

Litter size and fetal sex ratio adjustment in a highly polytocous species: the wild boar

Sabrina Servanty,^{a,b} Jean-Michel Gaillard,^b Dominique Allainé,^b Serge Brandt,^a and Eric Baubet^a

^aOffice National de la Chasse et de la Faune Sauvage, Centre National d'Etudes et de Recherches Appliquées sur les Cervidés-Sangliers, 85bis avenue de Wagram, 75017 Paris, France and ^bLaboratoire de Biométrie et Biologie Evolutive (UMR 5558), CNRS, Université Lyon 1, 43 boulevard 11 novembre 1918, 69622 Villeurbanne Cedex, France

For species in which reproductive success is more variable in one sex than the other, the Trivers and Willard model (TWM) predicts that females are able to adjust their offspring sex ratio. High-quality mothers should provide greater investment to one sex than the other. Previous tests of the TWM have been inconsistent, and whether the TWM applies to species with several offspring per litter is unclear due to possible trade-offs between size, number, and sex of the offspring. Williams' model (WM) accounts for confounding effects of these trade-offs on sex ratio variation. Lastly, the "extrinsic modification hypothesis" predicts changes in offspring sex ratio in relation to climatic conditions and population density. Using wild boar as a model, we tested 1) whether the WM fitted observed sex ratio variation and 2) whether sex ratio variations were related to maternal attributes (test of the TWM) and/or to resource availability (test of the extrinsic modification hypothesis). Females adjusted their litter size rather than their litter composition, so that the WM was not supported. Likewise, changes in resource availability did not influence the fetal sex ratio, so that the extrinsic modification hypothesis was not supported. The fetal sex ratio was negatively related to increasing litter size, providing some support for the TWM. Sex ratio was male biased for litter sizes up to 6 and then became female biased in larger litters. Our results provide the first case study showing marked changes in sex ratio in relation to litter size in a large mammal. *Key words*: litter size, primary sex ratio, sex ratio variation, *Sus scrofa scrofa*, Trivers and Willard model, Williams model. [*Behav Ecol* 18:427–432 (2007)]

Sex-allocation theory (Charnov 1982), and most specifically sex ratio variation, is one of the most often addressed topics in evolutionary biology over the last 2 decades (Hardy 2002). Skewed sex ratios have often been reported, but whether variation of offspring sex ratio is adaptive in vertebrate populations is still controversial (for reviews, Clutton-Brock and Iason 1986; Frank 1990; Hewison and Gaillard 1999; West and Sheldon 2002). Whereas our knowledge of the physiological mechanisms involved in sex ratio variation has recently improved (Krackow 1995; James 1997; Cameron 2004), most evolutionary models are intended to assess the pattern rather than the process of variation in sex ratio (for a recent review, see Sheldon and West 2004). Among these, the Trivers and Willard model (TWM; Trivers and Willard 1973) has been tested repeatedly in vertebrate populations. According to the TWM, high-quality mothers should provide a greater investment in sons than in daughters when males have a greater variance in individual fitness than females, providing that 1) sons benefit more than daughters from extra investment by mothers, 2) offspring quality is a good proxy of adult quality, and 3) offspring quality is related to maternal quality. In this context, females should be able to adjust their offspring sex ratio in response to factors that could modify both their own lifetime reproductive success and the reproductive success of their progeny (Clutton-Brock et al. 1984).

