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Extensive infanticide in enclosed European wild boars (*Sus scrofa*)

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ABSTRACT

Infanticidal behaviour, behaviour with wide welfare implications, is wide-spread among animals of various taxonomic groups, but has not previously been systematically studied in European wild boars, which are commonly kept in enclosures in Sweden and Finland for meat and recreation hunting. We studied the behaviour of wild boars in one enclosure during three reproductive seasons. Non-maternal infanticide was documented in 14 out of 22 litters, causing the deaths of all piglets in all but one affected litters. Infanticide was typically performed during or shortly after parturition by a sow which was older ($P<0.05$) and tended to be larger ($P=0.068$) than the victimised sow, and was not affected by whether or not the involved females were mother-daughter pairs. A questionnaire sent to 112 owners of a total of 116 enclosures in Sweden and Finland resulted in 62 valid responses. Non-maternal infanticide was reported to be the most common cause of piglet pre-weaning mortality, which in total (including all causes) was estimated to be 29.1 %. The occurrence of infanticide was unrelated to size of enclosure (less or more than 20 ha) and to variations in supplementary feeding routines (less or more than once a week) ($P>0.05$), which may suggest that the behaviour could be a part of the normal behavioural repertoire in European wild boars. The observed levels of infanticide constitute a major welfare problem in captive wild boars.

Keywords: Behaviour, Enclosure, Farrowing, Infanticide, *Sus scrofa*, Wild boar

1. Introduction

Wild animals in captivity may face a number of potential welfare problems. Some of them may result from normal behaviour of the species, expressed in an abnormal form or frequency, and many are related to stress caused by environmental conditions. In Sweden and other Scandinavian countries, keeping of wild boars in enclosures is relatively common, mainly for hunting purposes (in the enclosures) and meat production. Sweden has about 100 such enclosures with sizes ranging from less than 1 ha to about 300 ha, and Finland about 40 enclosures of about the same sizes. Since natural home ranges can be 1000 ha and more (Dardaillon, 1986), the restricted area in many of these enclosures could possibly limit the ability of sows to isolate during farrowing which may influence piglet mortality in connection with farrowing as shown in domestic pigs by Jensen (1988). Preliminary observations during studies of the maternal behaviour in captive wild boars (Andersson et al, 2011) showed a frequent occurrence of non-maternal infanticide. Based on this, the present paper reports a closer investigation on this behaviour.

Infanticide, the killing of an infant by a conspecific, has been reported from a wide variety of taxonomic groups (e.g. insects, birds and mammals) as reviewed by Hausfater and Hrdy (1984). This behaviour may exert an important selective pressure on a population (Hausfater and Hrdy, 1984; Hrdy, 1979) , since the impact of infanticide on offspring mortality can be significant in many mammals, e.g. European rabbits (Rödel et al., 2008) and prairie dogs (Hoogland, 1985). Also, it has resulted in the evolution of counter-strategies, such as territoriality or defence of young (Agrell et al., 1998; Ebensperger, 1998; Hrdy, 1979).

There are mainly four different hypotheses for how an infanticidal animal may gain fitness from the action (compiled and formulated by Hausfater and Hrdy, 1984; Hrdy, 1979): i) *Exploitation* where an infant is used as a food resource; ii) *Resource competition* where the death of an infant gives the perpetrator and its descendants increased access to resources, *e.g.* nest sites or food; iii) *Parental manipulation* where the death of an infant can improve fitness of the mother or the father by improving survival possibilities of other offspring; iv) *Sexual selection* where the killing of offspring increases the opportunities to mate for the infanticidal animal (usually a male) and reduces the reproductive success of the same-sex competitor. It has also been suggested that the behaviour can sometimes be caused by social pathology, where killing of an infant may in fact decrease both individual and inclusive fitness of the infanticidal animal (Hausfater and Hrdy, 1984).

In this paper, we present for the first time data on extensive non-maternal infanticidal behaviour in captive European wild boars (*Sus scrofa* L. 1758). Similar behaviour has been reported only once before, and then anecdotally, in the scientific literature (Gundlach, 1968). Our data suggest that infanticide is wide-spread among captive wild boars, and also allow some hypotheses to be formulated regarding the functional background. Furthermore, we suggest that infanticide may have been a significant aspect of the evolution of the maternal behaviour of the species (for example isolation and nest site choice; Andersson et al, 2011) and hence also of the domestic pig (Gundlach, 1968; Jensen, 1988). Importantly, it may constitute a major welfare problem for wild boars in captivity.

