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Regulation of Contact with Offspring by Domestic Sows: Temporal Patterns and Individual Variation

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ABSTRACT

We used a sow-controlled housing system to examine temporal and individual variation in the tendency of sows to associate with young. During a 5-week lactation, 22 sows and litters were housed in a pen where the sow could freely leave and re-enter the piglets' area by stepping over a barrier that the piglets could not cross. Despite this option, the sows remained with the piglets almost constantly during the 1st day after birth. Nineteen sows ('leavers') changed to spending most of their time away from the litter at some point in the lactation. The change was rapid, often within a single week, and occurred in week 2, 3, 4 or 5, depending on the individual. The time of rapid increase in time away was not related to characteristics of the sow or litter, including parity, litter size and sex ratio. Three sows ('stayers') did not increase their time away as lactation advanced, and rarely spent more than 15% of their day in the piglet-free area. Nearly all sows showed a clear preference to defecate in the piglet-free area. This study shows 1. that sows voluntarily reduce their contact with the young; 2. that the timing of this reduction varies greatly amongst sows for reasons that may relate to differences in maternal motivation, and 3. that sows do not abandon the litter if the young cannot follow. The clear preference that most sows developed for the piglet-free area reinforces physiological evidence that constant confinement with older litters is aversive for many sows.

Introduction

Animals differ a great deal in the amount of parental care they provide, with variation among taxa, populations, sexes and individuals (Clutton-Brock 1991;

Gowaty 1996). Individual variation in the level of maternal care has been noted for mice (Benus & Røndigs 1996), goats (O'Brien 1984), dogs (Wilsson 1984), cows (Day et al. 1987), peccaries (Babbitt & Packard 1990), and many species of non-human primates (see Fairbanks 1996 for a review). This variation is often described as differences in maternal 'style' which are thought to reflect individual differences in temperament (Altmann 1980; Maestriperi 1993). On the other hand, differences are also predicted by sociobiological and life history arguments concerning the optimal level of parental investment (Trivers 1972, 1974).

In mammals, maternal care is an important component of lifetime reproductive success (Clutton-Brock 1991). Variation in maternal care may have significant effects on the likelihood of the young surviving predation and starvation risks. Mortality in lion cubs has been reported due to maternal neglect (Packer & Pusey 1984). Individual differences in sow behaviour have been related to piglet mortality (Wechsler & Hegglin 1997). At a more extreme level, mothers sometimes attack and kill their offspring, and desertion of young has been reported in fish, birds and mammals (for reviews see Hausfater & Hrdy 1984; Clutton-Brock 1991).

A fundamental aspect of parental care is the spatial proximity of parents and offspring. Close proximity facilitates the provision of parental care (Altmann 1980). Proximity can also have a direct effect on infant mortality. For example, the first peak of mortality in vervet monkeys coincides with a reduction in carrying by the mother (Cheney et al. 1988). Mother-offspring proximity is often used as an indicator of the development of offspring independence. As offspring age increases, parental care decreases, and a gradual increase in the distance between mother and offspring occurs.

The temporal patterns of mother-litter contact have been examined in rats (Grota & Ader 1969; Cramer et al. 1990) and dogs (Malm & Jensen 1997) using multicompartment enclosures. These enclosures usually consist of a common nursing area and two other compartments, one accessible only to the mother, and the other accessible only to the offspring. A similar housing design, driven by animal welfare concerns rather than research interest in maternal behaviour, has been developed recently for swine.

In normal commercial housing, lactating sows are restrained in narrow 'farrowing crates'. A desire to provide animals with more natural environments has led to the development of 'sow-controlled' housing systems which allow the sow to leave her offspring at will, often by stepping over a low barrier (Bøe 1991). Previous studies on sow behaviour in such environments have reported a general decline in the amount of time mothers spend with their young as the litter ages, and large between-sow variability (Bøe 1991, 1993, 1994; Rantzer et al. 1995). In one study, Bøe (1993) reported that some sows abandoned their litters so early that piglets showed slow growth and poor health. This suggests that under certain conditions sows will not provide care if allowed to spend time away from the young, and that behaviour by the young is required to maintain contact between the offspring and the mother in some cases. Only one study has investigated the variation in the tendency of sows to remain with their piglets (Bøe 1994); however, the results are difficult to interpret because the study involved several farms with different management practices. In the present study we provide a quantitative comparison of animals housed in get-away pens vs. more conventional pens, using swine from the same stock and under the same management practices, and attempt to relate the variability in the amount of time sows spend away from their piglets to characteristics of the sow and litter. As part of a larger study on parent-offspring conflict over maternal provisioning (Pajor 1998), sows and litters were observed in a sow-controlled housing system throughout a 5-week lactation. In this paper we investigate temporal and individual variation in the amount of association with their young by sows in such environments.

