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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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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, mammal, phenotypic plasticity, reproductive tactic, *Sus scrofa scrofa*

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 & Jonzén 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

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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

Table 1. List of the 24 papers (out of 208 quoting Kaplan & Cooper (1984)'s paper on coin-flipping 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 diversification of developmental time

Order	Species	Traits	Coin-flipping validated	References
A				
Anura	Quacking frog (*Crinia georgiana*)	Eggs size within clutches	Yes	Dziminski, Vercoe & Roberts (2009)
Anura	Quacking frog (*C. 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 behaviour**	**Yes**	**Armitage (1986)**
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 (*P. australis*)	Developmental rates	Yes	Thumm & Mahony (2006)
Anura	Red-crowned toadlet (*P. 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)**

Warm-blooded organisms occur in bold.

with cold-blooded organisms as originally targeted by Kaplan & Cooper (1984). Only two studies dealt with warm-blooded species (house wrens, *Troglodytes 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 & 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 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 foetus 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.

Materials and methods

STUDY AREA AND DATA COLLECTION

We studied a wild boar population in north-eastern France in the 11 000 ha forest of Châteauvillain-Arc-en-Barrois. The territory is administratively divided into a core area that covers 8500 ha of national forest and a 2500 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 foetuses. Litter size was recorded and each foetus was weighed, measured (crown-rump length, in millimetres) and sexed. This information was available for 319 females and 1743 foetuses 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 foetus mass by gestation stage. To assess the gestation stage of a given litter, the mean length of foetuses in the litter was first calculated. Then, we applied the model provided first by Henry (1968) to link gestation stage to mean foetus length across litters [gestation stage (in days) = 23·43 + 0·32* mean length (in mm)]. The strength of this relationship was very high ($R^2 = 0{\cdot}86$, $N = 20$, Henry 1968). The gestation stage was thus estimated from Henry (1968)'s model for each litter. We then regressed individual foetus mass of the entire data set on the gestation stage and used the best model to standardize foetus mass at a given gestation stage. Because the relationship was quadratic (see Results), we corrected in all the following analyses the individual foetus mass by gestation stage and gestation stage^2 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 foetus mass. To do this, we used linear mixed models with normal error terms. We included individual foetus 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 foetus sex. AIC was used for model selection (Burnham & Anderson 2002).

WITHIN-LITTER VARIABILITY IN FETUS MASS

To provide a measure of within-litter variation in mass, we calculated the coefficient of variation (CV) of foetus mass for each litter. To correct foetus mass by gestation stage, we used the quadratic relationship linking foetus mass and gestation stage (see the section 'Linking mass of foetuses and gestation stage' for further details) and we standardized all foetuses 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 foetus mass corrected for gestation stage, we fitted a linear regression between CV of foetus mass and female body mass.

Moreover, we explicitly tested whether the variation in foetus 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 foetus mass and female body mass followed a Gaussian distribution with mean zero and a variance that equals σ^2*female body mass$^{(2*\delta)}$ where σ is the standard residual standard deviation and δ a parameter to be estimated. Including variance functions thus specifies that the variance in foetus 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).

Results

LINKING MASS OF FETUSES AND GESTATION STAGE

As expected, the mass of foetuses increased with the gestation stage, on a quadratic way (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; Appendix S1, Supporting information).

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 foetuses. 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.

