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RESEARCH PAPER

Rapid establishment of teat order and allonursing in wild boar (*Sus scrofa*)

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Abstract

Transfer of milk is the fundamental common characteristic of mammalian reproduction, but species differ considerably with respect to nursing strategies. The consequences of teat orders and allonursing have been studied intensively in domestic pigs. However, whether similar nursing strategies also exist in wild boar, the ancestor of domestic pigs is so far not known. The occurrence of allonursing in wild boar is only described anecdotally, and the question whether a teat order is established has not yet been investigated. Studying suckling behaviour of 29 piglets from six primiparous wild boar females in a semi-natural environment we found a surprisingly fast development of a rigid teat order among littermates, which established within 2.2 hr after birth. This suggests strong fitness benefits of this phenomenon that may ultimately explain the evolution and maintenance of this trait. We further found a strong synchrony of oestrus and delivery among the females of a group, as well as the occurrence of allonursing. By determining the amount of allonursing for the first time quantitatively, we demonstrate the importance of this trait and its presumably pivotal role for juvenile survival under truly natural conditions.

KEYWORDS

lactation, nursing behaviour, pig, suckling behaviour, udder preference

1 | INTRODUCTION

All mammals depend on milk during early development, and the transfer of milk from mothers to offspring is one of the fundamental common characteristics of mammals. However, with respect to nursing strategies and suckling behaviour, species may differ a lot. Juveniles of various polytocous species (i.e., species giving birth to multiple offspring at the same time) show a suckling order, either a preference to a particular region of the mother's udder (also called 'udder preference') or even evolved individual adherence

to a specific teat (described as 'teat fidelity' or 'teat order') (Skok, 2018). Exhaustive descriptions of udder preference can for example be found for several altricial species including felids (Glukhova & Naidenko, 2014; McVittie, 1978; Pfeifer, 1980), canines (Hudson et al., 2016), rodents (Bonath, 1972; McGuire, Vermeylen, & Bemis, 2011) and lagomorphs (Bautista, Mendoza-Degante, Coureaud, Martínez-Gómez, & Hudson, 2005). In contrast—and although also known from a number of species (for example see Ewer, 1959; Hoeck, 1976; Skok & Škorjanc 2014b; Skok, 2018)—detailed descriptions of the individual adherence to a specific teat, as well as the defence

Julia Nowack and Sebastian G. Vetter contributed equally to this work.

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of this teat and therefore the development of a stable teat order are only available for domestic pigs (*Sus scrofa domestica*) (Fraser & Jones, 1975; Hemsworth, Winfield, & Mullaney, 1976; McBride, 1963; Newberry & David, 1985; Rosillon-Warnier & Paquay, 1984; Skok & Škorjanc 2014b).

The establishment of a teat order has been reported to result in a less competitive feeding behaviour (McBride, 1963) and thus supposedly reduces stress and competition (Hoeck, 1976), increases body mass gain (Hemsworth et al., 1976) and ultimately survival of young (Skok & Škorjanc 2014b). In polytocous species, the access to the mother's milk is not necessarily equally distributed within a litter (Hofer, Benhaïem, Golla, & East, 2016), which could result in different growth rates of littermates. Furthermore, differences in growth rates may also result from the energetic costs of competing for access to milk (Skok, 2018; Skok & Prevolnik Povše, 2019). It therefore seems crucial for young to fight for an own teat and a favourable position in the suckling order of this main teat.

To date, most research on the establishment of a teat order has focused on domestic pigs. In this species, a preliminary teat order is already present twelve hours after birth (McBride, 1963) and stabilizes within the first 10 days after parturition (Skok & Škorjanc 2014b). Once established, the teat order remains relatively stable, meaning that piglets mostly suckle at the same one or two teats throughout the whole period of lactation (Rosillon-Warnier & Paquay, 1984). Cranial teats in domestic pigs seem to be preferred, which is likely related to the quantity of milk, as they seem to be more sensitive to stimulation (Algers & Jensen, 1991; Fraser, 1980) and hence result in higher body mass gain (Gill & Thomson, 1956). However, the quality of milk also seems to differ as cranial teats are reported to produce greater amounts of immunoglobulins A and G, which positively affect the immune system of piglets (Ogawa et al., 2014). In contrast to domestic pigs, not much is known about the establishment of a teat order and udder preference in their ancestor, the wild boar (*Sus scrofa*). Meynhardt (1990) first described the establishment of a teat order in wild boar piglets (*S. scrofa*) but claims that it is not stable until 4 weeks after birth.