Wild boars are matriarchal, i.e. they live in groups of closely related sows and their offspring (Dardaillon, 1988; Gundlach, 1968; Kaminski et al., 2005). The reproduction is usually synchronised within a female group (Delcroix et al., 1990). External cues such as e.g. increased food availability initiate the common oestrus (Fernández-Llario and Carranza, 2000; Mauget, 1982; Santos et al., 2006), which attracts the solitary males during mating periods (Briedermann, 1971; Dardaillon, 1988), and it is likely that pheromones are also involved. The wild boar sows have their main farrowing season in early spring when sows of the same group, with few exceptions, farrow within the same week (Delcroix et al., 1990). The sow undergoes significant behavioural changes in connection with farrowing. Aggression towards other group members often increases (Gundlach, 1968; Hirotani and Nakatani, 1987; Martys, 1982) and a couple of days before farrowing the sow isolates herself (apparently up to several kilometres) from the group, builds a nest, and gives birth to typically between four and eight precocial piglets (Carranza, 1996; Dardaillon, 1988; Gundlach, 1968).

The farrowing nest is most often situated in relatively protected habitats, e.g. dense forests and in the edge between open and dense areas (Andersson et al, 2011; Dardaillon, 1986; Janeau and Spitz, 1984). The sow and her piglets stay in the nest for up to two weeks during an isolation phase considered necessary to establish bonds between the sow and her piglets and decrease risk of predation (Fernández-Llario, 2004; Jensen et al., 1987). After the isolation phase the family groups join in nursing groups consisting of two or more sows with piglets of about the same age. By then, agonistic behaviours have normally decreased (Dardaillon, 1988; Delcroix et al., 1985; Teillaud, 1986). When domestic pigs are kept in enclosures outdoors, they show more or less the same overall pattern in their maternal behaviour (Jensen, 1986; Jensen et al., 1987).

The aim of this study was to examine the extent of infanticidal behaviour in enclosed wild boars, and to provide a quantified description of its occurrence.

Furthermore, we aimed to provide an initial analysis of the individual traits associated with both performers of the behaviour and victim sows, in order to suggest a functional explanation to infanticide in this species. The data were collected both through extensive field studies over three reproductive seasons in one confined group of animals, and by a questionnaire study covering in total 116 wild boar enclosures in Sweden and Finland.

2. Methods

2.1. Enclosure and animals

Field studies were carried out in February to April (the major farrowing period) during 2003, 2004 and 2005 in a wild boar enclosure, located in northern part of the province Östergötland, Sweden. The 10 ha large enclosure (approximately 400 x 250 m), was relatively hilly, and consisted of various habitats such as fields, rocks, dense spruce, leaf, open pine and mixed forests and a marsh. There were natural as well as artificial water sources. Normal husbandry routines for this enclosure were followed, which meant that the animal keeper fed the animals about once a week with raw potatoes, bread, household food waste and pig pellets spread on the ground. The food was spread over an area of about 50 m^2 and lasted for a couple of days. The animals could also obtain natural food in the enclosure, but it is clear that during winter, the availability of food was limited both in amount, and in protein content. During cold periods, water sources were frozen, and water intake was mainly from snow. During the three study seasons, the group varied in size from 10 to 30 individuals, consisting of one to two boars, four to ten sows, and their yearlings and piglets. Culling was done (outside the observation periods) by hunting or by the keeper shooting animals during feeding.

In total, 12 wild boar females were included in the study, of which four were observed for two consecutive seasons, and three for all three consecutive seasons (Table 1). Relatedness and parity were not fully clear for all individuals, but see DNA-results in 2.3.2. Five were nulliparous and six were multiparous at the time of our studies (one of unknown parity), all of them hereafter referred to as sows. Nine of the sows were habituated to humans and were not noticeably disturbed by being followed by an observer at a close distance (1-50 m). From these animals it was therefore possible to obtain detailed behavioural data. Three of the sows were not possible to follow by foot without severe disturbance; hence, these sows were used only for data collection on farrowing nest characters and litter sizes, which were possible to obtain without being in close contact with the animals.

In 2003 and 2004 the sows were paint marked on their coat for individual recognition and the markings were improved when needed. Apart from the paint markings, no interference was done with the sows. In 2005 the sows were ear tagged during anaesthesia as described below.