Methods

Twenty-two sows and their litters from the Centre for Food and Animal Research's minimum disease Yorkshire and Yorkshire × landrace research herd in Ottawa were tested between Apr. 1993 and May 1994. The animals were observed in one of four identical pens that permitted sows to leave their piglets at will. Each pen consisted of a 'nest area' (3.66 × 1.83 m), equipped with a heated piglet area in the back corner which contained two piglet feeders and a drinker, and a 'piglet-free area' (5.33 × 1.83 m). The two areas were separated by a piglet-proof partition. Sows were classified according to the number of previous litters: parities 2-3 ('young') and parities 4-6 ('old'). Each sow was moved into a test pen 1 week before the expected parturition date and was confined to the nest area. The piglet-proof partition was

installed within 24 h after parturition. The partition was mounted on a set of springs so that the sow's body weight depressed the partition temporarily while she crossed to the other part of the pen. A cylindrical roller along the top of the partition prevented the piglets from climbing over. Initially, the partition was set at its lowest height (15 cm), then raised to 23 cm when piglets reached 14 d of age, and to 31 cm when piglets were 21 d of age. The light cycle consisted of 16 h light (06.00-22.00 h) and 8 h dark. Dim light was provided during the dark phase to aid video recording. The first four sows in the study were given a single feeder and drinker located in the nest area. In subsequent tests, an additional feeder and drinker were provided in the piglet-free area for half of the sows to test whether food and water location affected the time sows would stay with their piglets. Sows were fed *ad libitum* at each feeder with a diet that was low in lysine (an essential amino acid) to increase the nutritional stress of lactation (King & Williams 1984) for the study of parent-offspring conflict over milk allocation (Pajor 1998). Piglets were provided with solid food at 14 d of age.

Behavioural records were obtained by video recording on day 0 (parturition), 3, 6, 13, 20, 27 and 34, for a 24-h period starting at 06.00 h. Above each pen a video camera (Burle TC651EA) was positioned to give a view of the entire nest area and some of the piglet-free area. A video recorder (Panasonic AG-6720) recorded images from eight cameras connected through a video switcher (Panasonic WJ-FS10). Behaviour was quantified by scoring the first frame of every minute (1440 frames/24 h). In each frame sows were scored as being either in the nest area or in the piglet-free area. These results were used to calculate the percentage time away from the piglets (i.e. in the piglet-free area) and the frequency of crossing the barrier. Occasionally, staff entered a pen during behavioural recording to clean pens. Such periods (plus the subsequent 10 min) were ignored in the video analysis.

The percentage of time the sow spent away from her piglets and the frequency of crossing were analysed principally by repeated measures analysis of variance using the General Linear Model Procedure of SAS (1990). Arcsine square root transformation was used for percentage data, but untransformed values are given in the tables, figures and text for clarity. Between-litter effects comprised litter size (treated as a linear effect with 1 df), parity class (young vs. old, 1 df) and the number of feeders (1 df), tested against the sow error term (19 df). Within litters and between days, we tested the effect of piglet age (the linear effect with 1 df, and the remaining, non-linear variation with 5 df) and the interaction between piglet age and the number of feeders (5 df); these were tested using the interaction of piglet age and sow as the error term (95 df). Within litters and within days we tested differences between day and night (1 df), and the interaction between day/night and piglet age (5 df) using the residual error. Because of the nested structure of the analysis, type 1 sums of squares were used for all tests. Tests for sphericity were performed on the covariance matrices (SAS 1990). Normality tests on the frequency distribution of percentage time away in each week were performed using the W-test (Shapiro & Wilk 1965) of the univariate procedure of SAS (1990).

Spearman rank correlations were used to test whether the sows' leaving patterns were correlated with features of their litters or other variables. We used the week in which a sow reached 60% time away as a simple measure of how early the sow left the litter. Sows that did not reach 60% time away by week 5 were given a score of 6.

The percentage of sow faeces in the piglet-free area was recorded each morning using a five-point scale reflecting the estimated proportion of the faeces in the piglet-free area: 0 (all faeces in the nest area), 25, 50, 75 or 100 (all faeces in the piglet-free area). Percentages were accumulated for each 3- to 7-d period between video recordings; an average was then calculated for each period and for the lactation as a whole. Detailed postmortem analyses performed by staff veterinarians were used to classify the deaths of all piglets as 1. stillbirths if piglets had not taken a breath; 2. crushing or trauma if there was evidence of

physical injury by the sow, or 3. other, including congenital defects, weakness at birth, starvation and infectious diseases.

Results

Sows crossed the barrier more often during the day than during the night ($p < 0.001$). However, since they spent less time away per visit during the day ($p < 0.001$), there was no difference between light and dark periods in the percentage time spent away from the piglets. Subsequent analyses are based on the entire 24-h period.

Although there was a gradual increase in the mean percentage time sows spent away from their litters as lactation progressed ($p < 0.001$), reaching $74.6 \pm 7.4\%$ time away in the 5th week, individual sows did not follow a trend of gradual increase. Of the 22 sows, 19 (subsequently called 'leavers') increased the amount of time they spent away from the piglets, usually in a sigmoid pattern, as lactation advanced (Fig. 1a). These sows all spent more than 40% of their time away by week 5, and many reached more than 80%. The remaining three sows (subsequently called 'stayers') failed to show this pattern of increase and rarely spent more than 15% of their time away (Fig. 1b).

The rate and time at which sows increased their time away varied greatly. Roughly, the middle 50% of sows started to spend half or more of their time away during the 3rd week of lactation (Fig. 1a). However, some sows reached this criterion by the end of the 1st week and others only at the end of the 5th week or not at all. Thus, there was a spread of at least 4 weeks in the total distribution. The tendency for sows to show a period of rapid increase in time away (varying among individuals) resulted in significant non-normality in the distribution of time away in each week ($p < 0.001$ by the Shapiro-Wilks' W statistic in all weeks; Fig. 2). Initially, the distribution was positively skewed, with most sows remaining largely with the piglets (Fig. 2a). As lactation advanced, the distribution appeared bimodal (Fig. 2c) and then negatively skewed with only a few intermediate sows (Fig. 2e). In all weeks, the three stayer sows were consistently at the low end of the distribution.

