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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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13 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

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 by decreasing the variance of annual reproductive success (Philippi & Seger 1989). In 45 unpredictable and variable environments, the life history tactic leading to the highest 46 47 individual fitness involves minimizing among-year variation in reproductive success rather than consistently maximizing reproductive success each year (Slatkin 1974; Philippi & Seger 48 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 (Charnov & Schaffer 1973, Schaffer 1974, Orzack & Tuljapurkar 1989, Gaillard & Yoccoz 52 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 their lifetime, mothers in long-lived iteroparous organisms may change the phenotype of these 58 offspring by allocating differentially among offspring within a given reproductive attempt 59 60 (see Kühl 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 developmental plasticity of offspring phenotypic traits or diversification of developmental 65 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

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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	(<i>Sus scrofa scrofa</i>) 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 <i>et al.</i> 2007) at each
92	reproductive attempt and face highly variable and unpredictable environmental conditions as
22	reproductive another and face inging variable and appreciedble environmental conditions as

they mostly feed on forest mast, the abundance of which fluctuates among years (Servanty *et 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
- 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,
- heart, lungs, liver, reproductive tract and blood) of each harvested female. Data on female

reproductive status were also collected based on the examination of uteri for the presence of

- embryos or fetuses. Litter size was recorded and each fetus was weighed, measured (crown-
- 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

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

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

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146 LINKING LITTER SIZE AND FEMALE BODY MASS

147 Under the hypothesis of individual optimization, large females should produce large litters of

large offspring, whereas small females should produce small litters of small offspring. We

thus first assessed whether larger females produced larger litters than smaller females by

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).

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154 LINKING MASS OF FETUSES WITH FEMALE BODY MASS

We assessed whether large females produced larger offspring than small females by assessing possible effects of maternal mass on fetus mass. To do this, we used linear mixed models with normal error terms. We included individual fetus mass as the response variable and mother identity as a random effect. In addition, we accounted for differences in gestation stage among litters (by including a quadratic regression as fixed effects) and for other potentially confounding factors, namely hunting season, female body mass, litter size, and fetus sex. AIC 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 σ^{2*} 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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184

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

(gestation stage: slope = -17.175, SE = 0.371; p-value << 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); $R^2 = 0.204$) 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

body mass. There was indeed a quite high variation in litter size both above and below the

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

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.

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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

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.

By including variance function into the different mixed models tested (Table 2B), we found

that the best model retained among all the models presented in Table 2 included effects of

hunting season, of mother body mass and of fetus mass as fixed effects, of mother identity as

- 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
- with the inclusion of the variance function. Consequently, in the best model retained the
- 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
- with the square of female body mass.

252 Discussion

253 We identified a continuum of reproductive tactics in wild boar females depending on their body mass. At one end, light females adjusted the size of their litters to their body mass. This 254 was consistent with the individual optimization process involving a strong positive link 255 between litter size and mother's phenotypic attributes usually reported in mammals (see 256 257 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), body mass of female wild boar had a little influence on offspring mass. Fetus mass was 261 262 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 marked among-year variation in fetus mass was also expected from the highly variable and 265 266 unpredictable food resources wild boars face with. Finally, we did not detect any effect of litter size on fetus mass. This absence of any evidence for a trade-off between fetus mass and 267 268 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.

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

reserves are not translated into additional offspring. This stabilization corresponds to 6 fetuses 277 278 on average. This could involve diminishing returns with increasing already large litters. Such diminishing returns have been reported in several studies (e.g., Jordan & Brooks 2010 on 279 280 guppies *Poecilia reticulate*). 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 despite a twofold variation in litter size has not been yet reported in any mammalian species 288 289 to our knowledge. Under the Lack model of optimal litter size (Lack 1948), selection should act on parents to maximize the number of offspring recruited, leading a trade-off to occur 290 291 between number and size of offspring produced (Smith & Fretwell 1974, Lloyd 1987, Winkler & Wallin 1987). Producing a lot of unviable offspring is obviously not a sustainable 292 293 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.

