



Research

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Population ecology

Fluctuating food resources influence developmental plasticity in wild boar

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To maximize long-term average reproductive success, individuals can diversify the phenotypes of offspring produced within a reproductive event by displaying the 'coin-flipping' tactic. Wild boar (*Sus scrofa scrofa*) females have been reported to adopt this tactic. However, whether the magnitude of developmental plasticity within a litter depends on stochasticity in food resources has not been yet investigated. From long-term monitoring, we found that juvenile females produced similar-sized fetuses within a litter independent of food availability. By contrast, adult females adjusted their relative allocation to littermates to the amount of food resources, by providing a similar allocation to all littermates in years of poor food resources but producing highly diversified offspring phenotypes within a litter in years of abundant food resources. By minimizing sibling rivalry, such a plastic reproductive tactic allows adult wild boar females to maximize the number of littermates for a given breeding event.

1. Introduction

In unpredictable and variable environments, optimal reproductive tactics of iteroparous organisms should minimize variance in reproductive success among years to maximize long-term average reproductive success [1,2]. To minimize among-year variation in reproductive success, individuals can minimize the variance in the number of offspring produced at each reproductive event (bet-hedging *sensu* [3]). Bet-hedging includes two non-exclusive mechanisms, risk-spreading and risk-minimizing. Producing the same limited number of offspring each year corresponds to risk-spreading. To minimize variance in reproductive success, individuals can also diversify the phenotypic quality of offspring produced at a given reproductive event (coin-flipping *sensu* [4]). Such developmental plasticity is widespread in invertebrates, fishes, amphibians and reptiles but not common in homeotherms [5].

Evidence of coin-flipping within a given reproductive event in warm-blooded species has been reported only in wild boar (*Sus scrofa scrofa*) [5]. Large wild boar females produce offspring with highly diversified phenotypes within a litter, whereas small females display the individual optimization tactic [6,7] by increasing litter size with mass and keeping fetus mass constant [5]. Coin-flipping in wild boar is thus a tactic which depends on female size. By feeding on forest mast, the abundance of which fluctuates greatly among years, wild boar face highly variable and unpredictable environments [8,9]. Therefore, we expect that fluctuating food availability should influence the magnitude of offspring phenotypic variance within a litter. Such a prediction has never been investigated for any species reported to display coin-flipping.

