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Comparative anatomy, physiology and ecology of pregnancy and lactation in wild pigs: a review

Abstract

The nutritional requirements of animals during pregnancy and lactation differ from the requirements of the growing animal, or the non-pregnant adult, as revealed by studies of the domestic species. However, relatively little information has been published to indicate the comparable requirements for pregnancy and lactation of most animals in the wild. Similarly, there is as yet surprisingly little information available from the study of animals in zoological collections. Analyses of the comparative anatomical and physiological data can contribute to our understanding of the problem. Similarly, behavioural and other data may help to indicate some aspects of the relationship between the pregnant or lactating animal and its environment.

As with many other widespread groups of animals, the nature of the relationships which exist between various Eurasian, African and Southeast Asian wild pig species and their respective environments during pregnancy and lactation has not attracted specific research attention. This review first seeks to gather together what is available, and on the basis of an analysis of this, to establish an investigative framework within which future studies may be undertaken. The anatomical and physiological changes which occur in different parts of the sow during pregnancy and lactation are described for the different species of pig, and the related changes in the behaviour and feeding patterns of the piglets and the sow are reviewed.

Keywords

body weight

1. Introduction

Although there have been a very large number of studies on animal nutrition, much remains to be learned about the nutrition of the pregnant and lactating mammal. Almost all our currently available understanding has been derived from studies of the human and a small group of domesticated mammals.

This review was undertaken to serve as a foundation, and a stimulus of ideas and suggestions which might aid future studies of the nutrition of wild mammals during pregnancy and lactation. The Family of pigs (Suidae) was chosen to enable comparisons to be made with the large data-set of information which has been gathered on the domestic pig. The terminology used in this paper for naming wild pigs is that published in the IUCN status survey and conservation action plan for pigs, peccaries and hippos (Oliver 1993); the one for naming the domestic pig (*Sus domesticus*), although different from the "*Sus scrofa*" more commonly used, is that recommended by Corbett & Clutton-Brock (1984). The five extant genera of wild pigs comprise 14 species which are found distributed over Eurasia, Africa and South-east Asia. There are two domesticated pig species, the one (*Sus domesticus*), with which we are most familiar and which has a world-wide distribution, and the other (*Sus celebensis*), which is found on a few islands of the Indonesian archipelago (Groves 1981).

Much of the nutritional data gathered for this review was very fragmentary, and many of the pieces of information concerning wild pig species were little more than anecdotal comments attached to studies which had a different focus of research attention. It was particularly striking that a number of these fragments lay as small clusters of observations in published and unpublished PhD theses. This is in sharp contrast to the substantial body of information on the domestic pig which has been reviewed regularly. Attention will be drawn to those reviews which have guided the present study. The literature describing and analysing the habitats and diets of wild pigs was surveyed recently by Leus and Macdonald (1997).

The duration of pregnancy varies considerably between the different species of pigs (Table 1). It ranges from about 114 days in a number of the *Sus* species, to about 171 days in the Common warthog (*Phacochoerus africanus*). Pregnancy length appears to be unrelated to either the size of the litter, or the neonatal weight of the piglets. It is relatively long (171 days) where the total litter weight may average less than 3 kg (Common warthog), and relatively short (115 days) where the average litter weight may be either 5 kg or more (Eurasian wild pig *Sus scrofa*), or less than 1 kg (Pigmy hog *Sus salvanius*).

2. The pregnant animal

2.1 Body weight

Pregnancy normally produces an increase in the body weight of the non-gravid female (Table 1). This has been clearly demonstrated in the domestic pig (Elsley et al. 1966; Whittemore 1998), and has been observed in other pig species

Table 1. Scientific name, common name, body weight of non-pregnant female (BWF), oestrus cycle length (OCL), gestation length (GL), numbers of piglets born in litter (NB), average number born (ANB), body weight of the neonatal piglet (BWN), number of functional teats on udder (T) and age at weaning (W) of fourteen species of wild pig, and the domestic pig. Data gathered from publications in the list of references