For the leaver sows, the increase in percentage time spent away resulted from changes in both the frequency and the duration of visits to the piglet-free area. The frequency of leaving increased rapidly and then remained roughly stable for many sows (Fig. 3a), while the mean duration of visits to the piglet-free area continued to increase over the 5 weeks (Fig. 3b). Sows varied not only in percentage time away but also in the combination of frequency and duration of visits by which they achieved this time away.

In weeks 2-5 of lactation there appeared to be a break in the distribution of percentage time away at 60% (Fig. 2). This provided a convenient criterion for subdividing leaver sows into 'early leavers' (those that spent more than 60% time away by week 3; $n = 12$) and 'late leavers' (those that did not; $n = 7$) for the purpose of further comparisons. Table 1 compares the percentage time away and the mean frequency of crossing for each of these categories as well as stayer sows. Both early leavers and late leavers reached a frequency of about 1 crossing every 2 h at week 2, and this level remained stable over the remainder of the experiment, while stayers crossed less frequently.

The number of feeders had no clear effect on behaviour (G -test = 2.52, ns), and sows with access to feeders in both areas showed no consistent pattern in their use. The three stayers were housed in pens with two feeders but never ate in the piglet-free area except for one sow that consumed 16% of her food from that feeder in week 5. Among leaver sows, there was no significant relationship between the number of feeders and the amount of time spent away. Three early leavers with two feeders never ate in the piglet-free area despite spending most of their time there, whereas another gradually increased her food consumption from the piglet-free area to just under 50% by week 5. Of the four late leavers with two

feeders, one ate exclusively from the feeder in the piglet-free area, one never ate from the piglet-free area feeder, and one gradually increased consumption of food from the feeder in the piglet-free area to 100% by week 4. The fourth sow fairly consistently ate 75% from the feeder in the piglet-free area starting in the 1st week.

Fig. 1: Percentage of time spent away from the piglets over the 5-week lactation, shown for a. five of the 19 'leavers', selected to represent the range of variation among these sows, and b. the three 'stayers' which failed to show the usual increase in time away from the young.

