	18.466631
24.410895	-17.348037	0.654100	0.210455	0.004599	1.368698	18.652701
24.183555	-17.339894	0.652306	0.210400	0.004587	1.280038	18.622173
24.337748	-17.333151	0.652400	0.210412	0.004587	1.035246	18.617337
24.111217	-17.323336	0.650661	0.210346	0.004575	0.926916	18.587900
21.871543	-17.363858	0.639170	0.209844	0.004505	NA	NA
21.866588	-17.385594	0.642490	0.210066	0.004527	NA	NA
21.986713	-17.373723	0.642152	0.209896	0.004526	NA	NA
21.751139	-17.375603	0.639511	0.210013	0.004506	NA	NA
21.953383	-17.293472	0.643980	0.209704	0.004547	NA	NA
21.85719	-17.27853	0.64152	0.20964	0.00453	NA	NA
21.585537	-17.307261	0.642423	0.209795	0.004536	NA	NA
21.488799	-17.290402	0.639943	0.209719	0.004519	NA	NA
24.088181	-17.3991	0.647400	0.2103	0.004557	3.1401	18.237696
23.978827	-17.3927	0.644850	0.2102	0.004540	2.8873	18.168100
23.929573	-17.4071	0.644307	0.2104	0.004534	3.1400	18.156731
24.040415	-17.4138	0.646914	0.2104	0.004551	3.3955	18.227937
24.162234	-17.3013	0.650873	0.2101	0.004590	3.4599	18.372177
23.978335	-17.2942	0.648613	0.2100	0.004575	3.4212	18.340809
24.064796	-17.2924	0.648641	0.2100	0.004575	3.2432	18.310563
23.883754	-17.2828	0.646425	0.2100	0.004561	3.1894	18.280356
21.565384	-17.2938	0.633440	0.2093	0.004480	NA	NA
21.616893	-17.3171	0.637273	0.2095	0.004504	NA	NA
21.695588	-17.2992	0.636818	0.2093	0.004503	NA	NA
21.485677	-17.3115	0.633831	0.2095	0.004481	NA	NA
21.656554	-17.2280	0.638784	0.2092	0.004524	NA	NA
21.538639	-17.2195	0.635754	0.2091	0.004503	NA	NA
21.328217	-17.2443	0.637000	0.2093	0.004491	NA	NA
21.210805	-17.2335	0.633926	0.2092	0.004491	NA	NA

nong female body bass. Displayed are the estimates and the associated SE for each fixed effect for all i

SE	Year 2009	SE	Mother body mass	SE	Litter size
15.619808	-26.341507	10.512601	0.336511	0.135132	-0.765974
15.569515	-26.756219	10.478344	0.351154	0.134593	-0.761081
15.557201	-26.979810	10.467356	0.306138	0.122347	NA
15.607521	-26.566817	10.501591	0.291162	0.122808	NA
15.757725	-24.087746	10.573349	NA	NA	0.215009
15.734505	-23.912606	10.533042	NA	NA	NA
15.721065	-24.408989	10.548713	NA	NA	0.261294
15.698815	-24.196305	10.509310	NA	NA	NA
NA	NA	NA	0.282717	0.133937	-1.200203
NA	NA	NA	0.193927	0.122168	NA
NA	NA	NA	NA	0.134642	-1.203652
NA	NA	NA	0.211577	0.121554	NA
NA	NA	NA	NA	NA	-0.409210
NA	NA	NA	NA	NA	-0.35464
NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA
15.447044	-23.3331	10.499089	0.3273	0.138936	-0.8522
15.380652	-23.5533	10.460556	0.3385	0.138557	-0.8335
15.372358	-23.8115	10.451039	0.2847	0.124049	NA
15.440075	-23.5974	10.490455	0.2725	0.124459	NA
15.556002	-21.1073	10.533739	NA	NA	0.1489
15.530104	-20.9634	10.485826	NA	NA	NA
15.496929	-21.2527	10.500213	NA	NA	0.2027
15.471946	-21.0580	10.452921	NA	NA	NA
NA	NA	NA	0.2856	0.957919	-1.2620
NA	NA	NA	0.1892	0.123598	NA
NA	NA	NA	0.2716	0.138223 1422	-1.2772
NA	NA	NA	0.2039	0.123032	NA
NA	NA	NA	NA	NA	-0.4280
NA	NA	NA	NA	NA	-0.3685
NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA

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SE	Sex	SE
0.948527	-11.539036	1.394038
0.944588	NA	NA
NA	NA	NA
NA	-11.538093	1.394039
0.870981	-11.589028	1.394132
NA	-11.590034	1.394016
0.868395	NA	NA
NA	NA	NA
0.951927	NA	NA
NA	-11.468746	1.394665
0.957026	-11.468034	1.394547
NA	NA	NA
0.872107	-11.514745	1.394530
0.86838	NA	NA
NA	-11.508937	1.394466
NA	NA	NA
0.958618	-9.9865	1.245208
0.954961	NA	NA
NA	NA	NA
NA	-9.9847	1.245326
0.865608	-10.0170	1.245028
NA	-10.0175	1.244922
0.862319	NA	NA
NA	NA	NA
0.957919	NA	NA
NA	-9.9093	1.244814
0.962904	-9.9099	1.244577
NA	NA	NA
0.864402	-9.9438	1.244606
0.859931	NA	NA
NA	-9.9381	1.244600
NA	NA	NA