As lactation is energetically costly, one would expect that lactating females will not provide milk to offspring other than their own. However, in some group-living species where group members reproduce and lactate simultaneously, cross feeding of juveniles can be observed. This so called allonursing, that is the nursing of non-descendent offspring as a form of alloparental care (Packer, Lewis, & Pusey, 1992; Roulin, 2002), occurs across a wide variety of group-living mammals, ranging from carnivores, over rodents, to ruminants, bats and primates (reviewed in Packer et al., 1992). Although allonursing (i.e., juveniles allosuckling) has been reported to occur in wild boar (Macheiner, 2015; Meynhardt, 1990) it is still unknown to what extent female wild boar nurse alien offspring and whether they distinguish between own juveniles and other females' offspring. Communal nesting seems to be absent in wild boar, as females are reported to leave their sounder to give birth in a solitary nest, and do not return to the group before approximately 1 week after farrowing (Martys, 1982). Further, females are reported to defend their nests

aggressively, not only against potential threats like predators or humans but also against group members (Martys, 1982).

In this study, we investigated the nursing behaviour of five primiparous wild boar females along with the suckling behaviour of their offspring in a semi-natural environment with a focus on teat order, udder preference and allonursing. We were interested in whether udder preference and the development of a teat order provides benefits to wild boar piglets with respect to body condition and body mass gain. We hypothesized (a) that a teat order in wild boar is established rapidly after birth, as described in domestic pig (McBride, 1963), and remains relatively stable over the lactation period, (b) that body mass gain is related to the location of a piglet's main teat, and (c) that piglets confined to less preferred teats at their mother show a higher tendency to engage in allosuckling.

2 | ANIMALS, MATERIAL AND METHODS

2.1 | Ethical note

All procedures have been approved by the institutional ethics and animal welfare committee and the national authority according to §§26ff. of Animal Experiments Act, Tierversuchsgesetz 2012 - TVG 2012 (BMFW-68.205/0171-WF/V/3b/2016).

2.2 | Study animals

Six nulliparous female wild boars (all approximately 2 years old), individually marked with coloured ear tags with individual letters, were kept and bred at the Research Institute of Wildlife Ecology (FIWI) at the Department of Integrative Biology and Evolution of the University of Veterinary Medicine, Vienna, Austria. Sows were trained once a day/five times a week to habituate them to human contact in order to ease management and to enable access to piglets. Mating occurred in November 2016 with one male wild boar (approximately 2 years old) and littering occurred in March 2017.

Nursing behaviour of all piglets was analysed from the day of birth until May 2017. Three piglets had to be euthanized in April because of dramatic weight loss, severe infection and critical low body temperature. Pathological examinations revealed severe infection with *Escherichia coli* in all three cases.

2.3 | Animal housing & maintenance

Study animals were kept in an outside enclosure of 2.5 ha which was divided in two areas. The larger part of the enclosure provided a natural environment with low human-animal contact. The second area contained three small 'farrowing enclosures' (each 160 m²), which allowed separation of animals during parturition and lactation. Each farrowing enclosures contained two sheltered, wooden hideouts (each approximately 2 m²), littered with straw, a water trough and two closable training boxes in which the animals were fed. Females were separated from the male from day 20 *pre-partum*

to about 6 weeks *post-partum* and separated in pairs into farrowing enclosures from day 20 *pre-partum* until 8–10 days *post-partum*. Thereafter, doors were opened, allowing contact among all females and piglets of all litters. This provided more space and opened the possibility for piglets to allonurse at all other mothers.

Animals were fed twice a day with a mixture of approximately 1.4 kg of pig feed pellets (Herbert Lugitsch und Söhne Ges.m.b.H., Austria) and corn, supplemented with some apples, bananas and carrots. Piglets were supplementary fed from day 22 *post-partum* onwards with a standard piglet starter (Porcimilk A, Provimi B.V., Netherlands, Rotterdam), and some Enteroferment® (Richter Pharma AG) for treating and preventing gastrointestinal infections.

2.4 | Data collection

Infrared cameras in the hideouts at a top shot position provided an overview of the 'nest' and allowed continuous video monitoring 24 hr/7 days a week from 3 weeks *pre-partum* to 6 weeks *post-partum*. Piglets were identified individually immediately after birth by their unique fur stripe patterns. On day 1 or 2 *post-partum*, piglets were also marked with coloured and numbered ear tags. To ease individual identification from a distance, we additionally marked the piglets with hair-dye (Schwarzkopf & Henkel, Düsseldorf -Wien) on day 7/8 *post-partum*. These markings were visible for about 4 weeks. Piglets were weighed five times during the study to the nearest gram, on day 1 (8.5–24 hr after birth), day 5, day 8–9, day 73–74, and day 140–158 *post-partum*. During the first 12 hr *post-partum*, we obtained detailed observations of all nursing bouts from continuous video recordings as mothers rarely left the farrowing boxes during this time, whereas piglets never left. Thereafter, we evaluated only one nursing bout/female/week until 6 weeks *post-partum* in order to verify persistence of the established teat order and to quantify allonursing. Selected bouts were equally distributed over the day, hence representing a random sample.