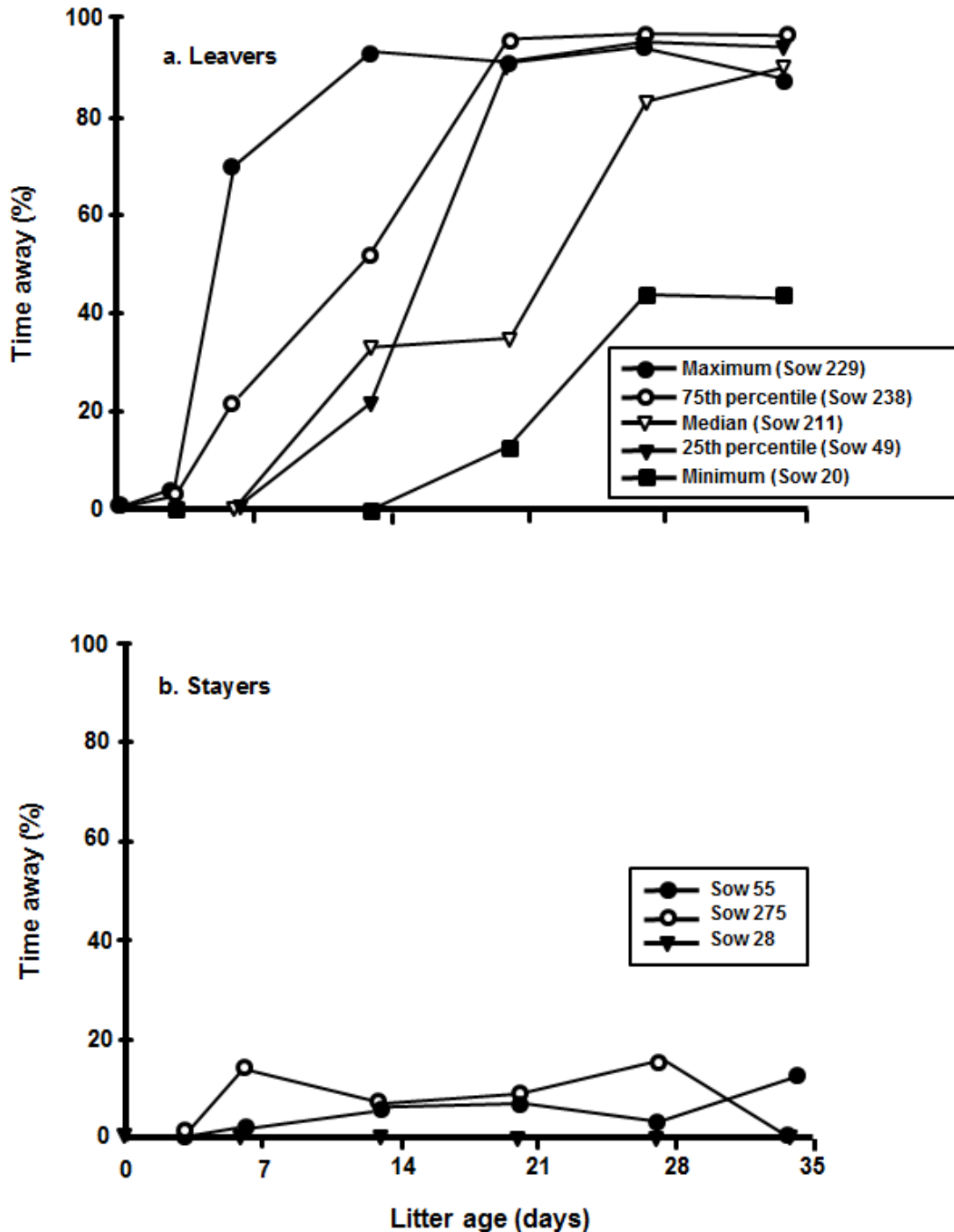


Fig. 3: a. Frequency of crossing into the piglet-free area, and b. mean duration of visits to the piglet-free area over the 5 weeks of lactation, shown for the five 'leaver' sows selected to represent the range of variation in percentage time away (see Fig. 1).

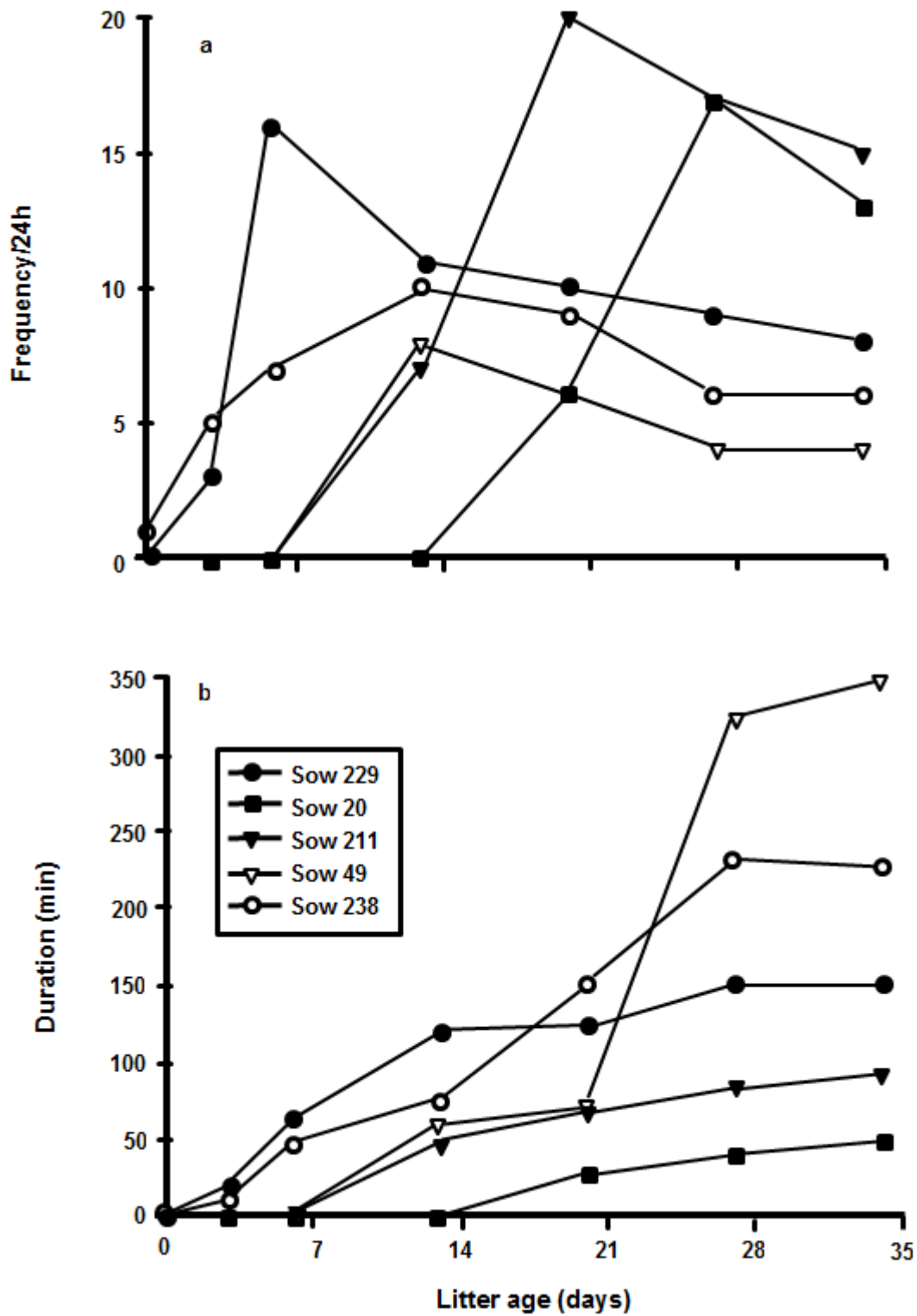


Table 1: Mean (\pm SE) percentage time away and frequency of leaving for the three categories of sows over a 35-d lactation.