Scientific name	Common name	BWF (kg)	OCL (d)	GL (d)	NB	ANB	BWN (g)	T	W (d)
Phacochoerus aethiopicus	Desert warthog	?	?	?	?	?	?	?	?
Phacochoerus africanus	Common warthog	~55–70	?	172	1–8	3	~840	4	50–150
Hylochoerus meinertzhageni	Forest hog	~100	?	151	2–4	3	?	4	42–56
Potamochoerus larvatus	Bush pig	~67	?	120	1–7	3.2	~900	6	<120
Potamochoerus porcus	Red river hog	~55	~30	120	1–6	3.4	650–900	6	<120
Babyrousa babyrussa	Babirusa	~40	28–42	158	1–3	1.8	~1000	4	~180
Sus celebensis	Sulawesi warty pig	?	?	?	1–8	5	?	12	?
Sus philippensis	Philippine warty pig	?	?	?	3–8	?	?	?	?
	Visayan warty pig	?	?	140	1–3	1–2	?	6	?
Sus *barbatus*	Bearded pig	~42	?	90–120	3–12	7	~550	12	?
Sus verrucosus	Javan warty pig	~44	?	?			?	12	?
Sus bucculentus	Vietnam warty pig	?	?	?	?	?	?	?	?
Sus salvanius	Pigmy hog	~6.5	21	110–120	1–7	4.7	~180	6	?
Sus scrofa	Eurasian wild pig	43–140	21–23	115	1–13	5.3	~900	8–12	90–120
Sus domesticus	Domestic pig	60–350	21	114	1–20	12	~1300	8–18	21–84

also. Pregnant Common warthogs less than three years of age were found to be heavier than similarly aged non-pregnant females, although older females did not show this increase in weight with pregnancy (Mason 1982). In a recent study of Bushpigs (*Potamochoerus larvatus*), the average body mass of pregnant adult females (71 kg) was greater than that (67 kg) in a comparable group of non-pregnant females (Seydack 1990). Two additional observations have been made, on the Babirusa (*Babyrousa babyrussa*). The body weight of a growing female increased from 35 kg at mating to 40 kg after 1 month, 42 kg after 2 months, 44 kg after 3 months, and 45 kg after 4 months; an older, multiparous Babirusa was similarly measured, and increased in body weight from 52 kg at about the time of conception to 60 kg some 130 days later (Leus, pers. comm). Although commercial sows frequently increase in weight by 50 kg during pregnancy, recent reviews suggest that increases in sow weight from one conception to the next should be from about 35 kg during the first pregnancy, to about 12 kg in the fourth pregnancy (Whittemore 1998).

The increase in body weight of the pregnant female is due in part to the growth of the uterus and placenta, the development of the fetuses, the increased volumes of fetal amniotic and allantoic fluids surrounding them, and latterly to the increase in weight of the mammary glands. However, the bulk of the increase in maternal body weight of the domestic pig is due to the growth in mass of her own muscle tissues and fat deposits (Elsley et al. 1966). The reason for the heavier weight increases seen in younger animals is that they are usually still growing, and part of the larger increase in their body weight during pregnancy reflects that growth. The pregnant Bushpig also has greatly enlarged stores of subcutaneous fat, as does the Eurasian wild pig, the domestic sow, and perhaps also the Bearded pig (*Sus barbatus*) (Seydack 1990, Briedermann 1990, Caldecott 1991, Whittemore 1998). Pregnant Bushpig also had more peritoneal fat relative to body mass than non-pregnant females and had bone marrow fat deposits which were larger in size than non-pregnant female Bushpigs (Seydack 1990). Importantly, there is also a retention of electrolytes during pregnancy with an accompanying expansion of body water. Maternal blood plasma volume increases during pregnancy as does total red cell volume. An increase in tissue hydration, and in the amounts of extracellular fluid is a feature of pregnancy and can persist into lactation (Lodge et al. 1979, Shields & Mahan 1983). These changes in body water and electrolytes are of central importance to the physiology of pregnancy (Stock & Metcalfe 1994).

There are also changes in the shape of the female as pregnancy nears term. The abdominal cavity expands in volume to accommodate the products of conception, and this is particularly noticeable in those species which carry larger litters.

2.2 Uterus and placenta

Information on the non-pregnant reproductive tract has been summarised for the Common warthog, the Forest hog (*Hylochoerus meinertzhageni*), the Babirusa, the Sulawesi warty pig, the Pigmy hog, the Eurasian wild pig and the domestic pig by Macdonald et al. (1984). The length of the uterine horn is relatively small in the Common warthog, and is particularly so in the Babirusa, which was consistent with the relatively small average litter sizes they carry (see Table 1). The size of the Pigmy hog uterus, although small in absolute terms (Figure 1), is still sufficiently long to accommodate up to seven fetuses (Table 1).