Polygynous and sexually dimorphic species are good candidates for the TWM, and among them, ungulates have been especially well studied (for reviews, see Hewison and Gaillard 1999; Sheldon and West 2004). However, results are often in-

consistent because of 1) the strict conditions that must be fulfilled for the TWM to apply (for recent case studies, see Leimar 1996; Blanchard et al. 2005; Hewison et al. 2005); 2) variable timing of the measure of maternal condition (i.e., before conception, near implantation, or during early stages of gestation; Cameron 2004; Sheldon and West 2004), and 3) possible confounding influences of environmental variation, including both extrinsic modification due to climate (Post et al. 1999; Mysterud et al. 2000; but see Weladji and Holand 2003) and a decrease in the proportion of males born with increasing population density (Kruuk et al. 1999). In addition, whether the TWM applies to polytocous species (i.e., species that produce several offspring per litter) is unclear. Whereas recent reviews have included polytocous species in comparative analyses (Hewison and Gaillard 1999; Cameron 2004; Sheldon and West 2004), possible trade-offs between size, number, and sex of offspring might complicate the test of the TWM in highly polytocous species (Carranza 2004). Williams (1979) generalized the TWM to polytocous species by including changes in litter size in the model.

Using data collected on the highly polytocous wild boar (*Sus scrofa scrofa*; mean litter size of 4.6; Mauget 1982; Carranza 1996), we tested 4 hypotheses. We first tested the Williams' model (WM) by investigating the relationship between maternal body mass and the specific sequence of litter composition. Only a few empirical studies have as yet tested the WM (but see Kucera 1991; Cassinello and Gomendio 1996; Allainé et al. 2000), and all focused on species with limited variation of litter size. Under the WM, we expected a positive relationship between a specific sequence of increasing production costs based on size and sex composition of the litters and maternal body condition. In this sequence, all litters are ranked along a continuum of increasing production costs based on the relative cost of producing a male or a female. For instance, given a maximal litter size of 3 and given that producing a male (M)

Address correspondence to J.-M. Gaillard. E-mail: gaillard@biomserv.univ-lyon1.fr.

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costs 1.1 times more than producing a female (F), the expected specific sequence should be as follows: 1F < 1M < 2F < 1M1F < 2M < 3F < 2F1M < 1F2M < 3M (Figure 1). According to the WM, we expected to find a positive relationship between the sequence of increasing production costs and relative maternal condition. Second, we tested the TWM to assess whether sex ratio variation was related to maternal attributes such as age and mass. According to the TWM, we expected more males than females to be produced by old and/or large females. Third, we tested for a possible extrinsic modification of sex ratio by assessing whether yearly changes in mast production influenced sex ratio. According to the extrinsic modification hypothesis, we expected to find an increasing proportion of males with increasing food resources. Finally, we also tested whether changes in litter size influenced sex ratio variation. Indeed, adjustment of the offspring sex ratio may vary in relation to litter size (Frank 1990). Equal allocation of resources to offspring may be prevented by a differential acquisition of maternal resources between sexes because males might be more efficient than females at converting dietary protein into biomass (Redondo et al. 1992) and/or by sibling competition (Mock and Parker 1997; Carranza 2004). We thus analyzed simultaneously the influence of phenotypic attributes of mothers and the influence of environmental drivers, as recommended by West et al. (2005), to apply general sex ratio theory to a specific case. Our study makes a novel contribution to the studies of sex ratio variation by 1) focusing on a highly polytocous species for which a much wider range of litter size and composition was available compared with previous studies (Kucera 1991; Fernández-Llario et al. 1999), allowing us to perform a firm empirical test of the WM, 2) examining simultaneously both the effects of maternal influence and environmental variation on sex ratio variation, and 3) providing the first case study showing marked changes in sex ratio in relation to litter size in a large mammal.