2.2. Data collection

2.2.1. Data collection for each farrowing

In total eight observers were involved in field data collection during the three farrowing seasons, and in each season, one to three observers worked in parallel. Data were collected using focal animal sampling. Before the start of a data collection period the observers spent at least five days, and about 6 h per day, following the animals in the enclosure in order to identify animals, behaviours and locations in the enclosure, and to habituate the animals to the observers. During data collection the focal animals were observed at a distance of about 1 to 50 m depending on vegetation. Data collection started at least 14 days before each sow's farrowing day, which was estimated from their latest oestrus in the autumn (oestrus signs were courtship and copulation) and, in 2005, from size of foetuses as measured during anaesthesia as described below.

Each sampling day started usually shortly after day-break with location of all sows to see if any of them showed signs of beginning isolation from the group, nesting, or farrowing. If so, that animal was followed by one observer until farrowing. The aim was to observe each farrowing at least until the placenta and foetal amnions were expelled and eaten and all piglets had found their way to the udder and had started to suckle. In 2003 and 2004 the data collection of ongoing farrowings was stopped at sunset and started again at sunrise. In 2005 ongoing farrowings were followed also at night if necessary, using night vision binoculars. During a farrowing, continuous notes on the progress were taken.

Data were collected during a total of 350 h of field studies in 2003, resulting in data from a total of six farrowing sows, three of them observed also during parturition, and 840 h in 2004, resulting in data from a total of seven farrowing sows, four of them observed during parturition. In 2005 the observations were focused on recording outcomes of farrowings in nine sows, resulting in about 150 field hours and attendance at four parturitions.

2.2.2. Variables collected for each farrowing

For each observed farrowing, the following variables were recorded:

- Date
- Litter size when the farrowing was considered to be finished
- Observed infanticide: piglets observed being killed
- Strongly suspected infanticide (as used by Leland et al. (1984)): circumstantial evidence of infanticide; e.g. a sow with blood remnants around the mouth staying in nest with a newly farrowed sow ; *or* when few or no piglets were left, while there were blood remnants or other bodily traces from piglets in or close to the nest; *or* when litter size had been strongly reduced over night when no observers were present
- When infanticide was observed: identity of the victimised and the infanticidal sow, and the date and time of the infanticide
- Whether a sow protected her nest and newborns against intruders (aggressive charges, threatening vocalisations (Schnebel and Griswold, 1983; Dardaillon and Teillaud, 1987)).
- Distance of farrowing nest to feeding area (which was a highly used area; Andersson et al, 2011).

2.2.3. Sampling during anaesthesia

In 2005, about four weeks before the first estimated farrowing, all sows were fully anaesthetised to enable measurement, blood sampling, and ultrasound examination.

The sows were immobilised either by combinations of Zalopine® (*medetomidin* 10 mg/mL, Orion Pharma, Orion Corporation, Espoo, Finland), Zoletil100® (*zolazepam 50 mg/mL* + *tiletamin 50 mg/mL*, Virbac, Carros, France) and Torbugesic® (*butorphanol*, 10 mg/mL, Fort Dodge Animal Health, Fort Dodge, Iowa, USA) or Large Animal Immobilon® (*acepromazin* 10 mg/mL + *etorfin* 2.45 mg/mL, Novartis Animal Health UK Ltd, Surrey, UK) and/or Stresnil® (*azaperone*, 40 mg/mL, Janssen–Cilag Pharma, Vienna, Austria). The sedatives were injected intramuscularly with a self-emptying projectile needle applied by air-pressure sedation gun or blowpipe. When fully anaesthetised the animals were transported to a warm nearby indoor locality, where ear tagging and data collection took place (see below for a description of the data collected). To enable ultrasound, part of the sows' abdomen was shaved. Animals immobilised by Large Animal Immobilon® were given antidotes of Revivon® (*diprenorphin* 3 mg/mL, Novartis Animal Health UK Ltd, UK) to end the anaesthesia and they woke up after having been transported back to the enclosure.

2.2.4. Variables collected in anaesthetised sows

- Number of foetuses (estimated by ultrasound examination, using a Draminsky portable ultrasound scanner) to certify pregnancy and estimate expected litter size)
- Size of foetuses (for further estimation of expected farrowing date)
- Weight
- Length from tip of nose to base of tail
- Height from hoofs to withers

- Thickness of abdominal fat layer (measured by ultrasound)
- Blood samples (for DNA-fingerprinting in order to estimate relatedness between sows).