In total, we analysed 201 nursing bouts. For each single suckling event of a piglet, we recorded: the ID of the mother and suckling piglets, the exact time of the start and end, along with the total duration of the suckling event (in seconds), the lying position of the mother (left or right lateral, see below), as well as the piglet's position along the udder (teat pair number). To locate piglets' position at the udder while suckling, teat pairs were numbered from 1–5 beginning from cranial to caudal. We only analysed nursing bouts when mothers were lying in a fully lateral recumbency, because only in this position all teats of an udder were accessible. The start of a nursing bout was defined when mothers were lying in this position and the first piglet started suckling. The end of a nursing bout was defined when the last piglet left the udder, or when the mother stood up. We were not able to distinguish between periods of milk flow, massaging of the udder or whether the piglet fell asleep (Devillers, Giraud, & Farmer, 2016; Gundlach, 1967) and therefore only recorded the total amount of time a piglet was attached to a specific teat.

We observed the first piglet eating solid food approximately 3 weeks after birth. When piglets reached the age of 3–4 months

mothers increasingly refused to nurse. However, weaning was not completed before removal of piglets at the age of 158 days.

2.5 | Statistical analyses

Data are presented as means \pm standard deviation (*sd*) if not indicated otherwise. All statistical analyses were conducted in R, version 3.5.2 (R Core Team 2018).

A binomial test was used to test whether the sex ratio of newborn piglets was balanced. Linear modelling was used to test (a) whether body mass at birth (measured at day 1) was linked to sex of the offspring, birth order, litter size or the mother, (b) whether it was related to the location of the main teat at mother's udder, established later in life, and (c) to test whether a piglet's main teat at its biological mother and whether allosuckling affected total body mass gain from day 1 to day 5. For the first model, we performed model selection with R-package MuMIn (Barton 2017), due to small sample size and in order to avoid overfitting. All models within Δ AICc of 4 as well as the null-model only containing the intercept are shown in the results. Also, to avoid overfitting, linear modelling instead of linear mixed-effects models was used as preliminary analysis based on the AICc revealed that including 'mother ID' as random effect did not improve the model and thus that the assumption of independence was not violated. This procedure regarding a potentially necessary inclusion of 'mother ID' as random effect was also followed in all analyses described below. In none of the analyses the inclusion of 'mother ID' was found to be necessary due to a violation of independence.

A segmented linear mixed-effects model was calculated to determine the time period necessary for establishment of a main teat at their mothers' udder, that is to analyse the proportional use of the main teat (i.e., time suckled at main teat in relation to total suckling time) and its change over the first 6 weeks of life utilizing the R-package lme4 (Pinheiro et al., 2016). Besides the random effect 'piglet ID', the model also included the teat pair number of the piglets' respective main teats to account for potential effects of the location of the main teat. Break point and its confidence interval were identified via a likelihood approach. Significance of the change of slopes in the variable time was determined via a linear hypothesis test. A chi-square test was performed to test whether the identified main teats of the piglets were uniformly distributed over all teat pairs.

A linear model was used to test the effect of total number of piglets and number of allosuckling piglets on nursing bout duration. Additionally, time after birth (weeks) was included to correct for potential age effects. A linear mixed-effects model with random effect 'piglet ID', to account for repeated measurements, was used to test the effect of a piglet's main teat on the proportional suckling time at allomothers (i.e., as percentage of total suckling time) during the first 12 hr after birth. Finally, a binomial model was used to analyse whether a piglet's tendency to allosuckle was influenced by the position of the main teat at its mother's udder. From this model, a variant including birth mass as additional fixed effect was

calculated in order to also analyse a potential effect of birth mass. This was done in a separate model because of the lower sample size in body mass data.

3 | RESULTS

3.1 | Birthing, litter size and body mass

Five of six study females gave birth to a total of 29 piglets. Littering occurred within 3 days from 20th to 22nd of March 2017. Total birth time per litter was on average 104 ± 51 min, and the birth time interval within litters between consecutive piglets was 21 ± 24 min. Litter size ranged from four to seven piglets (5.8 ± 1.1). Sex ratio of piglets was with a total of 59% males and 41% females not statistically different from 1:1 ($\chi^2 = 0.55$, $p = .46$). Birth mass of piglets (i.e., body mass at day 1) ranged from 1,293 g to 1,510 g ($1,421 \pm 28$ g). Relative litter body mass at birth (i.e., % of litter mass to the female's body mass 4 months *pre-partum*) ranged from 4% to 8.4% ($6.9 \pm 1.6\%$).

Four of the five females used an individual farrowing box for farrowing and piglets did not leave this box for the first twelve hours of life. One female joined a mother that had given birth approximately thirty hours before to give birth in the same farrowing box.

Body mass on day 1 after birth strongly correlated with body mass on day 5 ($r = .78$; $p < .001$) and day 8/9 (it was not possible to weigh all piglets on the same day) ($r = .56$; $p = .010$). In contrast, body mass on day 73/74 did not significantly correlate with body mass on day 1 ($r = -.09$; $p = .760$).