Day	% Time away			Frequency of leaving per 24 h		
	early leavers (n = 12)	late leavers (n = 7)	stayers (n = 3)	early leavers (n = 12)	late leavers (n = 7)	stayers (n = 3)
0	0.1 \pm 0.1	0.4 \pm 0.3	0 \pm 0	0.6 \pm 0.4	0.3 \pm 0.2	0 \pm 0
3	4.9 \pm 2.4	2.4 \pm 0.9	0.1 \pm 0.1	4.2 \pm 0.9	4.7 \pm 2.5	0.7 \pm 0.7
6	16.6 \pm 5.8	7.9 \pm 5.0	5.2 \pm 4.6	7.6 \pm 1.6	7.9 \pm 5.2	3.8 \pm 1.9
13	55.9 \pm 6.9	23.6 \pm 6.5	4.2 \pm 2.1	14.7 \pm 1.6	12.5 \pm 4.6	3.7 \pm 2.7
20	88.4 \pm 1.9	30.0 \pm 10.3	5.3 \pm 2.7	17.7 \pm 1.7	8.3 \pm 2.5	3.5 \pm 1.9
27	89.4 \pm 2.1	64.8 \pm 8.7	6.1 \pm 4.8	13.1 \pm 1.4	13.6 \pm 2.0	4.5 \pm 2.4
34	92.3 \pm 1.3	69.4 \pm 11.2	4.1 \pm 4.1	12.5 \pm 1.4	13.5 \pm 2.9	2.5 \pm 2.5

Table 2: Mean (\pm SE) percentage defecation in the piglet-free area for the three categories of sows¹

Days	Early leavers (n = 10)	Late leavers (n = 7)	Stayers (n = 3)
0	19 \pm 7	0 \pm 0	0 \pm 0
1–3	63 \pm 10	3 \pm 13	17 \pm 17
4–6	79 \pm 10	50 \pm 14	52 \pm 29
7–13	96 \pm 2	62 \pm 11	60 \pm 29
14–20	97 \pm 2	68 \pm 11	55 \pm 28
21–27	98 \pm 2	73 \pm 14	67 \pm 33
28–34	91 \pm 4	80 \pm 14	53 \pm 29

¹ Based on 20 sows with complete defecation records .

The week in which sows reached 60% time away was not significantly cor-related with sow parity, sow weight on the day of parturition, or characteristics of the litter such as size or sex ratio (for a complete list of variables examined see Pajor 1998). Restricting the analysis to the 19 leavers did not change this result. Moreover, early leavers, late leavers and stayers did not differ significantly in any of these variables (by analysis of variance and Wilcoxon test).

We also compared offspring survival between early and late leavers. At weaning, the number of piglets, the number of males, the number of females, and the proportion of males did not differ between the early and late leavers. However, the mortality rate among liveborn male piglets was significantly greater in the litters of late leavers compared to early leavers [proportion of males dying ($\bar{x} \pm$ SE): 0.26 \pm 0.08 vs. 0.05 \pm 0.03, Wilcoxon test, $p < 0.05$], apparently because more males were crushed in litters of late leavers than of early leavers (1.00 \pm 0.38 piglets vs. 0.17 \pm 0.11, Wilcoxon test, $p < 0.05$). This did not appear to be directly related to the amount of time sows spent with their piglets because all of the crushings occurred before piglets reached 5 d of age when sows were only spending, at most, 5% of their time away. There were no differences in the average number of stillbirths or deaths due to other causes.

Discussion

In an environment where sows could leave their piglets at will, most sows spent considerable time away from their young while still providing care. The time spent away by most (but not all) individuals followed a sigmoid pattern of increase as the litter aged. The timing of the period of rapid increase in time away varied considerably amongst individual sows.

The mean time that sows spent away from piglets (increasing to over 70% in weeks 4 and 5) is similar to values reported by Bøe (1991; 73% time away by week 5) and Rantzer et al. (1995; 75% time away by week 4). In our study, sows did not differ in the percentage time spent away during the day or night. This differs from the results of Bøe (1991) and Rantzer et al. (1995) who both found that sows spent more time with their piglets at night than during the day throughout lactation. Bøe (1993) found that sows spent more time with their piglets during the night in early lactation (week 2) but by weeks 3 and 4 there was no difference.

A gradual increase in the mean amount of time spent away by mothers has been reported for other species both in multicompartments enclosures (dogs, Malm & Jensen 1997; rats, Grota & Ader 1969; but see Cramer et al. 1990 for non-use of an offspring-free area by rat mothers) and other types of enclosures (guinea pigs, König 1985; cats, Martin 1986). The gradual increase in time away has often led to the conclusion that weaning is a gradual process. However, our results, showing that most sows had a rapid shift from staying mainly with the piglets to spending most of the time away, suggest that weaning by sows commonly involves a relatively sudden decline in the mother's tendency to remain with the young. The seemingly gradual change noted in other species may also be due in part to values being averaged over different animals.

When sows and piglets are kept in large outdoor enclosures, their proximity to each other decreases gradually (Jensen 1988). Sows build and occupy an isolated nest at the time of parturition and spend little time away from the piglets for the first 3 d of lactation (Jensen & Redbo 1987). Sows gradually increase the amount of time away from the nest, and the piglets start to follow for short periods after 7 d (Newberry & Wood-Gush 1988). The sow and young usually abandon the nest around 10 d after parturition (Jensen & Redbo 1987). Thereafter, the sow's contact with the young declines gradually over many weeks, presumably as a result of both sow and piglet behaviour (Jensen 1988).

