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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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Running headline: Coin-flipping in wild boar

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Summary

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

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

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

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

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

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Introduction

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 unpredictable and variable environments, the life history tactic leading to the highest individual fitness involves minimizing among-year variation in reproductive success rather than consistently maximizing reproductive success each year (Slatkin 1974; Philippi & Seger 1989). Bet-hedging includes two non-exclusive mechanisms, risk spreading and risk-minimizing (Seger & Brockman 1987). For instance, iteroparity corresponds to a risk-spreading tactic, which has been interpreted as a response to environmental variation (Charnov & Schaffer 1973, Schaffer 1974, Orzack & Tuljapurkar 1989, Gaillard & Yoccoz 2003). Likewise, producing each year the same limited number of offspring (Olofsson, Ripa & Jonsén 2009) and adjusting reproductive effort to a low level relative to available resources to avoid jeopardizing survival (Richard *et al.* 2002, Gaillard & Yoccoz 2003, Hamel *et al.* 2010, Nevoux *et al.* 2010, Jones 2011) correspond to a risk-minimizing life history tactic. 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 offspring by allocating differentially among offspring within a given reproductive attempt (see Kühl *et al.* 2007 for evidence of differential maternal allocation to male offspring according to litter composition in saiga antelope *Saiga tatarica*). Such a mechanism involving developmental plasticity among litter mates has been called coin-flipping by Kaplan & Cooper (1984). Few studies have reported a phenotypic plasticity in offspring traits (Table 1). 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 time. Most of them dealt with cold-blooded organisms as originally targeted by Kaplan & Cooper (1984). Only two studies dealt with warm-blooded species (house wrens, *Troglodytes*

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

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

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

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

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

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Materials and methods

STUDY AREA AND DATA COLLECTION

We studied a wild boar population in northeastern France in the 11,000 ha forest of Châteauvillain-Arc-en-Barrois. The territory is administratively divided into a core area that covers 8,500 ha of national forest and a 2,500 ha surrounding area of private or communal forest. These forests are mainly composed of oak (*Quercus petraea*), beechnut (*Fagus 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 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 1,743 fetuses collected during 14 hunting seasons.

LINKING MASS OF FETUSES AND GESTATION STAGE

Offspring mass is expected to differ markedly among litters. In particular, not all litters were 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 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 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* mean length (in mm)). The strength of this relationship was very high ($R^2 = 0.86$, N = 20,

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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.

LINKING LITTER SIZE AND FEMALE BODY MASS

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 linear regression model, a quadratic regression model, and a segmented regression model (Toms & Lesperance 2003). AIC was used for model selection (Burnham & Anderson 2002).

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).

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WITHIN-LITTER VARIABILITY IN FETUS MASS

To provide a measure of within-litter variation in mass, we calculated the coefficient of variation (CV) of fetus mass for each litter. To correct fetus mass by gestation stage, we used the quadratic relationship linking fetus mass and gestation stage (see the section "Linking mass of fetuses and gestation stage" for further details) and we standardized all fetuses at the same gestation stage of 110 days (110 days corresponds to the latest gestation stage observed in the dataset). To assess the effect of female body mass on the CV of fetus mass corrected for gestation stage, we fitted a linear regression between CV of fetus mass and female body mass.

Moreover, we explicitly tested whether the variation in fetus body mass increased with female body mass by including variance functions into the different models tested. We used the "varPower" variance function (Pinheiro & Bates 2000) because of its flexibility. Models including variance functions only differ from models without variance function in that the within-group errors are allowed to be heteroscedastic. More precisely, the residual term of the regression linking fetus mass and female body mass followed a Gaussian distribution with mean zero and a variance that equals σ^2*female body mass^(2*δ) where σ is the standard residual standard deviation and δ a parameter to be estimated. Including variance functions thus specifies that the variance in fetus mass changes with increasing female body mass (Pinheiro & Bates (2000); see Cleasby & Nakagawa (2011) for an application of variance functions). AIC was used for model selection (Burnham & Anderson 2002).

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

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Results

LINKING MASS OF FETUSES AND GESTATION STAGE

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 = 0.209, SE = 0.003; p-value << 0.01; $R^2 = 0.974$; Appendix S1).