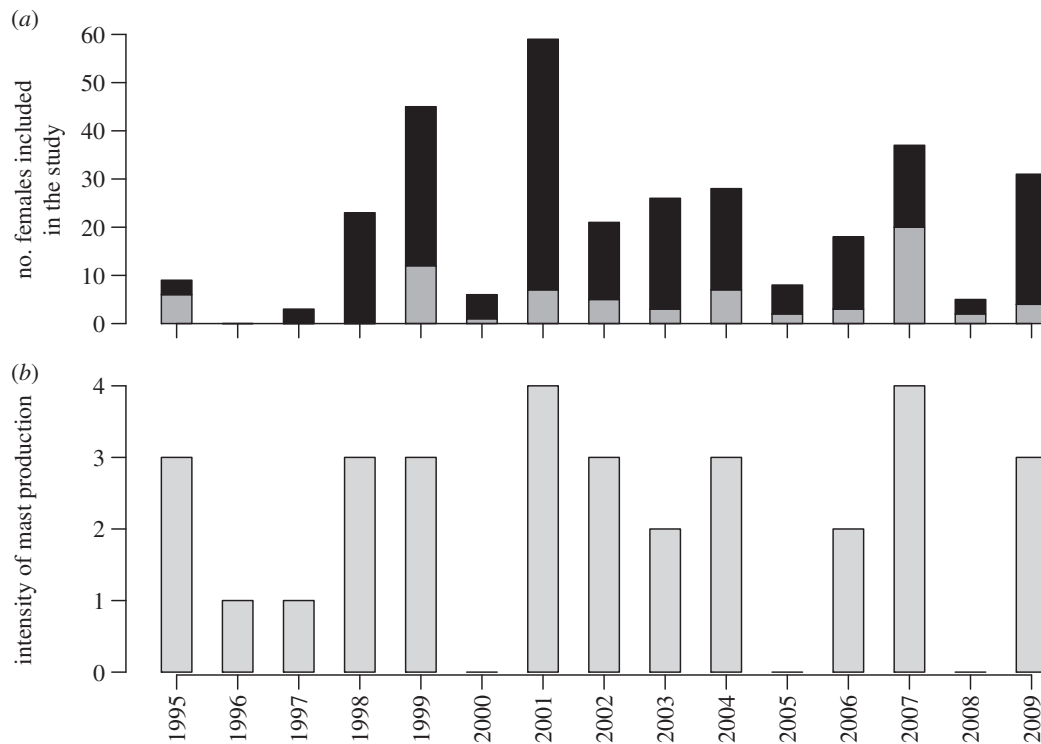


Figure 1. (a) Number of females shot in the population of Châteauvillain-Arc-en-Barrois, France, for which both litter size and fetus mass were measured in a given hunting season and at a given age (72 juvenile females and 247 adult females including 143 between 1 and 2 years of age and 104 older than 2 years of age). (b) Intensity of mast production (beechnuts + acorns) (from 0 corresponding to years without mast production to 4 corresponding to years with a very high mast production). Black shaded area represents females greater than 1 year of age and grey shaded area represents those less than 1 year of age.

Taking advantage of a long-term detailed monitoring programme for a heavily hunted population, we aim to fill the gap by testing whether female wild boar produce litters with increasingly variable phenotypes when there is increased masting.

2. Material and methods

(a) Study site and data collection

This study was conducted on a wild boar population in north-eastern France in the 11 000 ha forest of Châteauvillain-Arc-en-Barrois. This forest is mainly composed of oak (*Quercus petraea*), beech (*Fagus sylvatica*) and hornbeam (*Carpinus betulus*). Population size of wild boar fluctuated between 1200 and 1500 individuals over the course of the study [10]. Wild boar have no natural predators but are heavily hunted each year between October and February (see [11] for estimates of mortality owing to hunting). The hunting pressure was mainly oriented towards juveniles [10]. Between 1995 and 2009, we recorded the age class of each female shot (juvenile (less than 1 year of age) versus adult (older than 1 year of age)) based on tooth eruption pattern [12]. We examined uteri for the presence of fetuses. Changes in resource availability did not influence the fetal sex ratio [9]. Litter size was recorded and each fetus was weighed, measured (crown–rump length, in millimetres) and sexed. Measurements of 1743 fetuses from 319 females were collected during 15 hunting seasons (figure 1a).

(b) Mast production

Each year, food availability was measured indirectly through diet composition, using the analysis of stomach contents during the hunting period [13]. We recognized five categories depending on the quantity of beechnuts and acorns found in the stomachs (see [14] for further details, figure 1b).

(c) Statistical analyses

Not all litters were at the same gestation stage when shot, because mating of wild boar occurs throughout the year [10]. To correct fetus mass among litters by gestation stage, we standardized all fetuses at 110 days of gestation [5].

To assess whether females produced fetuses which were more diverse in terms of mass with increasing mast production, we first provided a measure of within-litter variation in mass by calculating the coefficient of variation (CV) of fetus mass corrected for gestation stage for each litter. We then fitted a generalized least squares (GLS) framework linking the CV of corrected fetus mass as a response variable to the fixed effects of age (categorical variable with two classes), mast production (treated as a continuous variable to describe the continuum of food resources availability) and their interaction.

We checked the expectation that fetuses are not heavier when food resources are abundant. We used linear mixed models with individual fetus mass corrected for gestation stage as the response variable, and mother identity as a random effect to account for the non-independence of fetuses within a litter. We then tested the fixed effects of age and mast production, and their interaction. We assessed whether larger litters are produced in years with abundant food. We fitted a linear regression including litter size as the response variable and mast production, age and their interaction as explanatory variables.

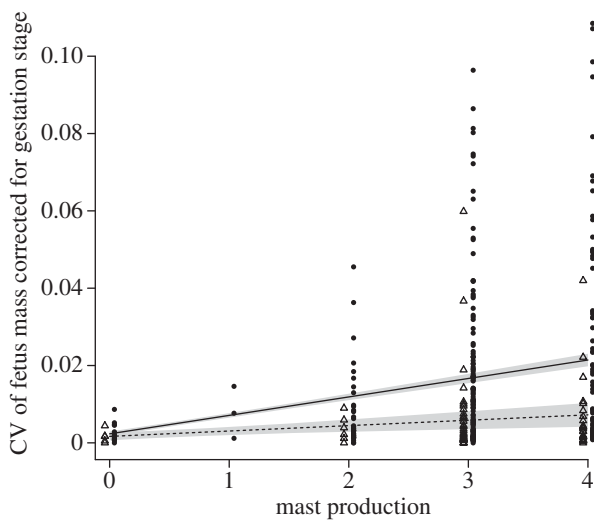
When necessary, we applied a correction for heteroscedasticity by using the ‘varIdent’ variance function [15] to account for different standard deviations among mast productions (performed with R v. 2.12.2 [16]). Data deposited in the Dryad repository: doi:10.5061/dryad.8hf1c.

