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### **Applied Animal Behaviour Science**

journal homepage: www.elsevier.com/locate/applanim



## Piglets call for maternal attention: Vocal behaviour in *Sus scrofa* domesticus is modulated by mother's proximity



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#### ARTICLE INFO

# Article history: Received 21 April 2015 Received in revised form 6 July 2015 Accepted 10 August 2015 Available online 22 August 2015

Keywords:
Behavioural development
Filial attachment
Vocalization
Social bond
Weaning
Domestic pig

#### ABSTRACT

Plasticity in the production of "separation distress" vocalizations, and seeking of caregivers beyond mere satisfaction of immediate physiological needs, are manifestations of attachment that we investigated in the domestic pig ( $Sus\ scrofa\ domesticus$ ). Female piglets from eight litters were either weaned (N=8) in pairs or stayed with their mother and remaining littermates (unweaned, N=8). After 48 h, they were placed individually in a test pen for 5 min in isolation (ISO) followed by 5 min in fence-line contact with their mother (Restricted Reunion, RR). The sows spent comparable time close to their weaned and unweaned piglets during the RR sessions, and gave a comparable number of vocalizations in their presence. Although unweaned piglets uttered more vocalizations overall than their weaned littermates (P=0.008), both weaned and unweaned piglets vocalized at a higher rate during the RR than the ISO session (P<0.02). Furthermore, during the RR session, the piglets in both groups gave more vocalizations when their mother was in close proximity than further away (P=0.04). In the ISO session, piglets uttered only grunt vocalizations whereas, during the RR session, they uttered both grunts and screams, with the ratio of screams to grunts increasing when their mother moved further away from them than when she was nearby (P=0.004). Thus, piglets modulated their vocalizations as a function of their mother's proximity, and psychological attachment persisted beyond weaning.

Published by Elsevier B.V.

#### 1. Introduction

According to attachment theory (Bowlby, 1969), attachment is evident in efforts by mammalian offspring to maintain, seek, and restore proximity and contact with their mother using physical approach behaviour and vocal signalling to which she responds.

Abbreviations: PND, postnatal day; ISO, isolation; RR, restricted reunion; UN, unweaned; WE, weaned.

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When offspring are separated from their mother, their level of vocalization varies according to their physical condition, suggesting that it provides an honest signal of their neediness for maternal care (Weary et al., 1997). Vocal "begging" (MacLean, 1985) plays a crucial role in infant survival when it is effective in attracting the attention of the mother and eliciting a prompt caregiving response (Grodzinski and Lotem, 2007; Illmann et al., 2008; Weary et al., 1996). It has been argued that this vocal behaviour represents a basic emotional response to separation, regulated by a neural "separation-distress system" (Panksepp et al., 1997) that indicates the infant's level of distress (Furlow, 1997). There is interest, therefore, in the use of these "separation distress" vocalizations in animal welfare assessment.

Whereas weaning in nature is typically a gradual process, domestic mammals are usually weaned abruptly through separation from their mother at an earlier age than would occur naturally (Newberry and Swanson, 2008). Humans then provision the young with nutritionally complete food and protect them from predators and weather extremes, enabling them to survive and grow in the

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absence of their mother. However, an attachment bond between mother and offspring implies more than the mere immediate satisfaction of the offspring's physiological need for nutrients, warmth, and safety but also involves an affiliative emotional relationship that survives temporary separations (Ainsworth, 1989). We can infer, therefore, that the strength of attachment bonding at weaning determines the extent to which separation at weaning impacts the psychological well-being of mother and young, as reflected by the amount of vocal "protest" exhibited by each party when they are separated. At weaning, the strength of offspring attachment to the mother, and the strength of maternal bonding to offspring, may not be symmetrical, with variation expected due to factors such as age, body condition, litter size, social organization, and degree of precociality (Newberry and Swanson, 2008).

The expression of attachment-related affect through "separation distress" vocalizations may also be modulated by the perceived availability of caregivers. Infant rhesus monkeys gave more vocalizations when their mother was present but inaccessible than when they were totally isolated (Levine et al., 1985). Similarly, degu (Octodon degus) offspring vocalized more when separated from the family group by a wire mesh than when in complete isolation from the family group (Colonnello et al., 2011). This ability to modulate vocal signalling may represent an evolutionarily conserved adaptation. Under natural conditions, it would presumably be adaptive for needy offspring to escalate vocal signalling when a caregiver is detected and limit vocalizations at times when caregivers are absent, considering that calling could also attract the attention of unwanted eavesdroppers (e.g., predators).