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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 <i>et al.</i> 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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368	

369 **References**

- 370 Armitage, K.B. (1986) Individuality, social behavior, and reproductive success in yellow-
- bellied marmots. *Ecology*, **67**, 1186–1193.
- 372
- Baubet, E., Van Laere, G. & Gaillard, J-M. (1995) Growth and survival in piglets. *Ibex*
- *Journal of Mountain Ecology*, **3**, 71.

375

- Blaxter, K.L. & Hamilton, W.J. (1980) Reproduction in farmed red deer. 2. calf growth and
- 377 mortality. *The Journal of Agricultural Science*, **95**, 275–284.

378

- Blouin-Demers, G. & Weatherhead, P.J. (2007) Allocation of offspring size and sex by female
- 380 black ratsnakes. *Oikos*, **116**, 1759–1767.
- 381
- Bowers, E.K., Sakaluk, S.K. & Thompson, C.F. (2011) Adaptive sex allocation in relation to
- hatching synchrony and offspring quality in house wrens. *The American Naturalist*, 177,617–

384 629.

385

- Brockmann, H.J. (2004) Variable life-history and emergence patterns of the Pipe-Organ mud-
- daubing wasp, *Trypoxylon politum* (Hymenoptera: *sphecidae*). *Journal of the Kansas*
- 388 *Entomological Society*, **77**, 503–527.

389

- Brown, C.A. (2004) Life histories of four species of scorpion in three families (Buthidae,
- 391 *diplocentridae, vaejovidae*) from arizona and new mexico. Journal of Arachnology, 32,193–

392 207.

393

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394	Burnham, K.P. & Anderson, D.R. (2002) Model selection and multimodel inference: a
395	practical information-theoretic approach. Springer.
396	
397	Charnov, E.L. & Schaffer, W.M. (1973) Life-History consequences of natural selection:
398	Cole's result revisited. The American Naturalist, 107, 791-793.
399	
400	Cleasby, I.R. & Nakagawa, S. (2011) Neglected biological patterns in the residuals a
401	behavioural ecologist's guide to co-operating with heteroscedasticity. Behavioral Ecology and
402	Sociobiology, 65 , 2361-2372.
403	
404	Clutton-Brock, T.H. (1991) The evolution of parental care. Princeton University Press.
405	
406	Dziminski, M.A. & Alford, R.A. (2005) Patterns and fitness consequences of intraclutch
407	variation in egg provisioning in tropical australian frogs. Oecologia, 146, 98–109.
408	
409	Dziminski, M.A. & Roberts, J.D. (2006) Fitness consequences of variable maternal
410	provisioning in quacking frogs (Crinia georgiana). Journal of Evolutionary Biology, 19, 144–
411	155.
412	
413	Dziminski, M.A., Vercoe, P.E. & Roberts, J.D. (2009) Variable offspring provisioning and
414	fitness: a direct test in the field. Functional Ecology, 23, 164–171.
415	
416	Edmunds, P. J., Cumbo, V. & Fan, T. (2011) Effects of temperature on the respiration of
417	brooded larvae from tropical reef corals. The Journal of Experimental Biology, 214, 2783 -
418	2790.

- 419 Frank, S.A. & Slatkin, M. (1990) Evolution in a variable environment. *The American*
- 420 *Naturalist*, **136**, 244-260.
- 421
- 422 Gaillard, J.-M., Andersen, R., Delorme, D. & Linnell, J.D.C. (1998) Family effects on growth
- 423 and survival of juvenile roe deer. *Ecology* ,**79**, 2878–2889.
- 424
- 425 Gaillard, J-M., Festa-Bianchet, M., Delorme, D. & Jorgenson, J. (2000) Body mass and
- 426 individual fitness in female ungulates: bigger is not always better. *Proceedings of the Royal*
- 427 Society of London. Series B: Biological Sciences, 267, 471-477.
- 428
- 429 Gaillard, J-M., & Yoccoz, N. G. (2003) Temporal variation in survival of mammals: A case of
- 430 environmental canalization? *Ecology*, **84**,3294–3306.
- 431
- 432 Gamelon, M., Besnard, A., Gaillard, J-M., Servanty, S., Baubet, E., Brandt, S. & Gimenez,
- 433 O. (2011) High hunting pressure selects for earlier birth date: wild boar as a case study.
- 434 *Evolution*, **65**, 3100–3112.
- 435
- 436 Glucksmann, A. (1974) Sexual dimorphism in mammals. *Biological Reviews*, **49**, 423–475.
- 437
- 438 Goode, J.M., & Ewert, M.A. (2006) Reproductive trends in captive *Heosemys grandis*
- 439 (*Geoemydidae*). Chelonian Conservation and Biology, **5**, 165–169.
- 440
- 441 Hakalahti, T., Häkkinen, H. & Valtonen, E.T. (2004) Ectoparasitic Argulus coregoni
- 442 (Crustacea: *branchiura*) hedge their bets studies on egg hatching dynamics. *Oikos*, **107**,
- 443 295–302.