3. Results

The CV of fetus mass was affected by a positive interaction between mast production and age (slope = 0.003 (s.e.: 0.0009);

Table 1. Effects of mast production and female age on (a) fetus mass (using linear mixed models) and (b) litter size (using linear regression).

response	effect	slope \pm s.e.	<i>p</i> -value
(a)			
fetus mass	mast production \times age	0.080 \pm 3.146	0.980
fetus mass	mast production	-0.697 \pm 1.340	0.603
fetus mass	age	1.357 \pm 3.509	0.699
(b)			
litter size	mast production \times age	-0.151 \pm 0.219	0.491
litter size	mast production	0.169 \pm 0.094	0.072
litter size	age	1.701 \pm 0.225	<0.01

**Figure 2.** Relationships between the CV of fetus mass and mast production for juvenile (triangles) and adult (circles) females collected in the wild boar population of Châteauvillain-Arc-en-Barrois, France. The lines correspond to the predicted values from the GLS linking the CV of fetus mass to mast production, age and their interaction (dotted line for juvenile females and solid line for adult females).

p -value \ll 0.01). In juvenile females, the CV of fetus mass increased with mast production (p -value \ll 0.01; figure 2), but the slope was weak (0.001 (s.e.: 0.0004)). A much stronger positive relationship between within-litter variation in fetus mass and mast production occurred in adult females (slope: 0.005 (s.e.: 0.0005), p -value \ll 0.01; figure 2).

We did not find any influence of mast production and age on fetus mass (table 1). A weak positive effect of mast production occurred on litter size for both juvenile and adult females (table 1). Both female categories increased their litter size only slightly in years of abundant food compared with non-masting years (from 3.65 to 4.32 in juveniles and from 5.35 to 6.02 in adults).

4. Discussion

Nutrition often shapes observed variation in growth of warm-blooded species [17]. Using a direct measure of nutrition for wild boar, we found that fetus mass and litter size are not markedly dependent on mast production. Such a noteworthy lack of effect of food resources on offspring mass and litter size does not mean, however, that wild boar

reproductive tactics are independent of food. Mast production strongly influenced the within-litter variation in fetus mass in adult females (figure 2).

By contrast, juvenile females produced fetuses of similar mass independent of food availability. Juveniles usually do not reproduce in wild boar and did here in response to the high hunting pressure [14,18]. Having reached only 33–41% of their full body mass [14], juvenile females have to allocate a large amount of energy to both growth and reproduction. This constraint might explain why juvenile females did not adjust the phenotype of their offspring to available resources.

Adult females diversified the phenotype of their offspring in masting years. Competition between siblings might be involved in this diversification of offspring phenotype. Sibling rivalry is common among species where young share the same litter [19]. In wild boar, variation in milk availability at different teats (teat order effect [20]) leads littermates to compete for the most productive teats [20,21]. Large offspring have an advantage over small ones in this competition [22]. By producing highly diversified offspring phenotypes, adult females match the mass variation of their offspring with variation in productivity among teats, leading to decreased sibling rivalry and thereby increasing the chance of rearing many offspring at a given breeding event. Adult females displayed a coin-flipping tactic involving the diversification of phenotypes within a litter only in masting years, while maintaining a constant mean fetus mass independent of resource availability. In masting years, females thus produce large fetuses requiring more energy allocation and also small ones requiring less allocation but likely to survive under good food conditions. On the contrary, in non-masting years, small fetuses are no longer viable [21], thus leading adult females to equi-allocate to offspring by producing fetuses of similar mass.

This study provides further support that wild boar females exhibit a unique life-history strategy among ungulates [23] by displaying different reproductive tactics to maximize the number of viable offspring in variable environments.