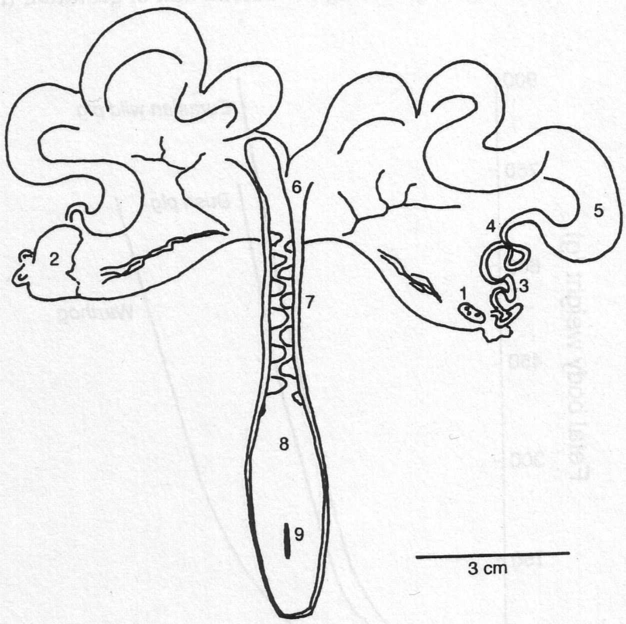

Fig. 1. Schematic diagram of the non-pregnant female reproductive tract of the Pigmy hog (*Sus salvanius*) (after Macdonald et al, 1984).
1: Right ovary; 2: infundibulum; 3: uterine tube; 4: utero-tubal junction; 5: right uterine horn; 6: uterine body; 7: cervix; 8: vagina; 9: urethral opening into the vestibule of the vagina.

The uterus of the domestic pig grows in weight progressively through pregnancy (Pomeroy 1960).

The gravid uterus of the near term Warthog female may comprise over 7 % of the female's body weight (Mason 1982).

2.3 Fetal development

The growth in weight of the embryo is small at the start of pregnancy, but fetal weight increases rapidly during the second half of gestation. Data for the fetal period of development are available for Common warthog, Bushpig, Eurasian wild pig and the domestic pig (Ullrey et al. 1965, Child et al. 1968, Gjesdal 1972, Stubbe and Stubbe 1977, Aumaitre et al. 1982, Mason 1982, Seydack 1990). Summarising the information from the three wild pig species, and plotting the results together reveals a similarity in the general pattern of growth, and particularly in the rates of growth during the second half of gestation (Figure 2).

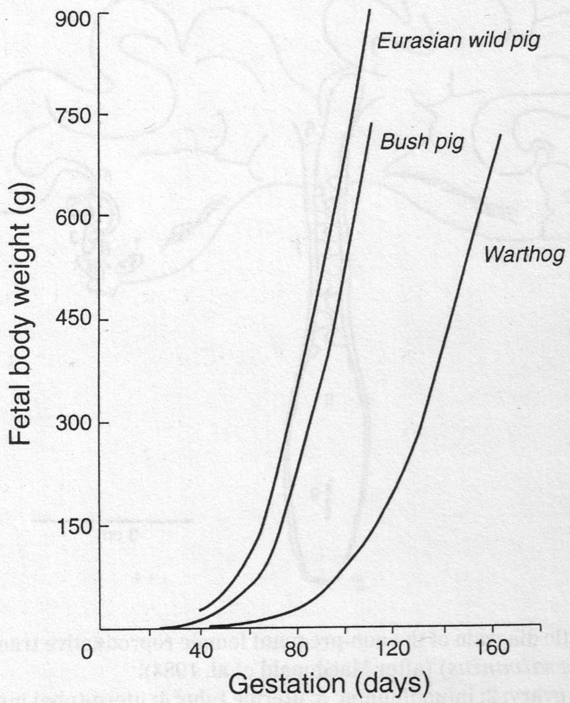

Fig. 2. The growth of the fetuses of the Eurasian wild pig (*Sus scrofa*), Common warthog (*Phacochoerus africanus*) and Bushpig (*Potamochoerus larvatus*) (redrawn after Aumaitre et al, 1982, Mason, 1982 and Seydack, 1990).

