

ORIGINAL INVESTIGATION

**Paternity assessment in free-ranging wild boar
(*Sus scrofa*) – Are littermates full-sibs?**

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Abstract

Multiple paternity within litters occurs in various groups of mammals exhibiting different mating systems. Using seven genetic markers (i.e., microsatellites), we investigated the paternity of littermates in free-ranging wild boar (*Sus scrofa*) in a Mediterranean habitat. Using the software CERVUS 2.0 we estimated the probability of detecting multiple paternity across all loci (D), the probability of paternity (W) and a statistic Δ that allows the assignment of paternity to the most likely male with strict and relaxed levels of confidence. Multiple paternity was inferred for one of the nine analysed litters at the 80% confidence level. This suggests that a single male may control the access to receptive adult females and it shows that multiple paternity is not very common in the studied free-ranging wild boar population. Despite the possible occurrence of sperm competition and/or female cryptic choice, mate guarding seems to play a significant role in sexual selection. To better understand the wild boar's mating strategies further studies analysing the reproductive success of both sexes and under different environmental conditions should be conducted.

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Introduction

Female sexual promiscuity seems to be rather common and several evolutionary benefits have been proposed for multi-male mating (Jennions and Petrie 2000; Gomendio 2002; Wolff and Macdonald 2004). The increasing use of molecular tools revealed that multiple paternities within single broods or litters are

frequent in a large range of different taxa (Birkhead and Møller 1998). Recently, microsatellite analysis revealed multiple paternity in natural ungulate populations, such as in wild pronghorn antelopes (*Antilocapra americana*) (Carling et al. 2003) and in white-tailed deer (*Odocoileus virginianus*) (Sorin 2004).

The social organization of wild boar (*Sus scrofa*) is very much related to its reproductive cycle, and accordingly adult males only join females groups in the rutting period (Dardaillon 1988). When an anoestrous period ends the females belonging to the same

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social unit resume cycling at the same time (Delcroix et al. 1990). According to the same authors, there is an extreme accurate synchronization that appears to result from interactions between females of the same group and is likely to have a functional significance. Bearing in mind that the oestrous period in the domestic sow is about 44 h (Sorensen Jr 1982), most probably in each group, formed by a few females (Fernández-Llario 1996), a single dominant boar is able to monopolize all the receptive females not allowing any other male to copulate. In fact, there is empirical evidence that dominant males exhibit agonistic behaviours during the rutting period in order to safeguard the sexual access to the receptive females, and that if necessary they will fight sneakers (males trying to usurp a copulation) using their large canine teeth (Barret 1986; Rushen and Pajor 1987). The walling behaviour in adult males during the rutting period may have a sexual function (Fernández-Llario 2005); the dry mud, mainly clay acts as a protection shield during the fights over the females. Male–male competition for accessing reproduction seems to begin early in life since pregnant females tend to invest more in males than in females foetuses, and also since across litters the heaviest piglet is a male in the large majority of cases (Fernández-Llario et al. 1999; Santos 2002). These results support the Trivers and Willard (1973) model's first prediction, showing that pregnant females in polygynous species tend to invest more in the sex with the higher biotic potential.

Besides male–male competition over copulation partners, post-copulatory competition may also be involved in sexual selection on wild boar. In fact, when compared to other livestock, adult domestic boars have relatively larger testes and produce higher semen volume (Sorensen Jr 1982), and it was shown that wild boar semen is not different from that of domestic boars (Kozdrowski and Dubiel 2004). These facts suggest sperm competition assuming that fertilization success of a given male depends on the relative amount of semen it can ejaculate. The testes size and the volume of sperm produced by wild boar could be male morphological adaptations to sperm competition and the consequence of a polyandrous mating behaviour. According to this hypothesis, multiple paternity could be a common event since heterospermic artificial insemination already showed that it may occur in domestic pig (Berger et al. 1996; Stahlberg et al. 2000). Another male adaptation to sperm competition might be the gel-like fraction of the boar ejaculate that forms a plug in the vagina of the mated sows (Hafez 1993). According to common knowledge, these copulatory plugs do not act like “chastity belts” neither seem to reduce female attractiveness to rival. However, it remains uncertain whether they can avoid further male insemination and egg fertilization or not. Nevertheless, multiple sired litters have been reported when gilts mate in rapid succession with different boars (Martin and Dzuk 1977). It is

frequently difficult to predict the present role of sperm competition-related male traits since they may compromise female fitness and so a fast evolutionary arms race between sexes in continuously ongoing (Chapman et al. 2003), and this is why so many different functions have been attributed to them in distinct species.

Though wild boar is generally considered a polygynous mammal, some morphological and physiological sperm competition-related male traits seem to point towards the possible occurrence of multiple paternity. This features inconsistency makes either single or multiple paternity plausible hypotheses. The aim of the present study was to investigate if multiple paternity within single broods occurred in foetuses litters on a Mediterranean environment (Alentejo, Portugal), using seven microsatellite markers.

Material and methods

Sample collection

Samples were collected in Alentejo (38°22'–38°35'N; 7°35'–7°43'W), a Portuguese county belonging to the Mediterranean Ibero-Atlantic Province where the Thermo-mediterranean bioclimatic type prevails (Rivas-Martínez and Loidi 1999). The elevation ranges from sea level to about 1000 m, the annual rain fall ranges from 500 to 700 mm, decreasing from the coastal to the inner zones, and the annual mean temperature ranges from 15 to 17 °C. The summer drought from June to September favours sclerophyllic evergreen Mediterranean vegetation and a secondary type of forest called *montado*, characterized by species like cork oak (*Quercus suber*) and holm oak (*Quercus rotundifolia*), dominates the landscape. In arable lands, oats (*Avena sativa*) and wheat (*Triticum* sp.) in autumn/winter, and sunflower (*Helianthus annuus*) and maize (*Zea mays*) in spring/summer, are the main crops. In rugged hilly areas mature stages of vegetation can still be seen. The hunting pressure is high and so is the number of wild boars taken per 100 ha of shooting area (Fernández-Llario et al. 2003). The hunting method is the so-called “*montaria*” and it consists in dog teams chasing wild boar towards hunters standing at fixed points spread along the shooting area.

Samples were obtained during the hunting season of 2001/2002 and were collected in different “*montarias*”. The uteri of pregnant females were removed during field necropsy and stored at –20 °C until genomic DNA extraction. These females were weighted (total life weight) and their age assessed according to the chronology of teeth eruption (Santos et al. 2006). For parentage analysis, samples of tissue were taken from foetuses (belonging to different litters) and from the respective mothers. The most prolific females were selected – litter size equal or bigger than five – in order to increase the chance of detecting multiple paternity.

Genetic analysis

(a) DNA extraction

DNA was extracted from tissue using Proteinase K digestion followed by extraction with standard

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