LINKING LITTER SIZE AND FEMALE BODY MASS

The segmented regression linking litter size with maternal mass provided the best fit to data (AIC = 174.1; intercept = -1.29 (0.31); slope= 0.76 (SE: 0.08) before the threshold; R^2= 0.219) when compared to the linear (AIC = 178.2; intercept= -0.67 (SE: 0.26); slope= 0.59 (SE: 0.06); R^2= 0.204) and quadratic (AIC = 176.3; intercept= -6.23 (SE: 2.89); log(Female Body Mass)= 3.53 (SE: 1.50); log(Female Body Mass)²= -0.38 (SE: 0.19); R^2= 0.214) models. The higher the female body mass is, the larger is the litter size until a threshold mass (Fig. 1). Above this threshold mass, litter size did not increase with body mass. This threshold corresponded to a female mass of 58.3 kg, at which litter size was about 6.2 fetuses. Nevertheless, the AIC of the three tested models were very close and the differences among 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 mass, but this relationship became weaker (quadratic model) or stopped to become constant (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 offspring females can produce on average.

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LINKING MASS OF FETUSES WITH FEMALE BODY MASS

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

WITHIN-LITTER VARIABILITY IN FETUS MASS

The heavier the female body mass is, the higher is the CV of fetus mass (intercept: -3.276e-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 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 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

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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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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

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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 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
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.

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

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

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

Wild boars are hunted in most European forests and have become short-lived animals despite of their large body size. The generation time in heavily hunted wild boar populations is around 2 years, which is closer to the turn-over of tit populations than to that of a 60 kg mammal (Servanty *et al.* 2011). Such unusual demographic patterns have led wild boar females to have only one or two breeding attempts during their lifetime, starting to breed at one year of age (Gamelon *et al.* 2011) at a low threshold body mass (between 20 and 25 kg, Servanty *et al.* 2009). Consequently, wild boar females could exhibit different reproductive tactics during their life according to their body mass. An investigation of coin-flipping in an un-hunted wild boar population in which individuals start to breed at a higher threshold body 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 (*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 (*Pseudophryne 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
Cyprinodontiformes	Poeciliid fish (*Heterandria formosa*)	Offspring size at birth	Yes	Henrich 1988
Cyprinodontiformes	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 (*Marmota flaviventris*)**	**Social behavior**	**Yes**	**Armitage 1986**

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Salmoniformes	Brook trout (*Salvelinus fontinalis*)	Eggs size	Yes	Koops, Hutchings & Adams 2003
Scleractinia	Scleractinian corals (*Pocillopora 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 (*Elaphe obsoleta*)	Offspring size among and within clutches	No	Blouin-Demers & Weatherhead 2007
B				
Anura	Red-crowned toadlet (*Pseudophryne australis*)	Developmental rates	Yes	Thumm & Mahony 2006
Anura	Red crowned toadlet (*Pseudophryne australis*)	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 (*Trypoxylon politum*)	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.

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

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mass~gestation+gestation²	17037.21	74.93	16910.72	68.65