The sharp rise in time away from the young seen in the present study has not been reported for domestic pigs kept outdoors. This could be because following by the young in outdoor environments compensates for avoidance by the mother (Newberry & Wood-Gush 1988). In our experiment, piglets would often attempt to cross the barrier. Failing this, they would vocalize, especially as the time since the last nursing increased. Piglets often vocalize when separated from their mother (Weary & Fraser 1995) and sows have been shown to respond to these calls (Weary et al. 1996). In addition, features of the piglet-free area itself could be associated with the dramatic increase in time away. Bøe (1993) reported a substantial acceleration in time spent away when an opportunity for social interaction between sows was provided and the distance between the sows' resting area and piglet nest area was increased over that provided in a previous study (Bøe 1991). Alternatively, focusing on means rather than individual sows may have obscured any evidence of a rapid increase in distance between sows and piglets in outdoor studies.

It is difficult to infer, from simple observations, the relative roles of the mother and offspring in maintaining proximity. Subtle maternal cues such as body posture or vocalizations may influence mother-offspring proximity (Ralls et al. 1987; Green 1992). Although maternal avoidance of young has been reported in experimental studies, studies in natural environments often conclude that offspring are responsible for the decrease in proximity to the mother. The willingness of the mother to maintain contact may be affected by her evaluation of offspring condition and worthiness of continued investment (Clarke & Ehlinger 1987; Bateson 1994). Mothers may desert their young if they have little chance of surviving (Carlisle 1982). The present study presents experimental evidence for a strong role of the mother in regulating contact with offspring in pigs and shows that offspring that cannot follow are not necessarily abandoned.

Differences amongst Sows

There are several possible reasons why sows differ in the amount of time they spend away and in the timing of the rapid increase in time away.

First, differences amongst individuals might reflect differences in the level of conflict over milk allocation between parent and offspring (Pajor 1998). For sows in better condition (with smaller litters and presumably a lower cost of lactation) or for sows nearer the end of their reproductive life-span, the cost of remaining with offspring would be less (Clutton-Brock 1984). However, this did not appear to account for our results because the number of weeks to reach 60% time away was not correlated with body weight, litter size or parity. Bøe (1991, 1993, 1994) was also unable to correlate the variation in time away with litter size or parity. In studies on primates, attempts to attribute individual differences in maternal behaviour to factors such as age, parity or social rank have had only limited success (Collinge 1987; Schino et al. 1995).

Secondly, maternal behaviour might be affected by the level of need of either the sow or the litter. Environmental quality, especially food availability, is known to affect maternal behaviour in some species (Berger 1979; Hauser & Fairbanks 1988). In our study, sows had constant access to food but maternal behaviour might still have been affected by individual differences in ability to store nutrients, metabolize body reserves, and/or absorb nutrients from the feed provided. The differences might also relate to offspring size and developmental stage and, hence, their ability to cope (in nature) without the mother or to follow the mother independently. Following such logic, we might expect some correlation between maternal behaviour and maternal weight loss, piglet growth weight, or sow food intake, but no such correlations were found (Pajor 1998). Although piglets were provided with solid food at 14 d of age they consume very little until 21-28 d of age (Pajor et al. 1991), after the differences in leaving patterns have been clearly established.

Thirdly, if some sows found the barrier more difficult to negotiate than others, this might influence the time they spent with their piglets. However, there is little evidence that this was the case. Early and late leavers crossed the barrier a similar number of times; the difference lay in how long they remained away after each crossing. Even two of the three stayers commonly crossed the barrier, presumably to defecate outside the nest area. Moreover, as the barrier height was increased, frequency of crossing did not decline. The one exception was a single stayer sow whose behaviour may have been inhibited by the barrier as she was never observed to cross.

Fourthly, some of the variation between sows could be due to their level of previous experience of raising young without being able to escape. The sows in this study had undergone 1-5 previous lactations, during which they had been confined in standard farrowing crates which prevented them from leaving their litters. If this previous experience had a strong effect then it should have been detected by the parity factor in the analysis, but no relation to parity was found.

Finally, individual variation in maternal behaviour may arise from individual differences in temperament or personality (Fairbanks 1996; Wechsler & Heggin 1997). In rhesus macaques, emotional reactivity has been demonstrated to account for more variation in maternal behaviour than other factors such as parity, rank or litter size (Maestriperi 1993). Consistent individual differences in measures of temperament have been reported for adult pigs (Lawrence et al. 1991). In addition to general differences in temperament, sows may also differ more specifically in tendency to provide maternal care. Price (1984) suggested that the human care of young farm animals may have resulted in relaxed selection for maternal traits; this could result in domestic sows differing widely in their degree of care for their young. Alternatively, differences in maternal behaviour could be a product of natural selection. Female wild boars can have

either one or two litters per year (Mauget 1981). The difference may be related to food availability and quality, but differences in maternal motivation could also be involved. Mothers that spend more time away from the young may nurse less frequently, and hence may return to oestrus sooner or in better condition, than mothers that stay with their young and nurse frequently (Pajor 1998). This could lead to selection for relatively low levels of maternal care. However there could also be selective pressure for prolonged care if, for example, it led to decreased mortality due to factors such as predation. If this explanation applies, then we would expect sows to be reasonably consistent in the level of care they provide to successive litters.