444	
445	Halkett, F., Harrington, R., Hullé, M., Kindlmann, P., Menu, F., Rispe, C. & Plantegenest. M.
446	(2004) Dynamics of production of sexual forms in aphids: Theoretical and experimental
447	evidence for adaptive" coin-flipping" plasticity. The American Naturalist, 163, 112-125.
448	
449	Hamel, S., Gaillard, J-M, Yoccoz, N.G., Loison, A., Bonenfant, C. & Descamps, S. (2010)
450	Fitness costs of reproduction depend on life speed: empirical evidence from mammalian
451	populations. Ecology Letters, 13, 915–935.
452	
453	Henrich, S. (1988) Variation in offspring sizes of the poeciliid fish Heterandria formosa in
454	relation to fitness. <i>Oikos</i> , 51 , 13–18.
455	
456	Henry, V.G. (1968) Fetal development in european wild hogs. The Journal of Wildlife
457	Management, 32 , 966–970.
458	
459	Holst, P.J., Killeen, I.D. & Cullis, B.R. (1986) Nutrition of the pregnant ewe and its effects on
460	gestation length, lamb birth weight and lamb survival. Australian Journal Agricultural
461	<i>Research</i> , 37 , 647–655.
462	
463	Jones, J.H. (2011) Primates and the evolution of long, slow life histories. Current Biology, 21,
464	708–717.
465	
466	Jordan, L.A. & Brooks, R.C. (2010) The lifetime costs of increased male reproductive effort:
467	courtship, copulation and the Coolidge effect. Journal of Evolutionary Biology, 23, 2403-
468	2409.

469

Kaplan, R.H. (1992) Greater maternal investment can decrease offspring survival in the frog *Bombina Orientalis. Ecology*, **73**, 280–288.

472

- 473 Kaplan, R.H., & Cooper, W.S. (1984) The evolution of developmental plasticity in
- 474 reproductive characteristics: An application of the "Adaptive Coin-Flipping" principle. *The*
- 475 *American Naturalist*, **123**, 393–410.

476

- 477 Koops, M.A., Hutchings, J.A. & Adams, B.K. (2003) Environmental predictability and the
- 478 cost of imperfect information: influences on offspring size variability. *Evolutionary Ecology*

479 *Research*, **5**, 29–42.

480

- 481 Kühl, A., Mysterud, A., Erdnenov, G.I., Lushchekina, A.A., Grachev, I.A., Bekenov, A.B. &
- 482 Milner-Gulland, E.J. (2007) The "big spenders" of the steppe: sex-specific maternal allocation
- 483 and twinning in the saiga antelope. *Proceedings of the Royal Society of London. Series B:*
- 484 *Biological Sciences*, **274**, 1293-1299.

485

Lack, D. (1948) The significance of Litter-Size. *Journal of Animal Ecology*, **17**, 45–50.

487

- 488 Lloyd, D.G. (1987) Selection of offspring size at independence and other Size-Versus-
- 489 Number strategies. *The American Naturalist*, **129**, 800–817.

490

- 491 McKee, D. (1997) Intra-clutch offspring size variability in the freshwater zooplankter
- 492 Daphnia magna. Hydrobiologia, **354**, 111–117.