MATERIALS AND METHODS

Study area

The Châteaullain-Arc-en-Barrois forest in eastern France (48°02'N, 4°55'E) is a homogenous broad-leaved deciduous woodland on a calcareous plateau. It covers 11 000 ha composed of hornbeam (*Carpinus betulus*) coppice with oak (*Quercus sessiflora*, 41%) and beech (*Fagus sylvatica*, 30%) stands. A national forest of 8500 ha constitutes the core of the forest, whereas the periphery (2500 ha) is private or communal. The study area is surrounded by a cultivated plain and a highway bordering the North–East side, limiting exchanges with other populations. Free-ranging populations of wild boar, red deer (*Cervus elaphus*), and roe deer (*Capreolus capreolus*) are present in the forest. The population size of these 3 ungulates is managed by hunting. In 2003, 250 roe deer, 250 red deer, and 760 wild boar were hunted in the national part of the forest. Each year between October and February, wild boars are intensively hunted during weekends using drives. In the national part of the woodland, hunters are posted around the hunted area (a patch of 250–500 ha) along roads or forest trails and wait for wild boar flushed out by trackers and dogs. In 2003, 44.7 ± 22.7 wild boars were culled on average each weekend of hunting.

Data collection

Since 1984, each harvested wild boar in the national part of the forest has been eviscerated and weighed (±1 kg; carcass mass after all the digestive system, heart, liver, lungs, repro-

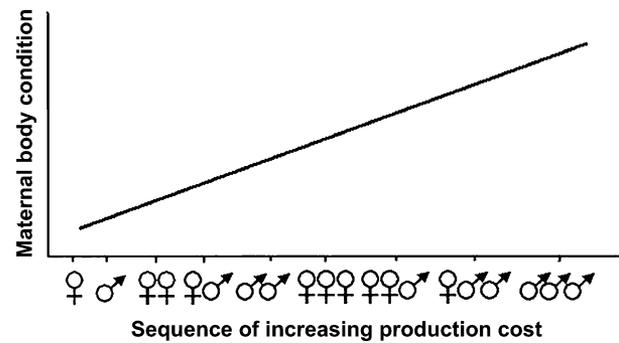


Figure 1

Relationship between maternal body condition and the specific sequence of increasing production costs expected under the WM. In this example, the relative cost of producing a male (M) compared with a female (F) is 1.1 (i.e., production cost of 1.1 for M, 1 for F). For instance, a litter of 3 with 2F and 1M costs 3.1 units, whereas a litter of 3 with 1F and 2M costs 3.2.

ductive tract, and blood have been removed). In this study, the dressed mass of females was used as the maternal body condition index.

Age was assessed by tooth eruption and replacement patterns (Matschke 1967; Baubet et al. 1994). Wild boars were classified into 3 age classes (Pedone et al. 1991): juvenile (less than 1 year of age), yearling (between 1 and 2 years of age), and adult (older than 2 years of age). In our population, the generation time was around 2 years due to high hunting pressure (Gaillard et al. 1987).

For each female, the reproductive tract was collected and, when gestation had already begun, fetuses were counted. We were able to sex fetuses visually without ambiguity from a length of 40–45 mm (i.e., about 1 month of gestation; Maugeat 1980) based on the presence of a vulva in females and the presence of a penis in males. The proportion of the litter that was identified did not depend on litter size ($\chi^2 = 4.392$, degrees of freedom [df] = 7, $P = 0.734$). Hence, there was no bias in the identification of sex composition within a litter in relation to the size of the litter.

In wild boar, many studies have reported a relationship between mast occurrence and the reproductive cycle of females (Matschke 1964; Maugeat 1982; Groot Bruinderink et al. 1994), so that gestation may begin at any time during the hunting season (i.e., from early October to late February). In our study site, mast production was assessed indirectly by the analysis of stomach contents (for a similar approach, see Bieber and Ruf 2005). Three cases were distinguished for the different hunting seasons: no mast production, beech mast year, and acorn mast year (Table 1).