Animal Welfare Implications

The results have important implications for animal welfare and housing. Physiological and behavioural measures suggest that forced confinement with the litter may be distressing for the sow (de Passillé & Robert 1989; Cronin et al. 1991; Pajor 1998). Sow-controlled housing allows sows to demonstrate their obvious preference for controlling the level of contact with piglets and may therefore reduce any stress caused by the constant confinement of the sow with the litter. Sow-controlled housing may also lead to reduced post-separation stress (Pajor et al., in press), because sows and piglets that have spent significant amounts of time away from each other maybe less disturbed by the sudden and permanent separation typical of commercial swine production.

Defecation away from the nest has been observed for pigs in semi-natural environments (Stolba & Wood-Gush 1989). Stangel & Jensen (1991) reported that, while in nests, sows clean piglets regularly and consume contaminated nest material. Such behaviour may prevent nest detection by predators as well as maintain hygiene. Conventional farrowing crates do not allow a separate area for defecation. In our experiment, like that of Bøe (1991), nearly all sows demonstrated a strong preference for defecating away from the nest, including those animals (stayers) that spent very little time away from the piglets. The lack of previous experience in this system did not prevent sows from rapidly forming the habit of dunging outside the nest. These results suggest that the inability to urinate and defecate away from their lying area maybe an additional stress associated with confinement.

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Literature Cited

- Altmann, J. 1980: Baboon Mothers and Infants. Harvard Univ. Press, Cambridge.
- Babbitt, K. J. & Packard, J. M. 1990: Suckling behavior of the collared peccary (*Tayassu tajacu*). Ethology 86, 102-115.
- Bateson, P. 1994: The dynamics of parent offspring relationships in mammals. Trends Ecol. Evol. 9, 399-403.
- Benus, R. F. & Rondigs, M. 1996: Patterns of maternal effort in mouse lines bidirectionally selected for aggression. Anim. Behav. 51, 67-75.

- Berger, J. 1979: Weaning conflict in desert and mountain bighorn sheep (*Ovis canadensis*): an ecological interpretation. *Z. Tierpsychol.* 50, 188-200.
- Bøe, K. 1991: The process of weaning in pigs: when the sow decides. *Appl. Anim. Behav. Sci.* 30, 47-59.
- Bøe, K. 1993: Maternal behaviour of lactating sows in a loose-housing system. *Appl. Anim. Behav. Sci.* 35, 327-338.
- Bøe, K. 1994: Variation in maternal behaviour and production of sows in integrated loose housing systems in Norway. *Appl. Anim. Behav. Sci.* 41, 53-62.
- Carlisle, T. R. 1982: Brood success in variable environments: implications for parental care allocation. *Anim. Behav.* 30, 824-836.
- Cheney, D. L., Seyfarth, R. M., Andelman, S. J. & Lee, P. C. 1988: Reproductive success in vervet monkeys. In: *Reproductive Success* (Clutton-Brock, T. H., ed.). Univ. of Chicago Press, Chicago. pp. 384-402.
- Clarke, A. S. & Ehlinger, T. J. 1987: Pattern and adaptation in individual behavioral differences. In: *Perspectives in Ethology*, Vol. 7 (Bateson, P. P. G. & Klopfer, P.H., eds). Plenum, New York. pp. 1-47.
- Clutton-Brock, T. H. 1984: Reproductive effort and terminal investment in iteroparous animals. *Am. Nat.* 123, 212-229.
- Clutton-Brock, T. H. 1991: *The Evolution of Parental Care*. Princeton Univ. Press, Princeton.
- Collinge, N. E. 1987: Weaning variability in semi-free-ranging Japanese macaques (*Macaca fuscata*). *Folia Primatol.* 48, 137-150.
- Cramer, C. P., Thiels, E. & Alberts, J. R. 1990: Weaning in rats: I. Maternal behaviour. *Develop. Psychobiol.* 23, 479-493.
- Cronin, G. M., Barnett, J. L., Hodge, F. M., Smith, J. A. & McCallum, T. H. 1991: The welfare of pigs in two farrowing/lactation environments: cortisol responses of sows: *Appl. Anim. Behav. Sci.* 32, 117-127.
- Day, M. L., Imakawa, K., Clutter, A. C., Wolf, P. L., Zalesky, D. D., Nielson, M. K. & Kinder, J. E. 1987: Suckling behavior of calves with dams varying in milk production. *J. Anim. Sci.* 65, 1207-1212.
- Fairbanks; L.A. 1996: Individual differences in maternal style. *Adv. Stud. Behav.* 25, 579-611.
- Gowaty, P. A. 1996: Field studies of parental care in birds: new data focus questions on variation among females. *Adv. Stud. Behav.* 25, 477-351.
- Green, W. C. 1992: The development of independence in bison: pre-weaning spatial relations between mothers and calves. *Anim. Behav.* 43, 759-773.
- Grata, L. J. & Ader, R. 1969: Continuous recording of maternal behaviour in *Rattus norvegicus*. *Anim. Behav.* 17, 722-729.
- Hauser, M. D. & Fairbanks, L. A. 1988: Mother-offspring conflict in vervet monkeys: variation in response to ecological conditions. *Anim. Behav.* 36, 802-813.

Hausfater, G. & Hrdy, S. B. 1984: Infanticide: Comparative and Evolutionary Perspectives. De Gruyter Aldine, New York.

Jensen, P. 1988: Maternal behaviour and mother-young interactions during lactation in free-ranging domestic pigs. *Appl. Anim. Behav. Sci.* 20, 297-308.