2.4. Questionnaire study

A questionnaire was sent to all of the 102 Swedish breeders who had permission from the Swedish county administrative boards to keep wild boars in a total of 104 enclosures, and to the 12 Finnish wild boar breeders affiliated to the Finnish association for the production of farmed game animals (Riistankasvattajat ry) at the time of the study (hence 116 enclosures owned by 114 persons). The questionnaire, which consisted of 18 multiple-choice questions on enclosure characteristics, animal husbandry and attendance, animal number, farrowing data and animal mortality, was sent out in June 2004, i.e. after the natural main farrowing period of wild boars in Scandinavia. A reminder was sent two weeks later to those who had not yet responded.

2.5. Data analysis

Each farrowing was treated as a statistically independent event, even though some farrowings were originating from sows that were included in two or three consecutive seasons. This was considered to be acceptable since the group composition was different between the years.

The data were divided into two groups, one with sows and litters subjected to observed and/or strongly suspected infanticide and one with sows and litters not subjected to infanticide. When the data allowed, mean values for age, distance to feeding area, weight, length, height and thickness of abdominal fat layer were calculated and differences between groups were analysed with Mann-Whitney U-test. Also, for the same variables, each pair of victim and infanticidal sows was compared using Wilcoxon's test for matched pairs (in any infanticidal event, data for the victim were compared to those of the perpetrator). The analyses were done using Statistica 8 (StatSoft Inc.).

Blood samples were genotyped (analysis performed by Dynamic code, Linköping, Sweden) for 11 polymorphic microsatellite markers (normally used for domestic pigs) to estimate relatedness among nine sows present in the enclosure during 2005. The markers used were S0059, S0070, S0122, SW1430, SW24, SW2411, SW72, SW840, SW936, SWC27 and TNFB (Nechtelberger et al., 2001). Three categories of relatedness between the sows were possible to determine from the data: 1) mother-daughter (genotype on all markers in common); 2) mother-daughter can not be excluded (one marker not in common); 3) mother-daughter can be excluded (two or more markers not in common). Categories 1 and 2 were merged and are hereafter referred to as relatedness of level 1, while category 3 is referred to as relatedness of level 2. The relatedness levels between the nine sows were established for 36 possible sow-sow combinations (36 combinations in 2005, 21 in 2004 and 3 in 2003). Of these, 14 were of level 1 and 22 of level 2. We then tested whether infanticide was randomly distributed with respect to relatedness, by comparing the expected frequency to the sum of observed and strongly suspected incidences, using Chi-square test (Statistica 8, StatSoft Inc.).

From the questionnaire data, the calculated variables were response rate, herd sizes, reproduction data, total mortality and its causes, enclosure size (smaller or larger than 20 hectares), and frequency of supplementary feeding (less or more than once a week). We analysed whether reported frequencies of infanticide were randomly distributed with respect to size of enclosures and frequency of supplementary feeding using Chi-square test (Statistica 8, Stat soft Inc.).

2.6. Ethical note

The studies were carried out under licence from the Linköping Ethical committee on animal experiments. In the field studies, when the infanticidal behaviour was first encountered, it was seriously considered whether to intervene or simply observe and record the behaviour. Since intervention was judged practically impossible, due to the fact that the observed animals were wild and only moderately habituated to humans (allowing observation, but not physical interaction), potentially dangerous, and no facilities were available for isolating animals, it was decided just to record the behaviour without intervention. It should be noted that the studies were conducted in a privately owned enclosure, and refraining from carrying out the studies would not have stopped the infanticidal behaviour.

3. Results

Twenty-two litters were born in the enclosure during the three consecutive years. The farrowings within the group were spread over 42, 32 and 30 days in 2003, 2004 and 2005 respectively.