3.2 | Teat order and udder preference

Piglets developed a teat order within the first 2.2 hr of life (95% CI 1.0–2.6 hr; increase of suckling time at the teat a piglet overall used mostly, $F_{1,602} = 36.86$, $p < .001$; linear hypothesis test for a change of slope, $\chi^2 = 36.82$, $p < .001$; Figure 1), that is piglets were thereafter found at the same teat, from here on referred to as 'main teat', for about 80% of the observed suckling time during the first 2 weeks. After the main teat was established the proportional use of this teat by the piglets showed a weak decrease but overall remained high ($F_{1,602} = 12.90$, $p < .001$; Figure 1). New-born piglets suckled on their mother's udder for the first time on average 20 ± 7 min after birth; typically, at a teat that was not the later established main teat (55.2% of 29 piglets observed). The main teat was firstly used on average 41 ± 15 min after birth.

TABLE 1 Model selection table for testing effects on body mass of piglets at day 1 after birth

Model	df	AICc	Δ AICc
sex	3	226.99	0.00
sex + birth order	4	229.10	2.11
sex + litter size	4	229.19	2.20
NULL	2	231.95	4.96

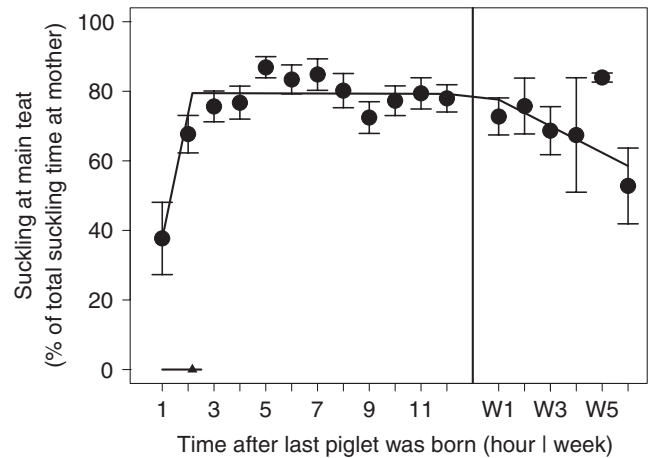


FIGURE 1 Partial effect of time after birth (hours 1–12 and week 1–6) on the proportional suckling time at the teat used mostly by a piglet (means \pm sem). Data for biological mothers only, the triangle and associated horizontal bars indicate location of the break point of segmented regression with 95% confidence interval

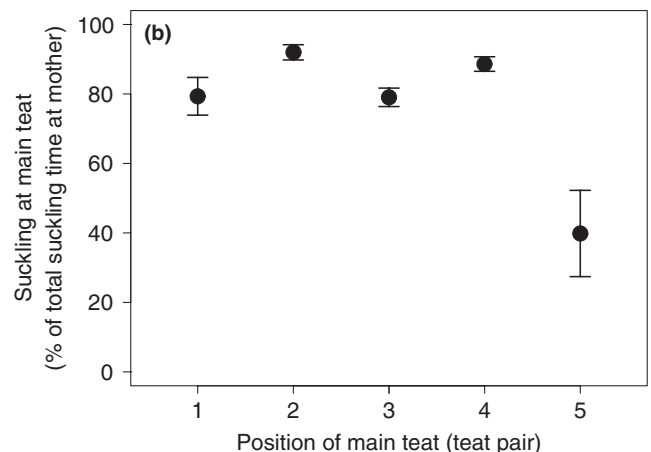
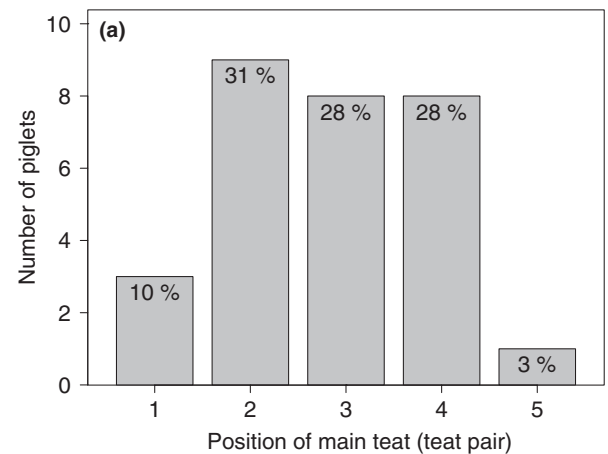


FIGURE 2 Udder preference of the piglets measured as (a) distribution of piglets' main teat at mothers' udders and (b) partial effect of the location of the main teat at mother's udder on the proportional use of main teats (means \pm sem). For the latter, no significant effect could be identified (see text)

Generally, piglets seem to have a preference for middle teat pairs (teat pairs 2–4) (Figure 2). Only 4 out of 29 piglets had their main teat located at teat pairs one or five, 25 at teat pairs 2–4 (Figure 2a; $\chi^2 = 8.751, p = .002$, computed by Monte Carlo simulation). However, piglets did not suckle longer on middle teats than on teats one or five ($F_{4,300} = 1.93, p = .139$; Figure 2b).