Journal of Animal Ecology

494	McNamara, J.M. & Houston, A.I. (1996) State-dependent life histories. Nature, 380, 215-
495	221.
496	
497	Meffe, G. K. (1987) Embryo size variation in mosquitofish: Optimality vs plasticity in
498	propagule size. Copeia, 3, 762–768.
499	
500	Menu, F. & Debouzie, D. (1993) Coin-flipping plasticity and prolonged diapause in insects:
501	example of the chestnut weevil Curculio elephas (Coleoptera: curculionidae). Oecologia, 93,
502	367–373.
503	
504	Menu, F., Ginoux, M., Rajon, E., Lazzari, C.R. & Rabinovich, J.E. (2010) Adaptive
505	developmental delay in chagas disease vectors: An evolutionary ecology approach. PLoS,
506	neglected tropical diseases, 4, e691.
507	
508	Moore, G.H., Littlejohn, R.P. & Cowie, G.M. (1988) Factors affecting live weight gain in red
509	deer calves from birth to weaning. New Zealand journal of agricultural research, 31, 279-
510	283.
511	
512	Murphy, G.I. (1968) Pattern in life history and the environment. The American Naturalist,
513	102 , 391–403.
514	
515	Nevoux, M., Forcada, J., Barbraud, C., Croxall, J. & Weimerskirch, H. (2010) Bet-hedging
516	response to environmental variability an intraspecific comparison <i>Ecology</i> 91 2416–2427
517	

519	between egg size and number. Proceedings of the Royal Society B-Biological Sciences, 277,
520	1149–1151.
521	
522	Orzack, H.S., Tuljapurkar, S. (1989) Population dynamics in variable environments. The
523	demography and evolution of iteroparity. The American Naturalist, 133, 901-923.
524	
525	Pettifor, R. A., Perrins, C.M. & McCleery, R.H. (1988) Individual optimization of clutch size
526	in great tits. <i>Nature</i> , 336 , 160–162.
527	
528	Pettorelli, N. & Durant, S.M. (2007) Family effects on early survival and variance in long-
529	term reproductive success of female cheetahs. Journal of Animal Ecology, 76, 908–914.
530	
531	Philippi, T. & Seger, J. (1989) Hedging one's evolutionary bets, revisited. Trends in Ecology
532	& Evolution, 4 , 41–44.
533	
534	Pinheiro, J.C. & Bates, D.M. (2000) Mixed-effects models in S and S-PLUS. Springer, New
535	York, USA.
536	
537	R Development Core Team. (2011) R: A language and environment for statistical computing.
538	R Foundation for Statistical Computing, Vienna, Austria.
539	
540	Reed, D.H., & Nicholas, A.C. (2008) Spatial and temporal variation in a suite of life-history
541	traits in two species of wolf spider. Ecological Entomology, 33, 488-496.
542	
543	Richard, A.F., Dewar, R.E., Schwartz, M. & Ratsirarson, J. (2002) Life in the slow lane?

Journal of Animal Ecology

544	Demography and life histories of male and female sifaka (Propithecus verreauxi verreauxi).
545	<i>Journal of Zoology</i> , 256 , 421–436.
546	
547	Roff, D.A. (2002) Life history evolution. Sinauer Associates Sunderland, Massachusetts.
548	
549	Russel, A.J.F., Foot, J.Z., White, I.R. & Davies, G.J. (1981) The effect of weight at mating
550	and of nutrition during Mid-Pregnancy on the birth weight of lambs from primiparous ewes.
551	The Journal of Agricultural Science, 97, 723–729.
552	
553	Sæther, B.E. & Heim, M. (1993) Ecological correlates of individual variation in age at
554	maturity in female moose (Alces alces) - The effects of environmental variability. Journal of
555	Animal Ecology, 62 , 482-489.
556	
557	Schaffer, W.M. (1974) Optimal reproductive effort in fluctuating environments. The American
558	Naturalist, 108, 783–790.
559	
560	Seger, J. & Brockman, H.J. (1987) What is bet-hedging? Oxford Surveys in Evolutionary
561	<i>Biology</i> , 4 , 182–211.
562	
563	Servanty, S., Gaillard, J-M., Allaine, D., Brandt, S. & Baubet, E. (2007) Litter size and fetal
564	sex ratio adjustment in a highly polytocous species: the wild boar. Behavioral Ecology, 18,
565	427–432.
566	
567	Servanty, S., Gaillard, J-M., Ronchi, F., Focardi, S., Baubet, E. & Gimenez, O. (2011)
568	Influence of harvesting pressure on demographic tactics: implications for wildlife