Data analysis

To take into account the difference in gestation stage among reproductive females, we used the observed sexual dimorphism in mass of fetuses to assess the relative cost of producing a male versus a female (for a similar approach, see Fernández-Llario et al. 1999). Male fetuses were on average 5.1% heavier than females in our sample (Office National de la Chasse et de la Faune Sauvage, unpublished data), so that the direct metabolic cost of producing a male was slightly greater than that associated with the production of a female (i.e., on average 1M = 1.051F; Table 2). We then calculated the costs of production of all litters. For instance, a litter of 2 females and 3 males costs $2 \times 1 + 3 \times 1.051 = 5.153$ production units, whereas a litter of 3 females and 2 males costs 5.102 production units. We looked for a relationship between

Table 1
Number of litters born to juveniles, yearlings, and adults available for each year (hunting season) and for each age class

Year (hunting season)	Mast production	Juvenile	Yearling	Adult
1989/1990	Acorn	6	9	7
1995/1996	Beechnut	6	2	2
1998/1999	Acorn	0	13	10
1999/2000	Beechnut	12	24	13
2000/2001	No mast production	1	3	3
2001/2002	Acorn	8	33	22
2002/2003	Beechnut	5	5	11
2003/2004	Acorn	3	16	7
2004/2005	Beechnut	8	14	7

The mast production for the considered hunting season is also indicated. Acorns were produced by oak (*Quercus sessiflor*), and beechnuts were produced by beech (*Fagus sylvatica*).

the sequence of increasing production costs and maternal dressed mass to test the WM (Figure 1). We also tested whether there were significant relationships among maternal dressed mass, litter size, and sex ratio.

Second, to assess whether maternal attributes, food resources, and litter size influenced sex ratio variation in wild boar, we fitted weighted logistic models as recommended by Wilson and Hardy (2002). Sex ratio (the dependent variable) was defined here as the proportion of males in the litter of a given mother and was treated as grouped binary data. To determine which of the candidate models provided the best description of the data, model selection was based on Akaike's information criterion (AIC; see Burnham and Anderson 1998). AIC quantifies the relative goodness of fit of different statistical models and then provides an objective way of determining which model among a set of models is the most parsimonious. Generally, the model with the lowest AIC was retained. However, when differences in AIC values between models were less than 2, the model with the lowest number of parameters was retained (parsimony criterion; Burnham and Anderson 1998). We tested whether sex ratio could be influenced by age, year, maternal dressed mass, and litter size, as well as the interactions among these factors. Then, we tested whether mast production could also account for between-year variation in sex ratio.

Once the best model was selected, we checked whether its residual mean deviance was close to 1 and when it exceeded 1.5, we corrected for overdispersion (e.g., Krackow and Tkadlec 2001; Wilson and Hardy 2002). We also checked that the standardized residuals of the selected model were randomly distributed around zero with respect to the fitted values and that the standardized residuals were normally distributed (Wilson and Hardy 2002).

In addition, we analyzed in more detail the relationship between sex ratio and litter size. To do so, we calculated the probabilities of occurrence of each litter composition for a given litter size expected under a binomial distribution of sex within litters. Then, because of the small sample size per litter of a given size, we pooled those probabilities of occurrence to obtain the expected probabilities of producing a male-biased versus a female-biased litter of a given size. Finally, we performed a chi-squared test using the observed numbers of male-biased and female-biased litters (Table 2).

We only included litters when all data were collected (i.e., female age, female dressed mass, number of males, and females within the litter) as recommended by Anderson and Burnham (2002) when a model selection procedure is used. Moreover, to test for between-year differences in sex ratio, we

Table 2
Observed distribution of males (M) and females (F) within each litter size