Strikingly, the similarities in the fetal growth during the first half of gestation, shown by the Bushpig and the Eurasian wild pig (and the domestic pig, although not shown in the figure) are in contrast to the slow or delayed growth in the embryos of the Common warthog. These graphs raise a number of questions, among which, what causes the Warthog embryo to be so slow to start growth? Does the Babirusa fetus, and perhaps those of the Forest hog and Visayan warty pig, also have a slow start to embryonic development?

The available data on the range in sizes of piglets born, the average litter size and the average neonatal weight of the different species of pig are listed in Table 1. It is important to note from the table that among individuals of a single species there may be considerable variation in the size of the litter. There is also considerable variation in the weight of the piglets at birth. Studies in the domestic pig indicate that body weights of fetuses and neonates may differ by as much as 100 % (Gjesdal 1972), and similar variation has been reported for Bushpig (Seydack 1990) and Warthog (Child et al. 1968).

2.4 Blood volume

The total blood volume of the domestic sow increases from about 11 litres at about the time of conception to 14 litres twelve hours after parturition, with most of this 28 % increase occurring between days 77 and 98 of pregnancy (Matte and Girard 1996). In another study, the blood volume per kilogram of sow's body weight decreased from conception (63 ml/kg) until about mid pregnancy (55.1 ml/kg), after which it increased to 62.3 ml/kg just prior to birth (Anderson et al. 1970). The total circulating haemoglobin rose from 1 kg at the start of pregnancy to 1.5 kg on the 110th day. In 9 older sows, the increase in total blood volume averaged 2.6 litres during an average gain in pregnant body weight of 22 kg.

The distribution of this increased volume of blood has not yet been studied in any pig species, and is incompletely studied in other species. The enlarged veins of the pig uterus seen at caesarean section are an indication of increased venous distensability. The additional heat loss required by the sow with actively growing products of conception is probably accomplished by a high rate of blood flow to the maternal skin. Cardiac output increases during pregnancy along with increased pulmonary blood flow, and an increased maternal consumption of oxygen is to be expected (Stock & Metcalfe 1994).

The blood volume of the fetal domestic pig averaged 100 + 5 ml/kg of fetal body plus placental weight during the last two weeks of pregnancy (Macdonald et al. 1986). No data on the blood volume of other species of pig were found.

2.5 Digestive system

The general anatomy of the digestive tracts of the domestic pig, Eurasian wild pig, Pigmy hog, Common wart hog, Bushpig and Babirusa have been studied (for references see Macdonald 1991). The structure of the stomach is largely the same although the cardiac gland region of the Babirusa stomach is enlarged relative to those of the other species and it has a much enlarged diverticulum (Leus et al. 1999). The structure of the intestinal tract in largely the same in each of these pigs.

There is almost no information on the direct effects of pregnancy and lactation on the biology of the digestive system of the pig. Studies on the domestic pig showed that pregnancy had no effect on the weights of the different components of the gastrointestinal tract (Pelletier et al. 1987). However, one recent study demonstrated that if the pregnant sow had access to a diet with a high energy content the weight of the digestive tract tended to be heavier at the end of gestation (Dourmad et al. 1996). The weight of the liver was not affected by the energy content of the diet. No specific studies of a directly comparable mature have been carried out on the other species of pigs. However, it may be worth noting that the weight of the abdominal contents (internal offal) of the pregnant female Warthog was heavier than that of the non-pregnant female (Mason 1982). In the rat, hypertrophy of all layers of the mucosa of the small intestine has been noted in late pregnancy and during lactation (Stock & Metcalfe 1994). This may lead to an increase in the total absorptive capacity of the intestine during pregnancy and lactation of this species. There is as yet no comparable histological information available to provide confirmation of this observation for any of the pig species.

3. The lactating animal

3.1 Mammary gland

The maximum haemodynamic load associated with gestation occurs shortly before delivery, when uterine blood flow is at its highest and mammary blood flow is rising in anticipation of lactation. The maternal haemodynamic commitment to reproduction does not end with the delivery of the young, but continues during lactation (Stock & Metcalfe 1994). Lactation involves an augmented blood flow to the digestive tract, including the liver, presumably related to increased food consumption and protein production. The number of functioning teats are shown in Table 1.