Body mass at birth was only affected by sex ($t = 2.92, p = .009$; Table 1) and not significantly linked to the position of an individual's main teat at a certain teat pair ($F_{4,15} = 1.86, p = .163$).

However, growth rates of piglets, evident from individual body mass gains between days 1–5 after birth, were significantly affected by the location of the main teat at mother's udder ($F_{4,13} = 3.29, p = .045$; Figure 3). Post hoc pair-wise comparisons revealed specific differences between teat pairs 2, 3 and 4 versus teat pair 5 (all 3 Tukey post hoc comparisons $p < .05$).

3.3 | Allonursing

Of all 29 piglets studied, 20 (69%) suckled at least occasionally at another mother than their own. For all nursing bouts analysed, 10% of the time spent suckling was at alien mothers. One piglet became even fully adopted by an alien mother one day after birth and completely stopped suckling at its biological mother. In case of the offspring of two females that gave birth in the same farrowing box, allonursing even occurred immediately after birth (three piglets within 10 min after birth), and in one case even during birth, with 30 hr old piglets suckling at the parturient mother. Duration of nursing bouts was strongly linked to the number of piglets suckling together at one mother ($F_{1,193} = 47.50, p > .001$, Figure 4a). However, the more alien piglets were involved, the shorter was the nursing bout duration ($F_{1,193} = 8.73, p = .004$; Figure 4b), independent of the effect of the total number of piglets suckling at an udder.

The probability as well as the amount of allonursing depended on the position of a piglet's main teat at its biological mother. Piglets

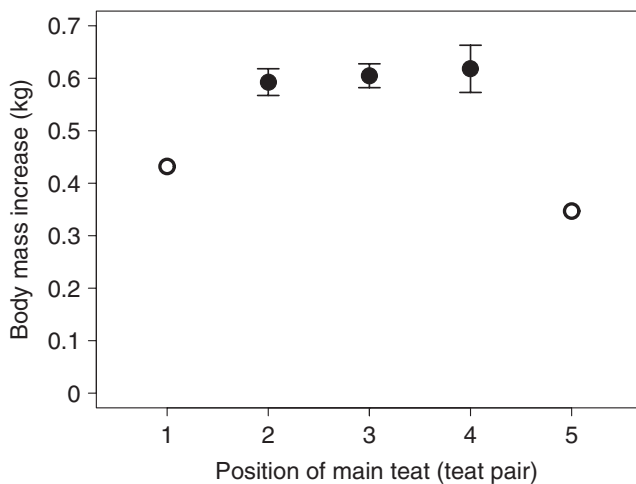


FIGURE 3 Partial effect of the location of the main teat on total body mass gain from day 1 to day 5 after birth (means \pm sem). Sample size at teat pairs 1 and 5 in this analysis was $N = 1$, indicated by open symbols and lack of error bars

owning a main teat at teat pairs 2–4 had a lower probability to suckle at alien mothers compared to piglets which had their main teat at teat pairs 1 or 5 ($F_{1,25} = 11.18, p = .002$; Figure 5a).

Further, piglets showed different proportions of allonursing according to the position of their main teat at mother's udder ($F_{4,404} = 70.88, p < .001$; Figure 5b). The piglet having its main teat at teat pair five spent a significantly higher proportion of total suckling time at allomothers (post hoc comparisons, $p < .001$; Figure 5b).

A piglet's probability of allonursing was not affected by its birth weight ($F_{1,16} = 0.26, p = .614$), and allonursing did not significantly affect its body mass gain from day 1 to day 5 after birth ($F_{1,13} = 2.17, p = .164$), when correcting for the influence of the location of the main teat at the biological mother (see above).

4 | DISCUSSION

Our study shows that wild boar piglets develop a clear teat order shortly after birth that remains roughly stable over the first 2 weeks of life but weakens again slightly in the following weeks. Furthermore,