Litter size	Observed sex composition within litter	Sample size	Sample size of biased litters	Theoretical probability
2	2F	N = 1		1/4
	1F1M	N = 5		1/2
	2M	N = 1		1/4
3	3F	N = 1	N = 13	1/2
	2F1M	N = 12		
	1F2M	N = 12	N = 16	1/2
3M	N = 4			
4	4F	N = 2	N = 5	5/16
	3F1M	N = 3		
	2F2M	N = 14	N = 18	5/16
	1F3M	N = 14		
4M	N = 4			
5	5F	N = 1	N = 26	1/2
	4F1M	N = 6		
	3F2M	N = 19		
	2F3M	N = 24	N = 34	1/2
	1F4M	N = 10		
5M	None			
6	6F	N = 3	N = 15	11/32
	5F1M	N = 2		
	4F2M	N = 10		
	3F3M	N = 16	N = 21	11/32
	2F4M	N = 12		
	1F5M	N = 7		
6M	N = 2			
7	7F	None	N = 21	1/2
	6F1M	N = 3		
	5F2M	N = 8		
	4F3M	N = 10	N = 16	1/2
	3F4M	N = 8		
	2F5M	N = 3		
	1F6M	N = 4		
7M	N = 1			
8	8F	None	N = 9	93/256
	7F1M	N = 1		
	6F2M	N = 1		
	5F3M	N = 7	N = 4	93/256
	4F4M	N = 6		
	3F5M	N = 1		
	2F6M	N = 3		
	1F7M	None		
8M	None			
9	9F	None	N = 5	1/2
	8F1M	N = 1		
	7F2M	None		
	6F3M	N = 2	N = 4	1/2
	5F4M	N = 2		
	4F5M	N = 2		
	3F6M	N = 1		
	2F7M	N = 1		
	1F8M	None		
9M	None			

Litters are classified according to their relative cost of production (from the lowest cost of production: 2F to the highest cost: 9M). Here the relative cost of producing a male is 1.051 times higher than the one for producing a female and is based on observed sexual dimorphism in mass of fetuses. Each theoretical probability is calculated using a binomial distribution of sex within litters. For instance, the probability to have a litter of 4 females and no male is $C_4^0 / (C_4^0 + C_4^1 + C_4^2 + C_4^3 + C_4^4)$. Then the calculated probabilities were summed in order to obtain those associated with the production of a male-biased or a female-biased litter for a given litter size.

only included years when at least 2 females per age class were collected (Table 1). However, we also included the 1998/1999 hunting season because large samples were available for 2 age classes although no data were available for juveniles (Table 1). The inclusion of this latter hunting season in our analysis did not change the results.

All analyses were performed with R 1.7.1. (R Development Core Team 2004).

RESULTS

We obtained complete data from 254 litters. Litter size varied between 1 and 14 fetuses (mean: 5.5 ± 0.1 standard error [SE]). However, data obtained for litter sizes of 1, 10, 11, and 14 were discarded because each was only represented by a single litter. Furthermore, maternal dressed body mass was not standardized in relation to culling date as the hunting month only explained 1.8% of variation in adult maternal dressed mass.

Test of the WM

Maternal dressed mass was positively related to the sequence of increasing costs of production ($r = 0.744$, $df = 41$, $P < 0.0001$). However, sex ratio did not contribute to that relationship, neither in interaction with litter size ($F = 0.64$, $df = 7$, $P = 0.723$) nor alone ($F = 2.041$, $df = 1$, $P = 0.154$). The observed relationship was therefore more an adjustment of litter size (i.e., number of fetuses; $F = 11.95$, $df = 7$, $P < 0.0001$) in relation to mass than an indication of adaptive offspring sex ratio variation within a given litter size. Hence, the WM was not supported.

Sex ratio variation

Neither maternal age, maternal dressed mass, year, nor mast production influenced the proportion of males in wild boar litters (Table 3). Furthermore, none of the interactions among those factors improved the model fit (Table 3). Hence, both the TWM and the extrinsic modification hypothesis were not supported. On the other hand, sex ratio decreased as litter size increased (slope ± 1 SE: -0.078 ± 0.034 , $\chi^2 = 5.25$, $df = 1$, $P = 0.022$). Sex ratio was male biased in small litters and female biased in large ones (Figure 2). Accordingly, the observed sex ratio in litters of a given size differed from a random distribution. Male-biased litters occurred significantly more often than expected for litter sizes of 4 ($\chi^2 = 16.93$, $df = 1$, $P < 0.0001$) and 6 ($\chi^2 = 6.57$, $df = 1$, $P = 0.01$), and litters were female-biased for litter size of 8 ($\chi^2 = 3.98$, $df = 1$, $P = 0.045$). This adjustment of offspring sex ratio in relation to litter size, involving higher sex ratio when more per capita resources are available, might support the TWM.