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Figure legends

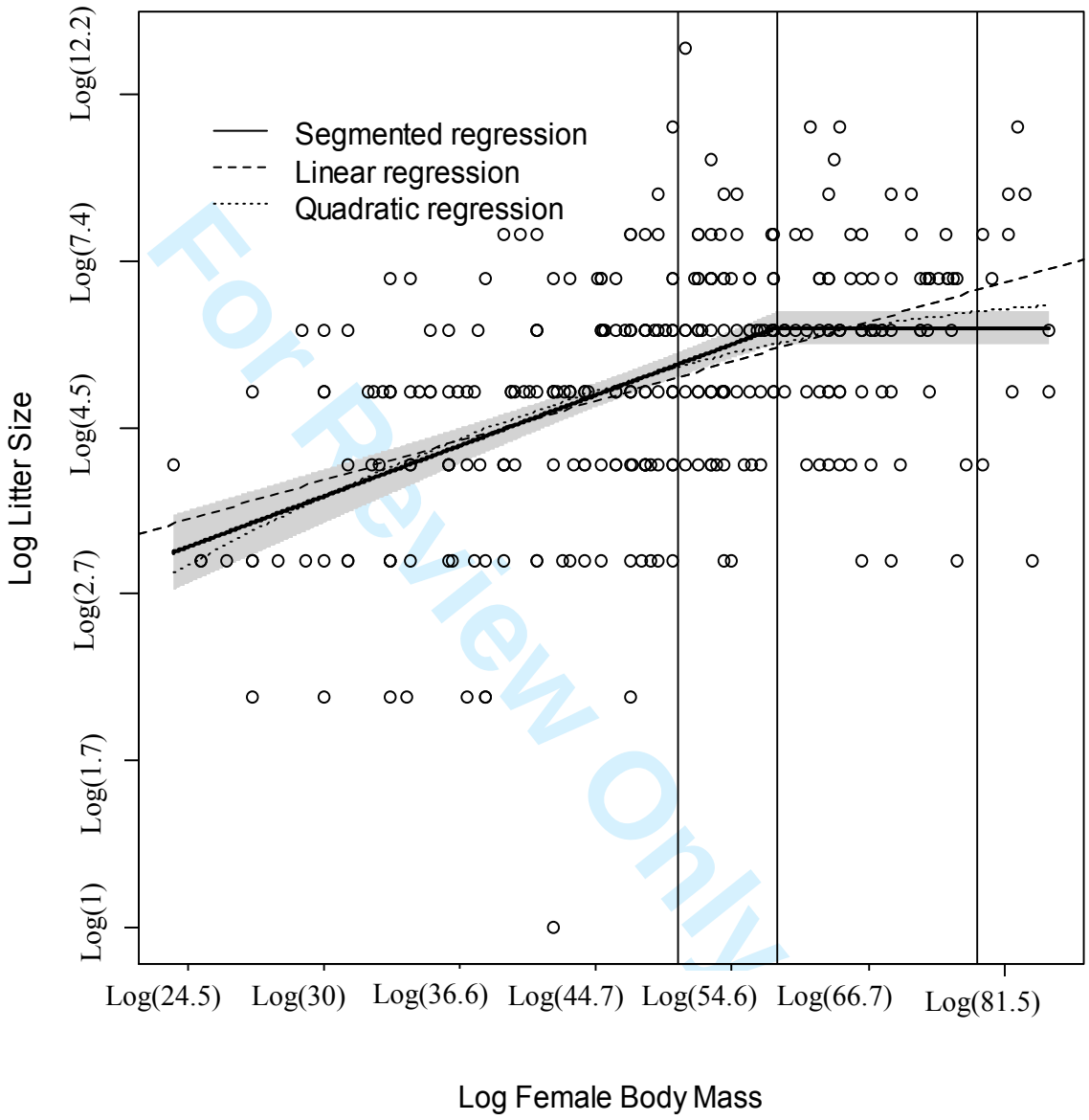
Figure 1. Relationship between litter size and female body mass (on a log-scale) in the wild boar population of Châteauvillain- Arc-en-Barrois, France. The best fitting model (segmented regression, solid line) and the linear and quadratic relationships (dotted lines) are displayed. The vertical solid 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 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: 1005.166; slope: 0.295 (SE: 0.117)).

Figure 3. Relationship between the CV of fetus mass and female body mass from females 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.**