- 569 management. *Journal of Applied Ecology*, **48**, 835–843.
- 570
- 571 Slatkin, M. (1974) Hedging one's evolutionary bets. *Nature*, **250**, 704–705.
- 572
- 573 Smith, C. C. & Fretwell, S.D. (1974) The optimal balance between size and number of
- offspring. *The American Naturalist*, **108**, 499–506.
- 575
- 576 Stearns, S.C. (1992) The evolution of life histories, vol. 248. Oxford University Press Oxford.
- 577
- 578 Tanaka, K. (1995) Variation in offspring size within a population of the web-building spider
- 579 Agelena limbata. Researches on Population Ecology, **37**, 197–202.
- 580
- 581 Thumm, K., & Mahony, M. (2002) Hatching dynamics and bet-hedging in a temperate frog,
- 582 *Pseudophryne australis (Anura: myobatrachidae). Amphibia-Reptilia*, **23**, 433–444.
- 583
- 584 Thumm, K., & Mahony, M. (2005) Is variable egg size the proximate cause of diversified
- bet-hedging in the hatching dynamics of the red-crowned toadlet (*Pseudophryne*
- 586 *australis*)(anura: *Myobatrachidae*)? Journal Information, **61**, 9–19.
- 587
- 588 Thumm, K., & Mahony, M. (2006). The effect of water level reduction on larval duration in
- the red-crowned toadlet *Pseudophryne australis* (Anura: *myobatrachidae*): Bet-hedging or
- 590 predictive plasticity? *Amphibia-Reptilia*, **27**, 11–18.
- 591
- 592 Toms, J. & Lesperance, M. (2003) Piecewise regression: a tool for identifying ecological
- thresholds. *Ecology*, **84**, 2034–2041.

594	
595	Tuljapurkar, S. (1990) Delayed reproduction and fitness in variable environments.
596	Proceedings of the National Academy of Sciences, 87, 1139–1143.
597	
598	Tuljapurkar, S. & Wiener, P. (2000) Escape in time: stay young or age gracefully? Ecological
599	Modelling, 133 , 143–159.
600	
601	Van Noordwijk, A.J. & de Jong, G. (1986) Acquisition and allocation of resources: their
602	influence on variation in life history tactics. The American Naturalist, 128, 137-142.
603	
604	Winkler, D.W. & Wallin, K. (1987) Offspring size and number: A life history model linking
605	effort per offspring and total effort. The American Naturalist, 129, 708–720.
606	
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Table 1. List of the 24 papers (out of 208 quoting Kaplan & Cooper (1984)'s paper on coinflipping on 12 January 2012) including tests of phenotypic polymorphism among offspring produced by a given individual. The species considered in the study, the taxonomic order, the offspring trait measured, the test outcome (coin-flipping (yes) or no (no)), and the reference of the study are provided. The table is divided into two parts. Part A brings together studies 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
Α				
Anura	Quacking frog (Crinia georgiana)	Eggs size within clutches	Yes	Dziminski, Vercoe & Roberts 2009
Anura	Quacking frog (Crinia georgiana)	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</i> australis)	Offspring sizes	Yes	Thumm & Mahony 2005
Anura	Fire-bellied toad (Bombina orientalis)	Eggs size	Yes	Kaplan 1992
Araneae	Wolf spider (Rabidosa punctulata, R. rabida)	Offspring size among clutches	No	Reed & Nicholas 2008
Araneae	Web-building spider (Agelena limbata)	Offspring size within and among clutches	Yes	Tanaka 1995
Chelonia	Giant Asian pond turtle (Heosemys grandis)	Number and size of eggs among clutches	Yes	Goode & Ewert 2006
Cladocera	Freshwater zooplankter (Daphnia magna)	Offspring sizes within clutches	No	McKee 1997
Cyprinodontifor mes	Poeciliid fish (Heterandria formosa)	Offspring size at birth	Yes	Henrich 1988
Cyprinodontifor mes	Mosquitofish (Gambusia affinis)	Embryo size	Yes	Meffe 1987
Homoptera	Bird cherry-oat aphid (Rhopalosiphum padi)	Production of sexuals or parthenogenetic females	Yes	Halkett et al. 2004
Rodentia	Yellow-bellied marmot (<i>Marmota flaviventris</i>)	Social behavior	Yes	Armitage 1986