DISCUSSION

In wild boar, females adjusted their litter size, rather than their litter composition for a given litter size, in relation to their condition (indexed here by their dressed mass). William's hypothesis was therefore not supported. However, the fetal sex ratio of wild boar decreased as litter size increased (Figure 2). So, for an increasing reproductive effort, mothers might not be able to provide extra investment in males in large litters. Although the sex ratio of wild boar was not influenced by maternal age or dressed mass, our result suggests that the Trivers and Willard hypothesis could be supported. Indeed, in small litters, mothers should have more resources for each individual offspring, and therefore, each offspring will be weaned in good condition. In these conditions, mothers

Table 3

Model selection for fetal sex ratio variation in wild boar

Models tested	AIC	Δ AIC
Logit (SR) = LS	773.6	0
Logit (SR) = LS + W	774	0.4
Logit (SR) = LS + M	774.45	0.45
Logit (SR) = LS + W + M	774.8	1.2
Logit (SR) = LS + LS ²	775.5	1.9
Logit (SR) = W \times LS	776.75	3.15
Logit (SR) = constant	776.9	3.3
Logit (SR) = M	776.9	3.3
Logit (SR) = LS + A	777.1	3.5
Logit (SR) = A \times LS	777.4	3.8
Logit (SR) = LS + A + M	777.9	4.3
Logit (SR) = W	778.9	5.3
Logit (SR) = A	780.7	7.1
Logit (SR) = A \times W	781.6	8
Logit (SR) = Y \times LS	784.2	10.6
Logit (SR) = LS + Y	786.0	12.4
Logit (SR) = LS + W + Y	786.7	13.1
Logit (SR) = Y	788.8	15.2
Logit (SR) = LS + A + Y	789.2	15.6
Logit (SR) = Y \times W	790.1	16.5
Logit (SR) = A \times Y	806.6	33

SR, sex ratio; LS, litter size; W, mother's dressed mass; A, mother's age class; Y, year (i.e., hunting season), M, type of mast production. The selected model occurs in bold.

should benefit from having male-biased litters. In large litters, there are fewer resources for each offspring, such that each individual will be weaned in poorer condition. Consequently, daughters would be a better investment because mothers will have a faster fitness return via female progeny, and this effect may be stronger in large litter sizes. Indeed, in wild boar, females become sexually mature and pregnant at approximately 8 months of age, whereas males become sexually mature at nearly 2 years of age (Mauget 1980). This result also is

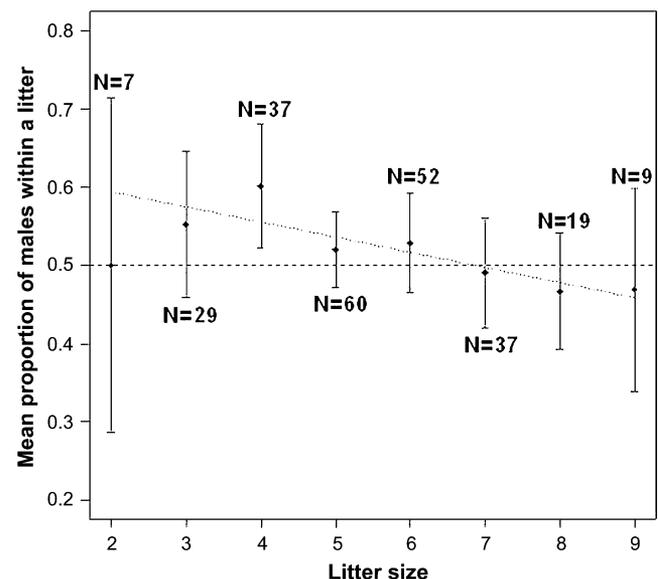


Figure 2

Mean proportion of males and 95% confidence interval in relation to litter size. The dotted line corresponds to the selected model (sex ratio decreased when the litter size increased; Table 3), and the dashed line corresponds to a balanced sex ratio. Sample sizes for each litter size are indicated.