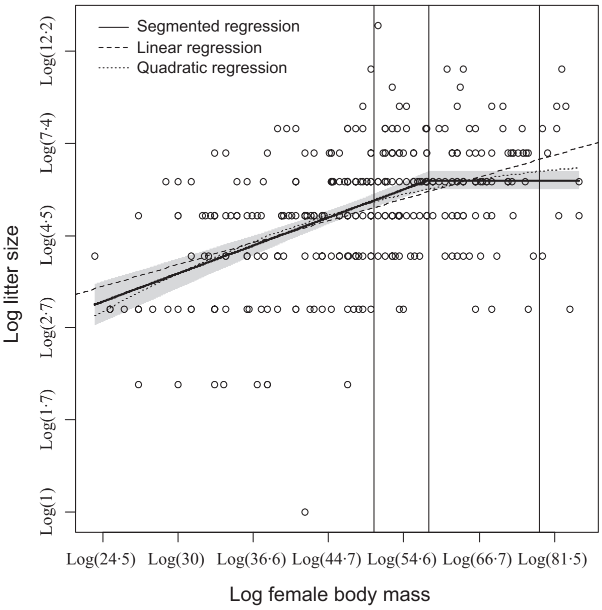

Fig. 1. Relationship between litter size and female body mass (on a log-scale) in the wild boar population of Châteauvillain-Arc-en-Barrois, France. The best fitting model (segmented regression, solid line) and the linear and quadratic relationships (dotted lines) are displayed. The vertical solid lines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

LINKING MASS OF FETUSES WITH FEMALE BODY MASS

The baseline model of variation in foetus 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 and foetus sex (Table 2 A; see Appendix S2, Supporting information for parameter estimates). Foetus mass thus depended on maternal mass. The heavier the females are the heavier the foetuses are (Fig. 2). Nevertheless, from a biological viewpoint, this relationship between foetus mass and female body mass was weak as shown by the small effect size [maternal mass effect = 0·295 (SE: 0·117)]. Moreover, we found no effect of litter size on foetus mass.

WITHIN-LITTER VARIABILITY IN FETUS MASS

The heavier the female body mass is, the higher is the CV of foetus 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 foetus 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 2 B), 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 foetus mass as fixed effects, of mother identity as random effect and included the variance function (AIC = 16842·07; see Appendix S2, Supporting information 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 foetus mass increases with female body mass. More precisely, δ was estimated to 0·984 (with a 95% confidence interval of 0·812–1·156) meaning that the variance increases with the square of female body mass.

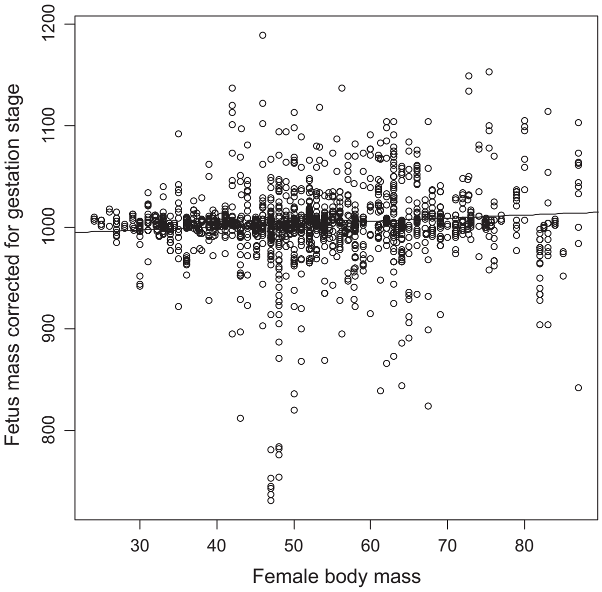

Fig. 2. Relationship between standardized foetus mass (i.e. corrected for gestation stage) and female body mass. The solid line corresponds to the estimates provided by the linear mixed model linking standardized foetus mass as a response variable, female body mass, foetus sex and hunting season as fixed effects and mother identity as a random effect [intercept: 1005·166; slope: 0·295 (SE: 0·117)].

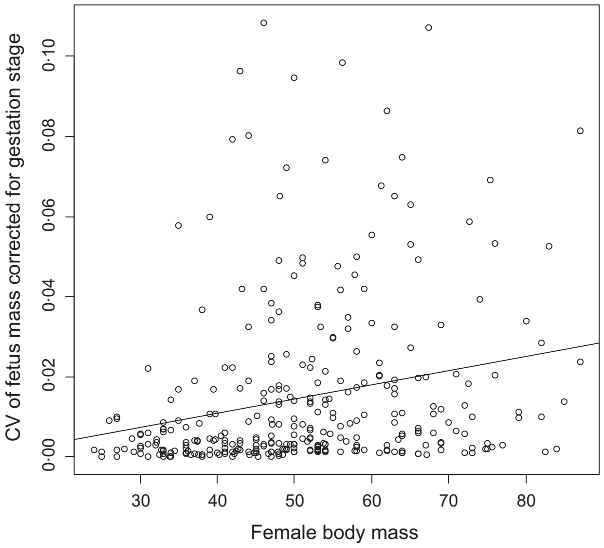

Fig. 3. Relationship between the CV of foetus mass and female body mass from females collected in the wild boar population of Châteauvillain-Arc-en-Barrois, France [intercept: −3·276e-03; slope = 3·545e-04 (SE: 8·478e-05); *P*-value << 0·01].