Salmoniformes	Brook trout (Salvelinus fontinalis)	Eggs size	Yes	Koops, Hutchings & Adams 2003
Scleractinia	Scleractinian corals (<i>Pocillopora</i> damicornis, Seriatopora hustrix, Stylophora pistillata)	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
В				
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 (Argulus coregoni)	Intra-clutch variability in hatching among eggs	Yes	Hakalahti, Häkkinen & Valtonen 2004
Coleoptera	Chestnut weevil (Curculio elephas)	Duration of diapause	Yes	Menu & Debouzie 1993
Hemiptera	Triatominas (Triatominae)	Developmental delays	Yes	Menu et al. 2010
Hymenoptera	Pipe-Organ Mud-daubing Wasp (<i>Trypoxylon politum</i>)	Synchrony or asynchrony of emergence pattern	Yes	Brockmann 2004
Passeriformes	House wrens (Troglodytes aedon)	Synchrony or asynchrony in hatching eggs and weight	Yes	Bowers, Sakaluk & Thompson 2011

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Table 2. Model selection of linear mixed models fitted with individual fetus mass (*mass*) as a response variable and mother identity (*mother*) as a random factor. The fixed effects correspond to gestation stage (*gestation*) and gestation stage² (*gestation²*), hunting season (*year*), fetus sex (*sex*), 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 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 column *Models* with a variance function specifying that fetus mass was allowed to differ in relation to female body mass. The selected models are in bold. Data come from wild boar females collected in the population of Châteauvillain-Arc-en-Barrois, France.

	I	4	B	6
Models	AIC	ΔΑΙΟ	AIC	ΔΑΙC
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+gestation ² +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

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Figure 1. Relationship between litter size and female body mass (on a log-scale) in the wild

652	Figure	legends
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- boar population of Châteauvillain- Arc-en-Barrois, France. The best fitting model (segmented
 regression, solid line) and the linear and quadratic relationships (dotted lines) are displayed.
 The vertical solid lines correspond to the threshold body mass estimated from the segmented
- regression and its associated confidence interval.
- **Figure 2.** Relationship between standardized fetus mass (*i.e.*, corrected for gestation stage)
- 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
- sex and hunting season as fixed effects and mother identity as a random effect (intercept:
- 662 1005.166; slope: 0.295 (SE: 0.117)).
- **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: -
- 3.276e-03; slope = 3.545e-04 (SE: 8.478e-05); p-value << 0.01).

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673 Fig. 1.



Log Female Body Mass

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678 **Fig. 2**.



Fig. 3.



- **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 << 0.01; gestation stage²: slope = 0.209, SE = 0.003; p-value << 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 res

A)	Intercept
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+gestation ² +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+gestation ² +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

ponse 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

Year 1998	SE	Year 1999	SE	Year 2000	SE	Year 2001
-2.087169	10.838650	-1.468700	10.115514	-11.898723	14.535547	-16.365803
-2.479462	10.802688	-1.641765	10.084674	-10.593128	14.488120	-16.722539
-3.005521	10.775402	-2.071703	10.063596	-10.648041	14.477794	-17.587640
-2.617202	10.811224	-1.900165	10.094448	-11.955087	14.525221	-17.236409
-1.995600	10.941400	-2.267436	10.205177	-11.638039	14.672503	-17.116154
-1.814267	10.899937	-2.161626	10.180680	-11.609089	14.650267	-16.855280
-2.394704	10.915006	-2.482863	10.183073	-10.320634	14.637820	-17.514605
-2.174998	10.874533	-2.353631	10.159236	-10.285891	14.616508	-17.198304
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
-0.2164	10.764390	0.4935	9.996430	-9.5220	14.367398	-14.8239
-0.5317	10.720737	0.3852	9.955803	-8.3161	14.305342	-15.1023
-1.1230	10.693832	-0.0836	9.936257	-8.4224	14.297463	-16.0622
-0.8213	10.738340	0.0152	9.977783	-9.6302	14.360791	-15.8054
0.2512	10.843358	-0.0213	10.069112	-9.1394	14.475021	-15.2668
0.4043	10.791111	0.0664	10.040533	-9.0968	14.449574	-15.0638
-0.0345	10.804591	-0.1384	10.033172	-7.9128	14.419611	-15.5509
0.1731	10.752858	-0.0190	10.005085	-7.8559	14.395004	-15.2758
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA