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1. Philippi T, Seger J. 1989 Hedging one's evolutionary bets, revisited. *Trends Ecol. Evol.* **4**, 41–44. (doi:10.1016/0169-5347(89)90138-9)
2. Starrfelt J, Kokko H. 2012 Bet-hedging: a triple trade-off between means, variances and correlations. *Biol. Rev.* **87**, 742–755. (doi:10.1111/j.1469-185X.2012.00225.x)
3. Slatkin M. 1974 Hedging one's evolutionary bets. *Nature* **250**, 704–705. (doi:10.1038/250704b0)
4. Kaplan RH, Cooper WS. 1984 The evolution of developmental plasticity in reproductive characteristics: an application of the 'adaptive coin-flipping' principle. *Am. Nat.* **123**, 393–410. (doi:10.1086/284211)
5. Gamelon M, Gaillard J-M, Baubet E, Devillard S, Say L, Brandt S, Gimenez O. 2013 The relationship between phenotypic variation among offspring and mother body mass in wild boar: evidence of coin-flipping? *J. Anim. Ecol.* **82** (doi:10.1111/1365-2656.12073)
6. Smith CC, Fretwell SD. 1974 Optimal balance between size and number of offspring. *Am. Nat.* **108**, 499–506. (doi:10.1086/282929)
7. Lloyd DG. 1987 Selection of offspring size at independence and other size-versus-number strategies. *Am. Nat.* **129**, 800–817. (doi:10.1086/284676)
8. Bieber C, Ruf T. 2005 Population dynamics in wild boar *Sus scrofa*: ecology, elasticity of growth rate and implications for the management of pulsed resource consumers. *J. Anim. Ecol.* **42**, 1203–1213. (doi:10.1111/j.1365-2664.2005.01094.x)
9. Servanty S, Gaillard J-M, Allainé D, Brandt S, Baubet E. 2007 Litter size and fetal sex ratio adjustment in a highly polytocous species: the wild boar. *Behav. Ecol.* **18**, 427–432. (doi:10.1093/beheco/arl099)
10. Gamelon M, Besnard A, Gaillard J-M, Servanty S, Baubet E, Brandt S, Gimenez O. 2011 High hunting pressure selects for earlier birth date: wild boar as a case study. *Evolution* **65**, 3100–3112. (doi:10.1111/j.1558-5646.2011.01366.x)
11. Toigo C, Servanty S, Gaillard J-M, Brandt S, Baubet E. 2008 Disentangling natural from hunting mortality in an intensively hunted wild boar population. *J. Wildl. Manage.* **72**, 1532–1539. (doi:10.2193/2007-378)
12. Baubet E, Brandt S, Jullien J-M, Vassant J. 2004 Valeur de l'examen de la denture pour la détermination de l'âge chez le sanglier (*Sus scrofa*). *Gibier Faune Sauvage* **11**, 119–132.
13. Brandt S, Baubet E, Vassant J, Servanty S. 2006 Régime alimentaire du sanglier (*Sus scrofa L.*) en milieu forestier de plaine agricole. *Faune Sauvage* **273**, 20–27.
14. Servanty S, Gaillard J-M, Toigo C, Brandt S, Baubet E. 2009 Pulsed resources and climate-induced variation in the reproductive traits of wild boar under high hunting pressure. *J. Anim. Ecol.* **78**, 1278–1290. (doi:10.1111/j.1365-2656.2009.01579.x)
15. Pinheiro JC, Bates DM. 2000 *Mixed-effects models in S and S-PLUS*. New York, NY: Springer.
16. R Development Core Team. 2011 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
17. Clutton-Brock TH. 1991 *The evolution of parental care*. Princeton, NJ: Princeton University Press.
18. Servanty S, Gaillard J-M, Ronchi F, Focardi S, Baubet E, Gimenez O. 2011 Influence of harvesting pressure on demographic tactics: implications for wildlife management. *J. Appl. Ecol.* **48**, 835–843. (doi:10.1111/j.1365-2664.2011.02017.x)
19. Mock DW, Parker GA. 1997 *The evolution of sibling rivalry*. Oxford, UK: Oxford University Press.
20. Fraser D, Thompson BK. 1991 Armed sibling rivalry among suckling piglets. *Behav. Ecol. Sociobiol.* **29**, 9–15. (doi:10.1007/BF00164289)
21. Drake A, Fraser D, Weary DM. 2008 Parent–offspring resource allocation in domestic pigs. *Behav. Ecol. Sociobiol.* **62**, 309–319. (doi:10.1007/s00265-007-0418-y)
22. Stockley P, Parker GA. 2002 Life history consequences of mammal sibling rivalry. *Proc. Natl Acad. Sci. USA* **99**, 12 932–12 937. (doi:10.1073/pnas.192125999)
23. Focardi S, Gaillard J-M, Ronchi F, Rossi S. 2008 Survival of wild boars in a variable environment: unexpected life-history variation in an unusual ungulate. *J. Mamm.* **89**, 1113–1123. (doi:10.1644/07-MAMM-A-164.1)