Seven out of the 22 litters (32 %) were subjected to observed infanticide and another seven (32 %) to strongly suspected infanticide; in one case two perpetrators were involved in the same litter, giving a total of 15 cases of infanticide. In one of the 14 litters, two out of nine piglets were killed, and in the remaining 13 litters, all piglets were killed during the infanticidal event or died shortly after (four of the attacked litters each had one piglet surviving the infanticidal event, but those four piglets all died within five days). An account of all the observed incidences and the involved individuals is provided in Table 2. All infanticide took place in direct connection to farrowing, and was performed by other sows than the mother, i.e. no maternal infanticide was observed. Out of the totally 12 observed sows, 11 were involved in infanticidal events. Four were observed to be perpetrators, three of them at more than one occasion. In two cases sows were victims in their own farrowings and later perpetrators towards other sows. All piglets which were directly killed by infanticide were eaten by the perpetrator during or directly after killing.

The typical series of events at the observed instances of infanticide was that a perpetrator sow approached the farrowing site when farrowing had already started, or towards the end of it. The perpetrator nosed in the nest and at the piglets, took one newborn (which usually started to scream) and ran off with it, killed it and ate it in the proximity of the nest before returning for the next piglet. Mostly, the mother sow did not show any attempts to protect its farrowing site or piglets, but in the few cases where she did, it was by threatening vocally or rushing up from the nest while threatening the intruder. It was never observed that a sow was able to protect the piglets successfully and stop an attempted infanticide.

When comparing the groups of victims and non-victims (table 3), the sows that were subjected to infanticide were significantly younger than the sows not subjected to infanticide (Mann-Whitney *U* test; $n_1 = 13$, $n_2 = 7$, $P = 0.008$,) (for two litters, sow age was unknown). The two groups did not differ significantly in distance between their farrowing nests and the feeding area (Mann-Whitney *U* test; $n_1 = 14$, $n_2 = 8$, $P = 0.4$). Among the sows where data on weight, length, height and thickness of abdominal fat layer were measured, only two out of nine were not subjected to infanticide, which made statistical comparisons between subjected and not subjected groups of sows impossible. Nevertheless, the numerical results showed that the medians of the two sows not subjected to infanticide were larger than the subjected sows (Table 3).

When comparing the traits of a perpetrator with those of their victims using paired comparisons, perpetrators were always older or of the same age as the victim sows (Wilcoxon's test for matched pairs; $n = 11$, $P = 0.012$). There was a tendency for weight and length to be higher in perpetrator sows, whereas height and thickness of abdominal fat layer did not differ significantly (Table 4). All sows that killed piglets were themselves pregnant or had already farrowed. The perpetrator performed the infanticide at a median of 11 days after she herself had farrowed, but the variation was considerable (range: day 30 pre-partum - 32 post partum, with no infanticide being performed within three days of the farrowing of the perpetrator, $n = 11$).

Perpetrators were seen to kill piglets of both their sisters and daughters as well as from less closely related animals, but never from litters of their mothers. Relatedness between perpetrator and victim sows as estimated by DNA analysis was known in nine infanticide occasions (Table 2). Out of these, six were performed with a relatedness of level 1 and three with a relatedness of level 2, and this was not significantly different from a random distribution (Chi-Square test; $df = 1$, $P = 0.21$).

Adoptions of about 10-day-old piglets were observed in several cases. These were not systematically recorded, but typically piglets from infanticidal or high ranked sows would occasionally start suckling victimised sows with lower rank than their mothers, eventually leaving their own mother completely (a few documented cases are provided in Table 2). In one case it was observed that an entire litter was adopted in this manner, and that the higher ranked mother then came into oestrus shortly after the event.

There were responses to the questionnaire for 88 out of the 116 enclosures (75.9 %); of these, 62 were still inhabited by wild boars. Based on those responses where the owner knew the requested data, or an estimate could be done, a total of 1418 piglets (*Mean* per enclosure = 38.3, range 1- 250, n = 37; *Mean* per sow = 4.8 piglets, range 1-12, n = 37), were estimated to be born in the enclosures during the year of investigation, out of which 1006 piglets (*Mea*n per enclosure = 27.2, range 0- 150, n = 37) survived to weaning, giving a total estimated piglet mortality of 29.1 %. The most common reported cause of piglet mortality was non-maternal infanticide (reported for 36 % of the 62 enclosures). The three most common reported causes thereafter were i) Piglets being stepped or laid upon (27 % of the enclosures); ii) Piglets killed by other species, e.g. raven or fox (18 %); iii) Maternal infanticide (15 %). The frequency with which owners reported that non-maternal infanticide had been observed was not significantly related to size of enclosure (smaller or larger than 20 ha), or to frequency of supplementary feeding (more or less than once a week) (Chi-Square test; $df = 1$, $P > 0.05$).