other body mass (mother body mass) and litter size (litter size) for (A) All possible models and for (

SE	Year 2002	SE	Year 2003	SE	Year 2004	SE
9.966127	-12.339041	11.061386	-3.696046	10.680154	-27.317094	10.615676
9.934405	-12.187252	11.024322	-4.276184	10.645879	-26.971466	10.581400
9.869286	-12.861533	10.984822	-4.605541	10.630610	-27.766500	10.527919
9.900715	-13.015398	11.021938	-4.028290	10.664810	-28.116613	10.562027
10.055567	-11.405323	11.160136	-3.648962	10.780992	-28.499368	10.705236
9.984980	-11.135213	11.089298	-3.536842	10.755132	-28.282855	10.653286
10.032485	-11.217519	11.132955	-4.234911	10.756089	-28.205192	10.680299
9.962937	-10.888894	11.062900	-4.099329	10.731061	-27.942114	10.629121
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
9.874083	-10.1903	10.985014	-1.7467	10.563426	-25.2605	10.495342
9.833907	-9.9763	10.940166	-2.1676	10.519298	-24.8568	10.451258
9.767130	-10.7131	10.901913	-2.5330	10.505572	-25.6635	10.404915
9.807992	-10.9419	10.947797	-2.1215	10.550558	-26.0893	10.449435
9.946630	-9.2764	11.060648	-1.3925	10.641847	-26.0517	10.569334
9.863709	-9.0750	10.983172	-1.2932	10.610159	-25.8931	10.514966
9.911099	-9.0350	11.021001	-1.7899	10.602543	-25.6548	10.530363
9.828685	-8.7617	10.944074	-1.6559	10.571462	-25.4411	10.476766
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA

Year 2005	SE	Year 2006	SE	Year 2007	SE	Year 2008
-7.141294	13.387191	-17.448597	11.290648	-7.348290	10.329227	-18.607765
-9.183713	13.339685	-17.416521	11.251443	-8.084024	10.297239	-16.510802
-9.725118	13.313372	-18.236120	11.197531	-8.378536	10.283594	-16.341329
-7.688232	13.360679	-18.272444	11.236626	-7.645570	10.315515	-18.438499
-9.264259	13.486754	-16.317363	11.389323	-8.087942	10.421873	-17.287493
-9.178423	13.461960	-15.988523	11.293477	-8.023455	10.403048	-17.286414
-11.417280	13.450719	-16.235961	11.360220	-8.869291	10.398751	-15.128002
-11.314250	13.426924	-15.836133	11.265335	-8.791587	10.380670	-15.127380
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
-5.6389	13.121377	-15.1559	11.244793	-5.7996	10.211670	-16.0265
-7.3007	13.055287	-15.0414	11.200227	-6.3634	10.169531	-14.1262
-7.9322	13.028436	-15.8554	11.155600	-6.7119	10.156492	-14.0323
-6.2857	13.095618	-15.9921	11.200667	-6.1566	10.199478	-15.9278
-7.2351	13.204879	-13.7649	11.313284	-6.1590	10.287333	-14.9017
-7.1479	13.173963	-13.5267	11.213588	-6.0904	10.263636	-14.8776
-8.9383	13.145211	-13.5854	11.273579	-6.7243	10.249975	-12.9681
-8.8205	13.115088	-13.2627	11.174752	-6.6316	10.226861	-12.9364
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA

[B) the all same models with a variance function specifying that fetus mass was allowed to differ an

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

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

the models . The selected

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

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	