Discussion

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 was consistent with the individual optimization process involving a strong positive link between litter size and mother's phenotypic attributes usually reported in mammals (see Clutton-Brock 1991 and Gaillard *et al.* 2000 for reviews). However, while previous studies of large mammals have reported that mothers in better than average condition produce heavier offspring (e.g. Russel *et al.* 1981 and Holst, Killeen & Cullis 1986 for sheep *Ovis aries*; 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. Foetus mass was mainly influenced by gestation stage, sex and year. The influence of gestation stage is trivial and simply corresponds to foetal growth during gestation. Males were heavier than females, as expected for a polygynous and dimorphic species like wild boar (Glucksmann 1974). The marked among-year variation in foetus mass was also expected from the highly variable and unpredictable food resources wild boars face with. Finally, we did

Table 2. Model selection of linear mixed models fitted with individual foetus mass (*mass*) as a response variable and mother identity (*mother*) as a random factor. The fixed effects correspond to gestation stage (*gestation*) and gestation stage^2 (*gestation*^{2}), hunting season (*year*), foetus 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 foetus mass was allowed to differ in relation to female body mass

Models	A		B	
	AIC	ΔAIC	AIC	ΔAIC
mass~gestation+gestation^2+year+mother body mass+litter size+sex+mother	16963·60	1·32	16843·23	1·16
mass~gestation+gestation^2+year+mother body mass+litter size+mother	17028·32	66·04	16903·93	61·86
mass~gestation+gestation^2+year+mother body mass+mother	17027·01	64·73	16902·73	60·66
mass˜gestation + 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
mass~gestation+gestation^2	17037·21	74·93	16910·72	68·65

The selected models are in bold. Data come from wild boar females collected in the population of Châteauvillain-Arc-en-Barrois, France.

not detect any effect of litter size on foetus mass. This absence of any evidence for a trade-off between foetus mass and litter size is especially noteworthy. This indicates that these females adjusted their reproductive effort mainly through variation in litter size and suggests that it pays more for females acquiring an energy surplus to produce more offspring than to produce heavier offspring. At this end of the continuum, we showed that light females produced foetuses that have very similar mass. Indeed, the CV of foetus mass was lower in litters produced by light females than in litters produced by heavy females, indicating little differences in foetus mass 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 foetuses 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 guppies *Poecilia reticulate*). Such a diminishing return can arise either because the marginal benefits of continued effort decrease or because the marginal costs of further reproductive effort increase (Jordan & Brooks 2010). In other words, when diminishing returns occur, a doubling of reproduction provides less than a doubling of relative success (Frank & Slatkin 1990). In our case, the litter size per-unit female body mass decreases as body mass increases, providing evidence for a marginal diminishing return. Therefore, heavy wild boar females did not show any evidence for an individual optimization of their reproductive effort. Such a total 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 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 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 reproductive tactic, and producing a lot of large foetuses is not possible. The reproductive tactic displayed by most females of large mammals in response to these constraints involves optimizing this number-size trade-off according to their condition (individual optimization, Pettifor, Perrins & McCleery 1988; McNamara & Houston 1996). In addition, we showed that CV of foetus mass was higher in litters produced by heavy females than in litters produced by light females, indicating marked differences in foetus mass within litters produced by heavy females. Such a pattern of variation in within-litter foetus mass variation according to female body mass provides support for coin-flipping in litters produced by heavy females.

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 foetus 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 (S. Devillard, L. Say, M. Gamelon, S. Brandt, D. Gonzalez & E. Baubet, 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, Van Laere & Gaillard 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 (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 1 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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