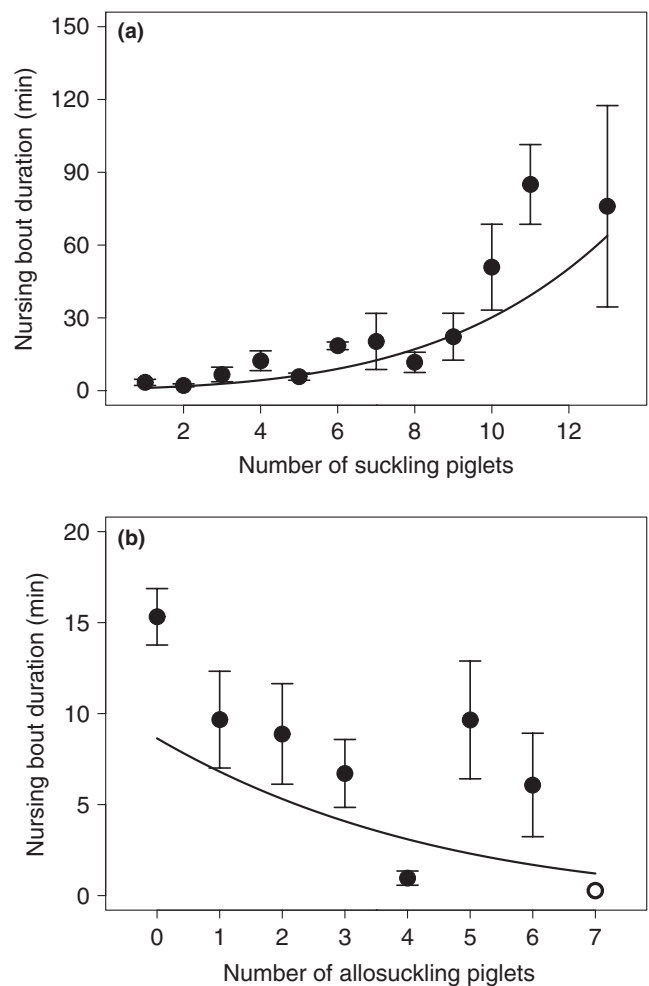


FIGURE 4 Partial effect of (a) the total number of suckling piglets and (b) the number of allonursing piglets on nursing bout duration (means \pm sem)

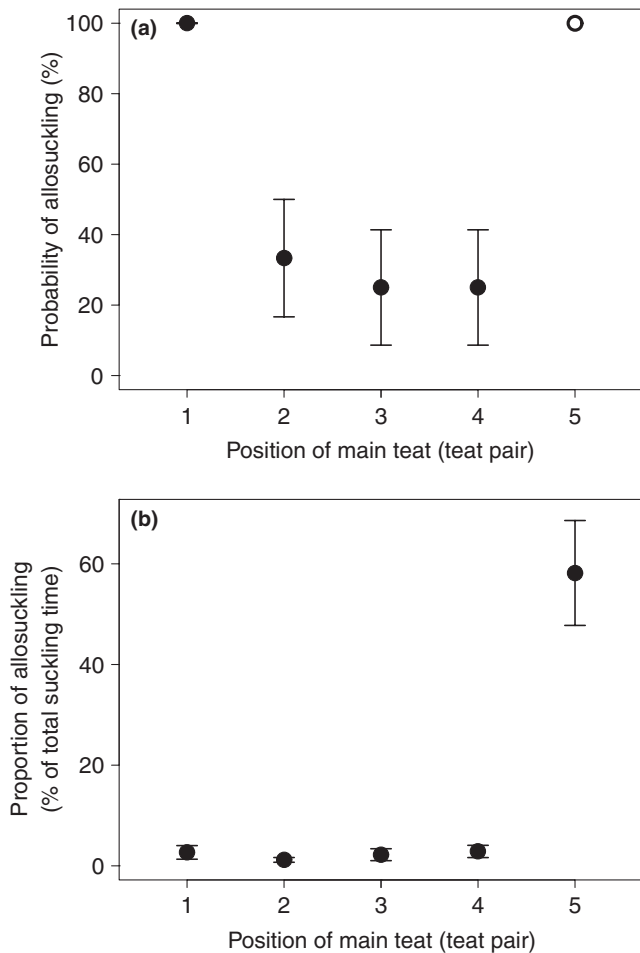


FIGURE 5 Effects of the main teat at the biological mother on (a) the probability of allosuckling (i.e., percentage of piglets having their main teat at a given teat pair \pm sem of this percentage); Only one individual had its main teat at teat pair 5 (open symbol without error bars) and (b) the average proportion of allosuckling during the first 12 hr after birth (means \pm sem)

we found a high tendency of allonursing, that is piglets suckling at other mothers than their own, and an almost perfect synchrony of littering among the five reproducing females. Interestingly, a piglet's probability to allosuckle was correlated with the location of the main teat at its biological mother. The existence of a rigid teat order in litters of *S. scrofa* is well known from extensive studies in domestic pig (Fraser & Jones, 1975; Hemsworth et al., 1976; McBride, 1963; Newberry & David, 1985; Rosillon-Warnier & Paquay, 1984; Skok & Škorjanc 2014b). Our data demonstrate that the consistent use of the same teat by individual offspring during the first days after birth and its defence against other piglets (McBride, 1963) is apparently an ancient trait that is already present in the wild ancestor of domestic pigs. The wild boar piglets studied developed a stable teat order within the first three hours after birth. Therefore, the teat orders were established earlier in our five litters than reported for litters of wild boar living in a natural environment (Meynhardt, 1990), and considerably faster than in litters of commercial pig breeds, where it takes seven to fourteen days *post-partum* until a stable teat order is

achieved (Rosillon-Warnier & Paquay, 1984; Skok & Škorjanc 2014b; Skok & Gerken, 2016). Wild boar piglets are described to first take solid food after 12 days post-partum (Gundlach, 1967). This might explain the observed weakening of teat order after 2 weeks and why nursing bouts were progressively terminated by the sows with increasing age of the piglets (anecdotal observations LA). The latter may reflect decreasing maternal investment (Trivers, 1974).