The domestic pig (Sus scrofa domesticus) is unusual among ungulates because it is a litter-bearing species producing precocial young that hide in communal nests (Newberry and Wood-Gush, 1985). Pigs have a rich vocal repertoire (Newberry and Wood-Gush, 1986; Schön et al., 1999), and the mother and offspring are highly vocal during early interactions such as suckling bouts and abrupt separations (Algers, 1993; Illmann et al., 2002). Piglets have a well-developed perceptual system at birth that allows them to discriminate between auditory, olfactory, visual and tactile stimuli (Parfet and Gonyou, 1991). They exhibit context-dependent plasticity in vocalization, calling more when in greater need of food (Weary and Fraser, 1995) and warmth (Weary et al., 1997), screaming when perceiving an imminent threat (Illmann et al., 2013), and modifying their vocal behaviour across isolation and reunion episodes (Colonnello et al., 2010). Moreover, they learn to recognize their mother's voice (Horrell and Hodgson, 1992) such that, during synchronized nursing bouts, they respond to the nursing calls of their own mother and run directly towards her rather than to other sows (Newberry and Wood-Gush, 1985). On the other hand, sows are not always responsive to piglet vocalizations, and do not appear to develop preferential bonds towards some piglets over others within a litter prior to weaning (Newberry and Wood-Gush, 1986). The domestic pig is, therefore, an interesting species in which to evaluate vocalizations as an indicator of the psychological impact of mother-young separation.

In the present study, we used "separation distress" vocalizations to assess attachment bonds between sows and piglets around the time of weaning. We investigated whether (i) piglets modulate the number and type of vocalizations uttered according to the proximity and accessibility of their mother, and (ii) piglet vocal responses to an inaccessible mother are influenced by two days of separation from their mother at weaning. We compared the responses of unweaned piglets still housed with their mother with those of same-aged littermates already weaned from their mother. The vocal responses of the two groups were observed during brief episodes of full and partial isolation (i.e., in proximity to a visible but inaccessible mother). We predicted that piglets would utter more

vocalizations in the presence of an inaccessible mother than when completely isolated, and that attachment would persist beyond weaning.

#### 2. Methods

#### 2.1. Subjects, housing, and husbandry

We used crossbred domestic piglets (genetic background: Large White sows and boars from Landrace, Yorkshire, Duroc and Hampshire lineages) born and housed at the Washington State University Swine Center, a facility accredited by the Association for Assessment and Accreditation of Laboratory Animal Care International. Sows were fed a standard lactation diet twice daily and provided with water ad libitum. Average litter size was 11 piglets (8-14 piglets). Sows were housed with their litters in 2.1 m  $long \times 1.8$  m wide pens. Room temperature was  $17 \pm 1$  °C, and a heat lamp in each pen provided supplementary heat. In accordance with standard practices in the USA, piglets were weighed at birth, tooth clipped, tail docked, ear notched, and vaccinated against atrophic rhinitis on postnatal day (PND) 2. Litters born within a 7-day farrowing window were weaned on the same day, at an average of PND 21. Piglets were familiarized with the weaning diet (a highly palatable starter diet) from PND 14. After weaning, piglets were housed in another room in nursery pens  $(1.5 \text{ m} \times 2.4 \text{ m})$  containing a heat lamp and enrichment objects, and provided with the starter diet and water ad libitum. In both rooms, fluorescent lighting was provided for 11 h daily (lights on at 05:30 h). The study was conducted in accordance with American guidelines for the care and use of agricultural animals in research and teaching (FASS, 2010), and approved by the Washington State University Institutional Animal Care and Use Committee.

#### 2.2. Experimental design and procedures

Two healthy female average-weight piglets from each of eight independent litters were selected and one was randomly assigned to the unweaned condition (UN, N = 8) while the other was assigned to the weaned condition (WE, N=8). This method ensured a comparable initial body weight distribution across conditions. Piglets in the UN group remained with their mother and littermates in their natal farrowing pen until weaning on PND 21, while WE piglets were weaned on PND 18 and housed with a sex-matched littermate in a nursery pen in a separate room (out of auditory contact with their mother). After 48 h (PND 20), the vocal responses of piglets from both groups were recorded during a two-session test: (1) isolation (ISO), and (2) restricted reunion (RR). During the ISO session, piglets were placed individually in a  $50 \, \text{cm} \times 50 \, \text{cm}$  pen, located in an empty room and adjacent to the centre of an empty 5 m by 1.5 m alley. The mother sow was then introduced into the alley for the RR session in which the piglet and sow were able to interact through the wire mesh fence between the pen and the alley. The fence allowed visual, auditory and olfactory contact, but not direct tactile contact. Each session lasted 5 min, with a 15-20 s interval between the two sessions. We elected not to include additional treatment groups controlling for session order for three reasons: (1) in our previous research, we consistently observed a decline in vocalization rate between two 7-min isolation sessions interspersed by a 1-min session alone in another empty pen or in full contact with the mother, another sow or littermates (Colonnello et al., 2010); (2) we were limited to using litters born in the first half of the sows' 1-week farrowing window (enabling testing of UN and WE pigs on PND 20, slightly prior to the facility's scheduled weaning date at an average of PND 21 when pigs were weaned into multi-litter groups segregated by sex and weight), and (3) we preferred to avoid

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