4. Discussion

We found extensive non-maternal infanticide in wild boars of Swedish and Finnish enclosures both in field observations and reported in a questionnaire study. Infanticidal behaviour was the single most common cause of piglet mortality as reported, and it was usually performed by sows other than the mother both in the field and in the questionnaire study. From the field study, we found that the sows most likely to be exposed to infanticide were younger and smaller than the perpetrators, whereas the relatedness between the sows was of no statistical significance. In the questionnaire, the occurrence of the behaviour was unrelated to size of enclosure and to variation in feeding routines, which all together may suggest that the behaviour is part of the normal behavioural repertoire in European wild boars, and may have evolved in the wild populations. The behaviour constitutes a major welfare problem which may need to be taken into account when designing enclosures for captive Wild Boars.

Whilst it was considered whether it was ethically acceptable to observe and record infanticidal events without intervening (in those cases where we did observe the behavior directly), it was concluded that intervention was not possible. Trying to capture and isolate affected animals would have caused severe stress to the animals, and confer substantial danger to the observers. Furthermore, no housing facilities were available, so it was judged to be practically impossible to affect the behaviour during the field studies.

Mortality in wild living wild boar piglets can be related to e.g. climate as discussed by Fernández-Llario and Carranza (2000), and has for the early life stage been estimated to be almost 60 % (Náhlik and Sándor, 2003). In the present studies of enclosed wild boars, we found that non-maternal infanticide was the main cause of piglet mortality, both as observed in the field, and as reported by owners of enclosures.

About two thirds of all litters in the field study were wiped out by non-maternal infanticide, a level of infanticide which has not been reported in any other animal species as far as we know. Mothers usually did not defend their new-born against intruders in the nests, and no sow was observed to be able to fend off an intruder. This suggests that active defense against infanticidal sows is not a common strategy in wild boars, in spite of casual reports from enclosure owners that sows readily defend their offspring against predators, such as dogs. Lack of defense of neonates has also been found in mice, where preceding suckling appears necessary in order to trigger maternal defensive aggression (Svare and Gandelman, 1976).

The risk of infanticide was affected by several traits. Young sows had a higher risk to lose their litters than older sows, and small sows had a higher risk than larger and heavier ones. Similar relationships between perpetrators and victims have been reported from other species, e.g. chimpanzees in both captivity and wild (Alford et al., 1986; Arcadi and Wrangham, 1999) and badgers (Cresswell et al., 1992).

Isolation from group members at farrowing might be one way for a sow to decrease the risk of infanticide. Spitz and Janeau (1995) have shown that sows prefer a more protective habitat, but the area available for isolation was limited in the studied enclosure. In the wild, an average distance of about 315 m (min 150, max 700) between nests is reported by Fernándes-Llario (2004). However, it is not clear how far from group members sows actually farrow in wild conditions. In free-ranging domestic pigs, Jensen (1988) found that increased distance between feeding places and farrowing nests increased the survival of the young, although infanticidal behaviour was not observed. Although the sows spent a large portion of their active time at the feeding area (Andersson et al, 2011), we did not find any effect of distance between farrowing nest and feeding areas on the infanticide, which again may indicate some limitations of the studied enclosure.

Infanticide events were not influenced by how closely the perpetrators and victim sows were related. Sows were seen to perform infanticide on distantly related litters as well as on litters of their own daughters and sisters, but never on those of their mothers (which also follows from the already mentioned effect of age and size). Maternal infanticide was never observed in the field study, although this is not uncommon in domestic pigs (Chen et al., 2009) and also has been reported from wild boars in semi natural conditions (Martínez-Rica, 1980) and more intense production systems (Harris et al., 2001).

Given the obvious fitness cost of losing offspring by infanticide, one might expect counter-strategies to have evolved. In rodents, periparturient hormone changes block infanticidal behaviour, (McCarthy and vom Saal, 1985; Soroker and Terkel, 1988), which indicates that synchronous breeding could act as a counter-strategy against female infanticide (Poikonen et al., 2008). In our study, no perpetrator performed infanticide closer than three days before or after its own farrowing, and synchronisation of births is known to occur normally among wild boars (Delcroix et al., 1990). Synchrony in wild boar oestrus is affected by food availability (Fernández-Llario and Carranza, 2000; Santos et al., 2006) and the following synchronised farrowing has been suggested to be a means of rearing piglets communally (Delcroix et al., 1990). An additional possibility suggested by our results is that synchronisation of farrowings in wild boars may have evolved as a counter-strategy against infanticide (Agrell et al., 1998). In the enclosed groups studied here, farrowings were not obviously synchronised, which may have contributed to the high levels of infanticide observed. The same may be true for isolation before farrowing, which is usually considered in the context of anti-predation behaviour and establishing of bonds between the mother and offspring (Fernández-Llario, 2004) . We suggest that this isolation may be part of an adaptive strategy to avoid infanticide, which is supported by the lack of active defence of neonates in the nest in our observations.