Jensen, P. & Redbo, I. 1987: Behaviour during nest leaving in free-ranging domestic pigs. *Appl. Anim. Behav. Sci.* 18, 355-362.

King, R. H. & Williams, I. H. 1984: The effect of nutrition on the reproductive performance of first litter sows. 2. Protein and energy intakes during lactation. *Anim. Prod.* 38, 249-256.

König, B. 1985: Maternal activity budget during lactation in two species of *Cavidae* (*Cavia porcellus* and *Galea musteloides*). *Z. Tierpsychol.* 68, 215-230.

Lawrence, A. B., Terlouw, E. M. C. & Illius, A. W. 1991: Individual differences in behavioural responses of pigs exposed to non-social and social challenges. *Appl. Anim. Behav. Sci.* 30, 73-86.

Maestriperi, D. 1993: Maternal anxiety in rhesus macaques (*Macaca mulatta*) II. Emotional bases of individual differences in mothering style. *Ethology* 95, 32---42.

Malm, K. & Jensen, P. 1997: Weaning and parent-offspring conflict in the domestic dog. *Ethology* 103, 653-664.

Martin, P. 1986: An experimental study of weaning in the domestic cat. *Behaviour* 99, 221-249.

Mauget, R. 1981: Behavioural and reproductive strategies in wild forms of *Sus scrofa* (European wild boar and feral pigs). In: *The Welfare of Pigs* (Sybesma, W., ed.). Martinus Nijhoff Publishers, The Hague. pp. 3-13.

Newberry, R. C. & Wood-Gush, D. G. M. 1988: Development of some behaviour patterns in piglets under semi-natural conditions. *Anim. Prod.* 46, 103-109.

O'Brien, P. H. 1984: Leavers and stayers: maternal post-partum strategies in feral goats. *Appl. Anim. Behav. Sci.* 12, 233-243.

Packer, C. & Pusey, A. E. 1984: Infanticide in carnivores. In: *Infanticide: Comparative and Evolutionary Perspectives* (Hausfater, G. & Hrdy, S. B., eds). De Gruyter Aldine, New York. pp. 31---42.

Pajor, E.A . 1998: Parent-offspring conflict and its implications for maternal housing systems in domestic pigs. PhD Thesis, McGill Univ., Montreal.

Pajor, E. A., Fraser, D. & Kramer, D. L. 1991: Consumption of solid food by suckling pigs: individual variation and relation to weight gain. *Appl. Anim. Behav. Sci.* 32, 139-155.

Pajor, E. A., Weary, D. M., Fraser, D. & Kramer, D. L., in press: Alternative housing for sows and litters: I. Effects of sow-controlled housing on responses to weaning. *Appl. Anim. Behav. Sci.*, in press.

de Passillé, A. M. B. & Robert, S. 1989: Behaviour of lactating sows: influence of stage of lactation and husbandry practices at weaning. *Appl. Anim. Behav. Sci.* 23, 315-329.

Price, E. O. 1984: Behavioural aspects of animal domestication. *Q. Rev. Biol.* 59, 1-32.

- Ralls, K., Lundrigan, B. & Kranz, K. 1987: Mother-young relationships in captive ungulates: spatial and temporal patterns. *Zoo. Biol.* 6, 11-20.
- Rantzer, D., Svendsen, J. & Westrom, B. 1995: Weaning of pigs raised in sow-controlled and in conventional housing system. 2. Behaviour studies and cortisol levels. *Swedish. J. Agric. Res.* 25, 61-71.
- SAS Institute, Inc. 1990: SAS Procedures Guide, Version 6. SAS Institute, Inc., Cary.
- Schino, G., D'Amato, F. R. & Troisi, A. 1995: Mother-infant relationships in Japanese macaques: sources of inter-individual variation. *Anim. Behav.* 49, 151-158.
- Shapiro, S. S. & Wilk, M. B. 1965: An analysis of variance test for normality (complete samples). *Biometrika* 52, 591-611.
- Stangel, G. & Jensen, P. 1991: Behaviour of semi-naturally kept sows and piglets (except suckling) during 10 days post partum. *Appl. Anim. Behav. Sci.* 31, 211-227.
- Stolba, A. & Wood-Gush, D. G. M. 1989: The behaviour of pigs in a semi-natural environment. *Anim. Prod.* 48, 419--425.
- Trivers, R. L. 1972: Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man* (Campbell, B., ed.). Aldine, Chicago. pp. 136-179.
- Trivers, R. L. 1974: Parent-offspring conflict. *Am. Zool.* 14, 249--264.
- Weary, D. M. & Fraser, D. 1995: Calling by domestic piglets: reliable signals of need? *Anim. Behav.* 50, 1047-1055.
- Weary, D. M., Lawson, G. L. & Thompson, B. K. 1996: Stronger sow response to isolation calls associated with greater levels of piglet need. *Anim. Behav.* 52, 1247-1253.
- Wechsler, B. & Hegglin, D. 1997: Individual differences in the behaviour of sows at the nest site and the crushing of piglets. *Appl. Anim. Behav. Sci.* 51, 39-49.
- Wilsson, E. 1984: The social interaction between mother and offspring during weaning in German shepherd dogs: individual differences between mothers and their effects on offspring. *Appl. Anim. Behav. Sci.* 13, 101-112.