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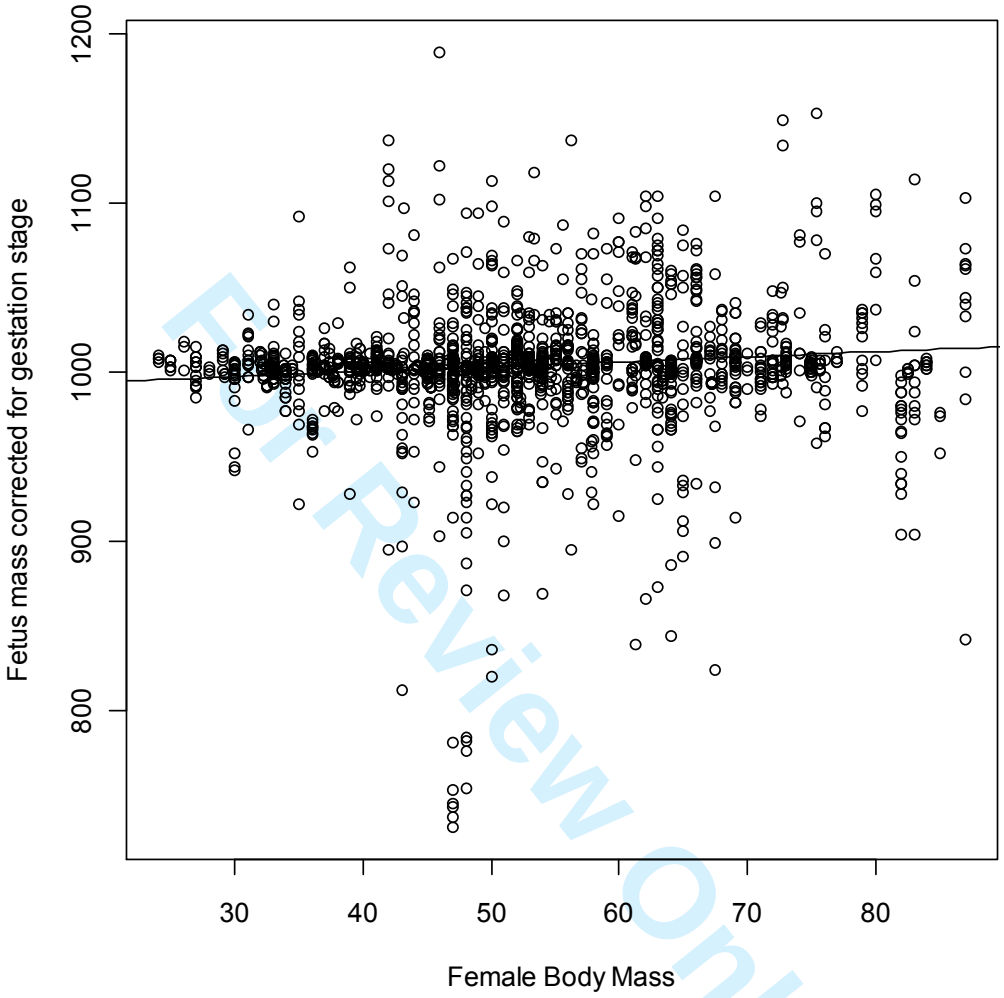
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678 **Fig. 2.**



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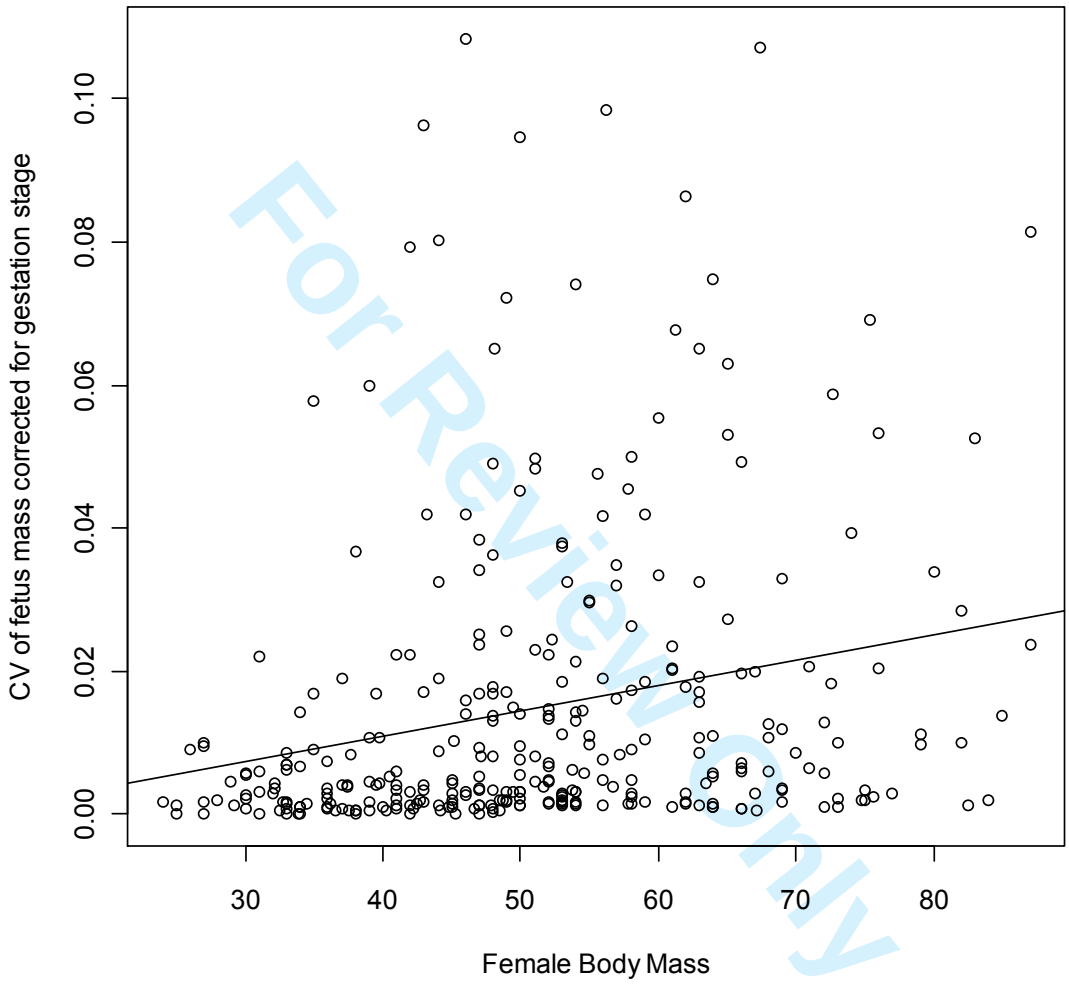
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685 **Fig. 3.**