Preference for particular regions of the mother's udder and the formation of a teat order is mostly reported in altricial species (Bautista et al., 2005; Bonath, 1972; Ewer, 1959; Glukhova & Naidenko, 2014; Hudson et al., 2016; McGuire et al., 2011; McVittie, 1978; Pfeifer, 1980). Further, Skok (2018) argued that teat orders develop mainly in species with lower maternal investment, such as low breeding frequency, monogamy, biparental care and lower litter birth mass. This holds also true for wild boar, as they usually have a low breeding frequency of one litter a year and a relative birth mass under 21% of the mothers body mass (this study, Skok, 2018). Overall, the establishment of a teat order is suggested to result in a calm and ordered feeding behaviour (McBride, 1963), and thus in increased body mass gain (Hemsworth et al., 1976) and survival of the young (Skok & Škorjanc 2014b). Teat orders are assumed to potentially reduce mother-offspring conflict, as unused teats stop producing milk (Kim, Easter, & Hurley, 2001) and once fully established may also serve to reduce conflicts among littermates by preventing foraging competition. Such effects would be in fact very important in wild boar where juvenile body mass was found to have long-lasting effects on adult reproductive success (Vetter et al., 2016).

Skok and Škorjanc (2014a) suggest that teat orders in pig develop in order to ensure sufficient access to colostrum. This product of the mammary gland containing immunoglobulins is only available during the first 24 hr of lactation, immediately after delivery (Rooke & Bland, 2002). Obtaining colostrum is pivotal for piglets, because this is the only way to achieve immunoglobulins from their mother (Schnorr & Kressin, 2006). Immunoglobulins in pigs cannot be transferred during pregnancy from the mother to offspring due to the epitheliochorial placenta type of this species, which is impermeable for such macromolecules (Schnorr & Kressin, 2006). Therefore, development of a functional immune defence in new-borns depends on access to colostrum immediately after birth, that is in the first 24–36 hr (Kruse, 1983; Rooke & Bland, 2002). Moreover, the milk ejection is very short in pigs, lasting only for 13–17 s (Horrell, 1997). Hence, it is crucial for new-born piglets to reduce the time of searching and fighting for teats and instead maximize the nursing duration to obtain large quantities of colostrum-rich milk. Ensuring exclusive intake of colostrum by own progeny may also explain why wild boar females separate from the social unit to give birth (Martys, 1982). However, contradicting to these anecdotal reports, we observed one female giving birth next to a mother that had given birth approximately thirty hours before. As a result, the one-day old piglets obtained colostrum from the parturient mother by allosuckling before the female's own offspring were born. Other benefits, for example from social huddling, must substitute for the cost of reduced access to colostrum if joint farrowing is an adaptive trait.

Establishing a teat order is energetically costly for offspring, because it is accomplished by strong disputes among littermates (Hudson & Distel, 2013). Therefore, it seems to be a behavioural trait caused by stronger littermates, who are able to defend their main teat and acquire potentially beneficial positions at the udder (e.g., teats which were more sensitive to stimulation (Algers & Jensen, 1991; Fraser, 1980) or teats at positions providing thermoregulatory benefits (see below) (Fernández-Llario & Mateos-Quesada, 2005; Skok & Škorjanc, 2014a). In contrast, Skok and Prevolnik Povše (2019) suggest that teat orders are more important for weaker neonates who could compensate growth rates by choosing an ordered foraging strategy, although they may end up with less milk intake than stronger and intermediate littermates. In our study, sibling rivalry was already obvious during the first hours after birth, that is piglets fought over acquisition of their main teat (anecdotal observation LA). Interestingly, even piglets with lower body mass, thus potentially weaker individuals, were able to successfully defend their main teat.

Teat orders may also develop from preferences for and fighting over specific regions of the udder (e.g., Fraser & Jones, 1975). In fact, some authors speculate that milk quality may differ according to udder region (Ogawa et al., 2014; Šamanc et al., 2013; Wu et al., 2010). The piglets studied showed a clear preference for teat pairs 2–4 (middle pairs), whereas the cranial, and the caudal teat pairs were less likely to be used as main teats. This finding is in line with the result of Skok and Gerken (2016), who found a preference for middle teat pairs in mini-pigs. Fernández-Llario and Mateos-Quesada (2005) found a preference for caudal teats in 51 female wild boar culled while lactating, but did not include the most caudal teat pair in the study as it was never used. In contrast, a preference for cranial and middle teat pairs was found in domestic pigs (Algers, 1993; Fraser & Jones, 1975; Gill & Thomson, 1956). In the present study, the one piglet having its main teat at the caudal teat pair showed a high tendency to suckle at alien mothers, presumably to achieve surplus milk in order to compensate for lower productivity of the mammary glands of the caudal teat pair. This interpretation is supported by a lower rate of body mass gain and a lower proportional suckling time of the piglet at the main teat at its biological mother.