The questionnaire study suggested that non-maternal infanticide is an important cause of neo-natal mortality among captive populations of wild boars. The occurence of reported infanticide did not differ between enclosures of different sizes which was a bit unexpected since larger enclosures should increase the possibilities of sows to isolate and thereby succeed in raising young. It is possible that even the larger enclosures were too small to allow sows to isolate properly. Few of the owners supervised farrowings regularly, which indicates that the reported level of infanticide may have underestimated the true situation.

There is a possibility that the presence of observers in the field studies somehow triggered the infanticidal behaviour. Either the observers could have been a source of stress, or they could have provided a visual cue indicating the position of a farrowing sow, or both. However, this possibility appears unlikely, since about half of the field study cases occurred outside observation periods, and the behaviour was reported to be common in the questionnaire, which did not involve the presence of observers. Another possibility could be that the behaviour is copied by sows, which would spread the behaviour throughout the group. Again, the fact that the behaviour was so common in so many different enclosures in two countries, as shown by the results from the questionnaire, suggests that while copying may have occurred it was not the most important factor.

Our results indicate that infanticide is a wide-spread phenomenon in captive wild boars. The fact that we found no relationship between the extent of infanticide, and the size of enclosure or feeding routines suggests that it might not be an abnormal behaviour caused by stress from the captive environment. Assuming that the behaviour may be part of the normal repertoire of wild boars, its evolutionary background is interesting to consider. Functional explanations for infanticidal behaviour have been suggested by Hrdy (1979) and Ebensperger (1998), and based on our observations, wild boar infanticide seems best to fit the categories “resource competition”, and “exploitation of the young as a food resource”. Evidence for this is that only adult females were perpetrators, and they clearly benefited from the behaviour in terms of food (all piglets were eaten), and increased reproduction, sometimes mediated by adoption of their own piglets by exposed sows. The benefit of extra nutrition may have been augmented by the fact that food abundance in the enclosure was limited, as it would be under natural conditions during winter, when wild boars normally farrow.

It is also important to note that the inclusive fitness of the victim sow would depend on the relatedness to the perpetrator. In a wild population, sows in the same group would normally always be closely related (e g Gundlach, 1968), and therefore victimised sows may gain indirect fitness by the increased survival of the offspring of the perpetrator. This could be further augmented by the direct investment in those offspring shown in those cases where victims were observed actually to nurse the offspring of perpetrators.

The general pattern of infanticidal behaviour observed in the wild boars bears resemblance with that seen in certain canids. Hausfater and Hrdy (1984) provides a general account of infanticidal behaviour in this group of animals. Both in foxes and wild dogs, subordinate females regularly get their offspring killed by dominant individuals, and similar observations have been reported from brown hyenas. McLeod (1990) reported two cases in which female wolves killed pups of subordinate animals. Often, the subordinate females helped raising and suckling the offspring of the perpetrator, and hence, Hausfater and Hrdy (1984) suggest that non-maternal infanticide may be an adaptive strategy of the dominant female,.

5. Conclusions

We have reported a previously unknown extent of infanticide in captive European wild boars, where non-maternal infanticide constituted the single largest estimated cause of piglet mortality. Our results suggest that this behaviour might have evolved as an adaptive behaviour, where sows utilise young of others as food resources or benefit through resource competition. We suggest that counter-strategies have evolved, such as synchronised farrowings and isolation of the females prior to birth, but that these may be difficult to adopt for animals in enclosures, where feed and the available area are limited. Consequently, the results raise serious welfare concerns with respect to how wild boars are kept in captivity in enclosures in Sweden and Finland.

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Table 1

The animal population in the enclosure (numbers of animals, n, of each category, and the age of the adult females) during each of the three farrowing seasons (at the start of each study season).