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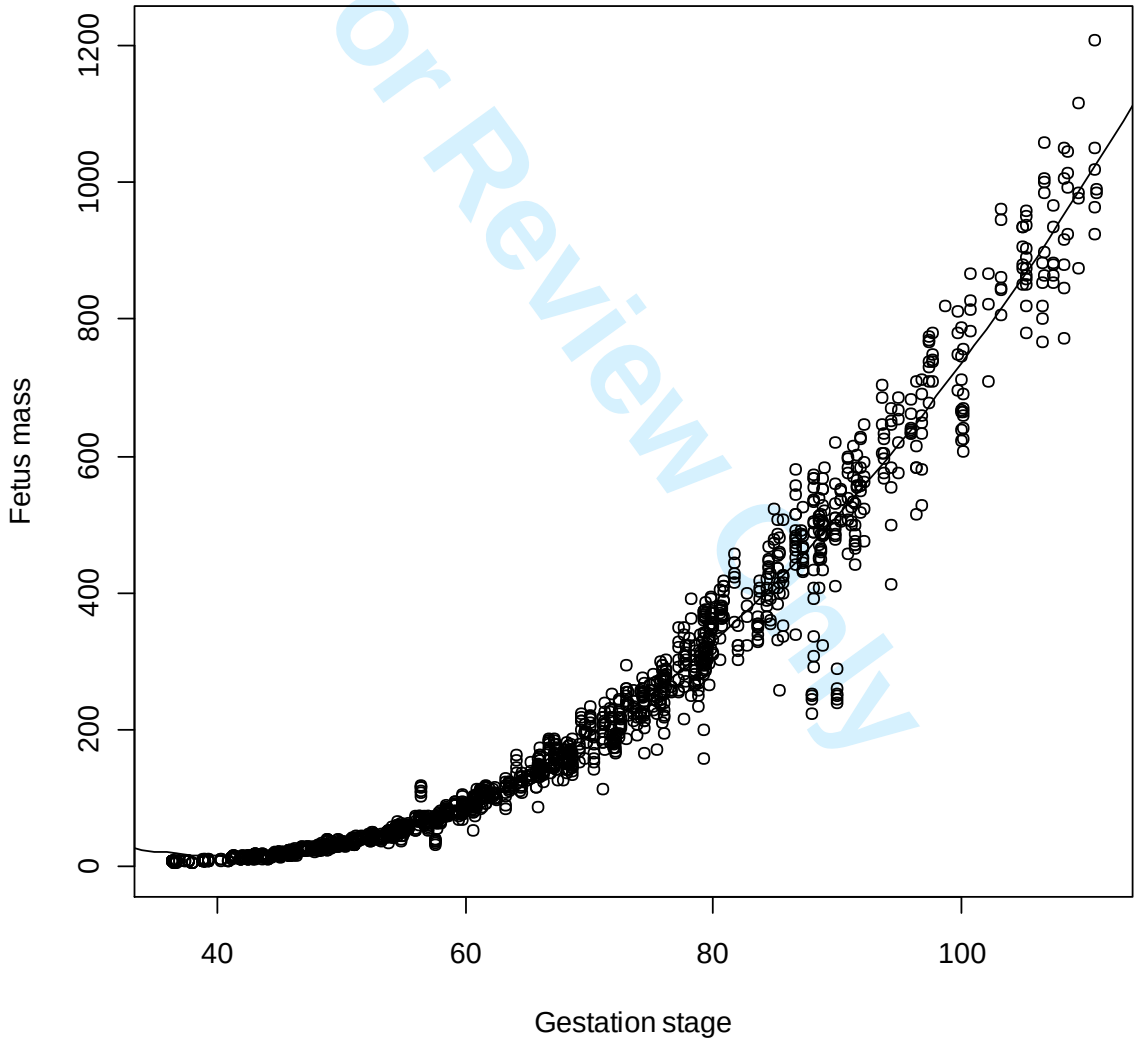
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Supporting Information