Another explanation for a preference of specific teats is a potential thermoregulatory benefit associated with the position of the suckling piglet. Fernández-Llario and Mateos-Quesada (2005) view the preference for teat pairs 3–4 in wild boar as a result of seeking a thermoregulatory advantageous place between the hind legs providing extensive contact to the nursing female's bare skin. Indeed, avoiding heat loss seems to be of particular importance in wild boar as piglets are known to be vulnerable to low ambient temperatures (Briedermann, 2009). Further, both wild boar and domestic piglets have been reported to huddle extensively (Gundlach, 1967), which facilitates the reduction of heat loss (Gilbert, McCafferty, Giroud, Ancel, & Blanc, 2012; Sukhchuluun, Zhang, Chi, & Wang, 2018). This is supported by our observations that the piglets were mostly lying closely together in one farrowing box while sleeping, especially when ambient temperatures were below 0°C (anecdotal observation

by LA). Similar thermoregulatory benefits may exist at the middle teat pairs, because laying in-between two litter mates provides close contact to warm bodies at both body sides.

Milk yield and quality as well as different thermal conditions lead to potential energetic consequences of the position of a main teat, and the two explanations are not mutually exclusive. In fact, our results suggest a combination of factors: the caudal teat pair might be avoided by piglets due to a lower sensitivity to stimulation (Algers & Jensen, 1991; Fraser, 1980) or accessibility of these glands as indicated by the increased tendency of allosuckling and the decreased body mass gain of the single piglet with a caudal teat as main teat. In contrast, the first teat pair, which is also less likely to be the location of a main teat, is used as frequent as teat pairs 2–4, and three piglets that had their main teat at teat pair one did not show an increased proportion of allosuckling. Although we can only speculate, this might indicate that sensitivity of the most cranial glands is comparable to those at teat pairs 2–4 and suggests that this position is less preferred because of thermoregulatory disadvantages. The fact that such an avoidance of the most cranial teat pair is not evident in domestic pigs (Algers, 1993; Fraser & Jones, 1975; Gill & Thomson, 1956; Jeppesen, 1982), which might result from the highly regulated thermal conditions within commercial pig breeding facilities.

Although our data suggest that mothers try to limit the number of allosuckling piglets, as suckling bout duration decreased with the number of allosuckling piglets, we found a surprisingly high occurrence of allonursing in the present study. The occurrence of this phenomenon for wild boar was so far only described anecdotally (Meynhardt, 1990). As lactation is one of the costliest aspects of maternal care (Clutton-Brock, Albon, & Guinness, 1989), it seems crucial that transfer of milk is restricted to own progeny. However, wild boar sounders are typically composed of closely related females (Meynhardt, 1990; Podgórski, Lusseau, Scandura, Sönnichsen, & Jędrzejewska, 2014), suggesting that allonursing could have evolved because of indirect fitness benefits gained through improved reproductive success of close kin (Packer et al., 1992). Highly synchronous farrowing of wild boar females within social groups (this study, Canu et al., 2015), a prerequisite for extensive allonursing, supports this view. However, it has to be noted that allonursing of alien offspring in the wild will likely occur at a later stage than found in this study, as most anecdotal observations report that wild boars separate from the group when giving birth (Martys, 1982; Meynhardt, 1990). From the recipients' point of view, receiving surplus milk from allomothers should always be beneficial. Nevertheless, it has been reported that frequent allosuckling correlates with lower body mass gain and decreased growth rates in red deer (Bartoš, Vankova, Hyaneek, & Šiler, 2001), river buffalo (Paranhos da Costa, Andriolo, Simplício de Oliveira, & Schmidek, 2000) and also pig (Olsen, Dybkjær, & Vestergaard, 1998). However, it seems that in these cases offspring tried to get milk from alien mothers but were unable to fully compensate insufficient provision by the biological mother. In contrast, full compensation is possible in domestic piglets, as shown by Illmann, Pokorná, and Spinka (2007). These authors found no relation

between the degree of allosuckling and body mass gain. In line with this, we also could not identify such an effect in wild boar piglets.

5 | CONCLUSION

Two features underline the importance of living in social groups for reproduction in wild boar: synchrony of oestrus and delivery, and allonursing. In this study, we observed both features to occur in wild boars and our study is the first to describe allonursing quantitatively for this species. The surprisingly fast development of a rigid teat order after birth among littermates suggests strong fitness benefits of this phenomenon that may ultimately explain the evolution and maintenance of this trait.

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CONFLICT OF INTEREST

The authors declare no conflict of interests.

AUTHOR CONTRIBUTIONS

JN, SGV and LA conceived and designed the study; MH and JN trained the animals; LA collected data with help of MH, JN, SGV; LA analysed the data; SGV conducted the statistical analyses; LA, JN and SGV wrote the first version of the manuscript; all authors have seen and commented on the manuscript; JN, SGV and JT supervised the project.

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