Year	Females (*n*)	Female age (*years*), median and range	Males (*n*)	Yearlings (*n*)
2003	6	5.5 (3 – 6)	1	18
2004	7	4 (2 – 7)	1	17
2005	9	3 (2 – 8)	2	11

Table 2

An account of all 15 cases of observed or suspected (implicated by indirect observations) cases of infanticide. For each case, the table provides date of observation (YYMMDD), whether the infanticide was observed or suspected, identity (ID, the individual number of the sow) and age in years of perpetrator (P) and victim (V), their relatedness according to a DNA-analysis, the number of offspring surviving from each of P and V during the field observation period, and comments with further details in some of the cases. Un= Unknown.

Case	Date	Obs or susp	P ID	V ID	P age	V age[1]	Relation P vs V	Nrs surviving offspring of P	Nrs surviving offspring of V	Comments
1	030312	Susp	Un	2	Un	6	Un	Un	0	
2	030320	Obs	4	1	5	5	Un	4	7	P:s piglets suckled sow 3
3	030417	Obs	1	3	5	5	Level 1	7	0	1 piglet survived the infanticidal event, but died within five days
4	030422	Obs	1	11	5	3	Un	5	0	
5	040311	Obs	2	7	7	2	Level 2	3	0	4 out of 7 piglets of P died from disease at 3 weeks; P adopted the litter of sow 3.
6	040316	Susp	2	6	7	2	Level 1	3	0	1 piglet survived the infanticidal event, but died within five days; for P, see case 5; V

7	040317[4]	Obs	2	5	7	2	Level 2	3	0	adopted one piglet of sow 1 1 piglet survived the infanticidal event, but died within five days; for P, see case 5
8	040317[4]	Obs	7	5	2	2	Level 1[2]	0	0	P lost its own piglets in case 5, came into new estrous (outcome unknown). For V, 1 piglet survived the infanticidal event, but died within five days
9	050301	Susp	Un	7	Un	3	Un	Un	0	V was P in case 13
10	050311	Susp	Un	3	Un	7	Un	Un	0	
11	050312	Obs	1	6	7	3	Level 1	4	0	
12	050312	Susp	Un	8	Un	Un	Un	Un	0	
13	050313	Susp	7	5	3	3	Level 1[2]	0	0	P was V in case 9
14	050313	Obs	2	9	8	2	Level 2	6	0	
15	050313	Susp	2	10	8	2	Level 1[3]	6	0	

[1]All ages >3 yr given as estimated by the keeper; [2]Known to be sisters. [3]Known to be mother and daughter; [4]Two perpetrators, one victim

Table 3

Median, range and numbers of observations (*n*) for different variables for the group of sows which had litters subjected to infanticide and for the group of sows which had litters that were not subjected to infanticide. *P*-values as obtained by Mann-Whitney U-test (- signifies that statistical analysis was not meaningful).

	Subjected to infanticide			Not subjected to infanticide			
	Median	*Range*	*n*	*Median*	*Range*	*n*	*p*
Age (*yr*)	3	2 - 7	13	6	3 - 8	7	0.008
Nest distance to feeding area (*m*)	128	65 - 310	14	135	70 - 310	8	0.4
Weight (*kg*)	114	77.5 - 147	7	-	136 - 143	2	-
Length (*cm*)	150	133 - 160	7	-	159 - 165	2	-
Height (*cm*)	79.5	70.9 - 85.3	6	-	80.3 - 83.8	2	-
Thickness of abdominal fat layer (*cm*)	2.5	1.8 - 4.5	7	-	3.0 - 3.0	2	-

Table 4

Median, range and numbers of observations (*n*) for different variables for perpetrator and victim sows in a given pair at the infanticidal event. *P*-values generated by Wilcoxon's test for matched pairs.

	Perpetrator sows		Victim sows			
	Median	*Range*	*Median*	*Range*	*N*	*p*
Age (*yr*)	7	3-8	2	2-5	11	0.012
Weight (*kg*)	143	136 - 147	102	77.5 - 137	4	0.068
Length (*cm*)	163	159 - 165	146	133 - 154	4	0.068
Height (*cm*)	83.8	80.3 - 83.8	77.7	70.9 - 81.3	3	0.285
Thickness of abdominal fat layer (*cm*)	3.0	3.0 - 4.0	2.3	1.8 - 4.0	4	0.109