in agreement with the Byers and Moodie (1990) hypothesis. These authors postulated that male-biased energy allocation to offspring is constrained in species that have high reproductive output because mothers cannot allocate extra resources to males. Mothers should thus face a trade-off between total maternal expenditure and the magnitude of male-biased allocation of maternal care.

A negative relationship between litter size and sex ratio has recently been observed in domestic pigs (Górecki 2003) but has not been yet reported in wild boar. In Spain, Fernández-Llario et al. (1999) analyzed wild boar fetal sex ratio variation but did not report any influence of litter size. However, the low sample size ($N = 58$ litters) and the low range of observed litter sizes (mean litter of 3.69, range 1–7) in that study could account for the absence of a significant relationship between sex ratio and litter size. Litter sizes of wild boar in Mediterranean countries such as Spain or Italy are generally smaller than those observed in more eastern countries of Europe (Pedone et al. 1991; Table 1 in Bieber and Ruf 2005), probably due to a drier climate and lower resource availability.

Primary sex ratio adjustment could occur at 3 different stages: 1) gamete selection, 2) differential implantation of embryos, and 3) differential mortality of fetuses (Krackow 1995). Here, sex-specific fetal mortality (e.g., Gosling 1986) is unlikely to be the mechanism behind the observed variation. Indeed, during the whole study period, only 5 cases out of the 483 pregnant females that were examined showed evidence of fetal mortality (i.e., nonfresh stillborn piglet or mummified fetuses; van der Lende and van Rens 2003). Moreover, the possibility that large fetal litters of all males are so costly that they are already lost by the time we took our measurements is unlikely to be the case here. Observed embryonic mortality was on average 15% (e.g., mean percentage of *corpora lutea* not represented by fetuses, van der Lende et al. 1990; Hewison and Gaillard 2001), and the mean embryonic mortality was even less for large litter sizes, reaching only 6% for a litter size of 6 or more (Office National de la Chasse et de la Faune Sauvage, unpublished data). Hence, even if mothers were selectively reabsorbing embryos from only one sex, this level of embryonic mortality would have been too small to account for the effect we reported here.

The observed pattern of sex ratio variation in wild boar highlights the determinant role of litter size. Producing large female-biased litters may be an adaptive adjustment to avoid strong sibling competition during lactation and hence to optimize the growth and the survival of the whole litter. Indeed, in farmed wild boar, piglet fighting is more intense in male-biased litters than in female-biased ones (Harris et al. 2000). Moreover, in domestic pig, piglets that fail to establish consistent use of a teat are likely to die or to suffer severe reduced weight gain (de Passillé et al. 1988). This behavior has not been substantially modified through domestication, and a strong teat order also occurs in wild boar (Horrell 1997; Gustafsson et al. 1999). Thus, low within-litter competition may lead to a reduction of begging by the piglets and an improvement in milk utilization (Dostálková et al. 2002) that might increase the survival of most offspring within a litter (e.g., Carranza 2004). Access to a teat during the release of milk is then likely to be more important to piglets than a decrease in milk received when the litter size increases (Fraser 1990). A few observations of postnatal survival of large litters in our population seem to confirm this hypothesis (Brandt S, personal observation).

Hence, the production of one sex can be favored when the allocation of maternal expenditure in one sex is more profitable in terms of fitness returns. Even when the production of large female-biased litters might result in a decrease of performance for each individual offspring of the litter (e.g., the

daily gain in weight will probably be lower than in smaller litters), the total return from the whole litter will be higher. Nevertheless, further studies of postnatal survival of piglets in relation to litter composition are needed.

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