The mammary gland of the domestic pig has been described by Turner (1952). The mammary gland of the Babirusa near the end of gestation is illustrated in Figure 3. Most sows of the latter species have four glands, one pair inguinally located and the other pair on the abdomen, but an additional pair has sometimes been reported slightly cranial to the others (Leus et al. 1992). There is a pronounced increase in the volume of the Babirusa mammary glands one day before birth. The mammary gland of the Bushpig comprises three pairs of glands, although their location has not been defined (Seydack 1990). The udder of the non-lactating Warthog comprises two pairs of mammary glands which are small and flat, the caudal pair located in the inguinal region and the cranial pair in the abdominal region just behind the umbilicus (Owen 1851, Clough 1969). From about 20 days before birth there is a clear increase in their size (Figure 3), and small amounts of viscous secretion can be expressed from the teats at this time (Mason 1982). The weights of lactating mammary gland tissue from eleven Warthogs were found to lie between 300 g and 960 g (Mason 1982). Involution of the udder tissue follows weaning.

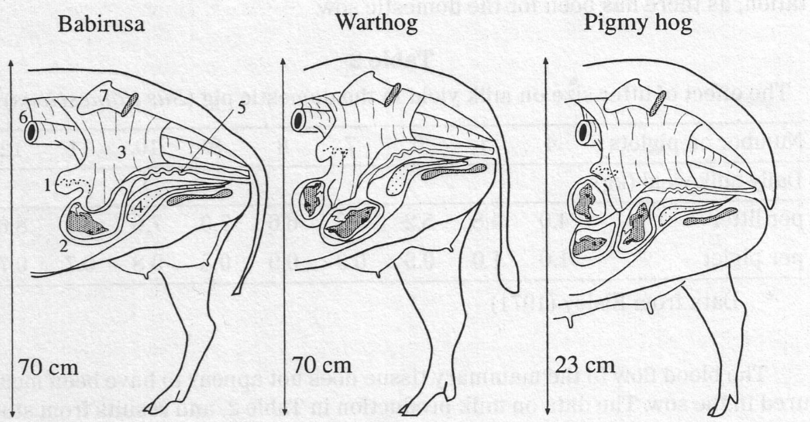

Fig. 3. The relative positions of the reproductive organs and mammary glands of the pregnant Babirusa (*Babyrousa babyrussa*), Common warthog (*Phacochoerus africanus*), and Pygmy hog (*Sus salvanius*); two of the three pairs of abdominal mammary glands of the Pigmy hog are illustrated. The intestines have largely been removed for clarity.
1: ovary; 2: pregnant uterine horn; 3: broad ligament of the uterus; 4: bladder; 5: cervix; 6: descending colon: 7: cut section of the pelvis.

The Pigmy hog is reported by Garson (1883) to have three pairs of abdominal mammary glands (two of which are shown in Figure 3). The teats of the cranial pair are smaller than the other two pairs, and were observed to swell gradually about 7 to 3 weeks before birth (Narayan et al. 1997). About four weeks before birth there is also a change in the structure of the mammary gland of the Eurasian wild pig (Martys 1982). The teats grow longer and the udder becomes heavier. As early as about 9 days before birth it may be possible to obtain liquid from the teat (Martys 1982). In most sows this is possible one or two days before birth.

The production of milk by the mammary gland of the domestic sow increases to a maximum by about four weeks of age and declines thereafter (Elsley 1971). The amount secreted is increased by the number of piglets suckling (Table 2), and although the yield also varies according to the breed and age of the neonates, litter size has the greatest positive influence on total production of milk from sows (Elsley 1971, Hartmann et al. 1997). The composition of the milk samples obtained from five different species of pig are shown in Table 3. It is worth noting that although these samples were obtained within the first few weeks of lactation and are roughly comparable, there has not been the same type of systematic study in wild pigs of milk composition during lactation, as there has been for the domestic sow.