Appendix S1

Relationship between fetus mass and gestation stage in the wild boar population of Châteauvillain-Arc-en-Barrois, France (gestation stage: slope = -17.175, SE = 0.371; p-value << 0.01; gestation stage^2: 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 resp

A)	Intercept
mass~gestation+gestation²+year+mother body mass+litter size+sex+mother	380.634381
mass~gestation+gestation²+year+mother body mass+litter size+mother	374.019765
mass~gestation+gestation²+year+mother body mass+mother	372.598006
mass~gestation+gestation²+year+mother body mass+sex+mother	379.211825
mass~gestation+gestation²+year+sex+litter size+mother	386.581145
mass~gestation+gestation²+year+sex+mother	387.333558
mass~gestation+gestation²+year+ litter size+mother	380.227457
mass~gestation+gestation²+year+mother	381.145422
mass~gestation+gestation²+mother body mass+litter size+mother	366.037266
mass~gestation+gestation²+mother body mass+sex+mother	369.833861
mass~gestation+gestation²+mother body mass+litter size+sex+mother	372.879994
mass~gestation+gestation²+mother body mass+mother	362.987829
mass~gestation+gestation²+litter size+sex +mother	377.763622
mass~gestation+gestation²+litter size+mother	371.22766
mass~gestation+gestation²+sex+mother	375.960021
mass~gestation+gestation²	369.662583

B)	
mass~gestation+gestation²+year+mother body mass+litter size+sex+mother	377.1696
mass~gestation+gestation²+year+mother body mass+litter size+mother	371.4549
mass~gestation+gestation²+year+mother body mass+mother	370.2911
mass~gestation+gestation²+year+mother body mass+sex+mother	375.9730
mass~gestation+gestation²+year+sex+litter size+mother	382.5391
mass~gestation+gestation²+year+sex+mother	382.9819
mass~gestation+gestation²+year+ litter size+mother	376.9891
mass~gestation+gestation²+year+mother	377.5949
mass~gestation+gestation²+mother body mass+litter size+mother	364.3586
mass~gestation+gestation²+mother body mass+sex+mother	367.4411
mass~gestation+gestation²+mother body mass+litter size+sex+mother	370.1793
mass~gestation+gestation²+mother body mass+mother	361.6615
mass~gestation+gestation²+litter size+sex +mother	375.0776
mass~gestation+gestation²+litter size+mother	369.4921
mass~gestation+gestation²+sex+mother	373.2981
mass~gestation+gestation²	367.9610

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

SE	Gestation	SE	Gestation²	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

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estation stage (gestation) and gestation stage² (gestation²), hunting season (year), fetus sex (sex), m

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

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ıother 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

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

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

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

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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the models . The selecte

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

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