Table 2

The effect of litter size on milk yield in the domestic pig (*Sus domesticus*)*

Number of piglets	4	5	6	7	8	9	10	11	12
Daily milk yield (kg)									
per litter	4.0	4.8	5.2	5.8	6.6	7.0	7.6	8.2	8.6
per piglet	1.0	1.0	0.9	0.9	0.9	0.8	0.8	0.7	0.7

* Data from Elsley (1971)

The blood flow to the mammary tissue does not appear to have been measured in the sow. The data on milk production in Table 2, and results from studies of other species are consistent with the presence of a high mammary blood flow at the end of gestation and for the first month of lactation (Stock & Metcalfe 1994).

Table 3

Composition of milk from different pig species.

Pig species	Total solids (%)	Fat (%)	Protein (%)	Sugar (%)	Reference
Phacochoerus africanus	19–20	7.3	7.0	3.4	Roth 1967, in Child et al. 1968
Potamochoerus larvatus	24.2	10.4	9.4	3.0	Seydack 1990
Babyrousa babyrussa	23	13	7.8	2.7	Bowles (pers. comm.)
Sus scrofa	16	4	9	2	Haber 1969, in Briederman 1990
Sus domesticus	20	7–9	5–7	5	Elsley 1971

3.2 Body weight

Much of the body weight increase which the domestic sow has made during pregnancy may be lost during lactation (Shields and Mahan 1983). The body weight of the Bushpig was also significantly lighter (60 kg) during lactation than during pregnancy (71 kg) (Seydack 1990). This is due in part to the delivery of the young, but in addition, the subcutaneous, peritoneal and bone marrow fat deposits were significantly reduced in the lactating Bushpig when compared to those in the pregnant animal. Both the duration of lactation and the size of the litter adversely influence the body condition of the Bushpig sow, which is shown as reduced body fat stores (Seydack 1990).

The Bearded pig also loses weight during lactation, and it is reported that the females accompanied by small piglets are invariably thin or very thin (Caldecott et al. 1993). For the Warthog, an indication of the body weight of lactating sows may be derived from their dressed carcass weights. Mason (1982) noted that they remained low following the onset of the rainy season, despite the improved grazing, and suggested that this was probably the consequence of the demands of nursing the young. There is no data on the change in body condition of the lactating Babirusa sow or any of the other wild pigs.

3.3 Digestive system

It has been shown in a number of mammalian species that with the high metabolic demands of lactation there is an enlargement in the liver, the walls of the stomach and the gastrointestinal tract. Lactating domestic sows also have heavier empty intestinal tract weights than non-pregnant sows (Shields & Mahan 1983). Liver weights are larger in lactating sows than in non-pregnant domestic sows, and sows nursing twelve piglets had heavier livers than those nursing eight (Pelletier et al. 1987). Similarly, the liver of the lactating Eurasian wild pig is larger, relative to body weight, than that found in the non-lactating sow (Koslo 1975 in Briederman 1990). However, studies on other species of mammals show that these effects can be modified by dietary factors, with food restriction reducing the increase in liver and gut size during lactation (Robinson 1986). Although information might be available in a systematic way from the annual cull of Eurasian wild pig and could be related to the measured availability of food during that season, it was surprising that no data specific to the effect of diet on the digestive system of the lactating wild pig has been found. Similarly, it would be possible to gather information from annual culls of African pig species and similarly relate these to the differences in the local availability of plant (and animal) nutrients.

3.4 Blood volume

In 20 domestic sows studied during their second parity from parturition to weaning at 4 wk of lactation, blood volume decreased linearly by approximately 9 % (Matte & Girard 1996). No data seem to be available for other species of pigs.

4. Comparative ecology of pregnancy and lactation

The ecology of pregnancy and lactation embraces a wide range of topics, such as habitat, social organisation, diet and predation. There appear to have been no specific studies of these with respect to the state of pregnancy and lactation in any of the wild species of pigs. However, for a number of years, the ecology of the managed domestic pig has been the subject of increasing interest, and information on the diet and nutrient utilisation of the sow has been intensively studied (e.g. Mroz et al. 1995, Foxcroft 1997, Mahan & Vallet 1997, Noblet et al. 1997, Trottier 1997, Varel & Yen 1997, Mackenzie & Revell 1998; van der Peet-Schwering et al. 1998, Vestergaard & Danielsen 1998, Whittemore 1998). The reader is referred to these reviews for detailed information.

4.1 Social groups

There is a gradually increasing amount of information on the social structure of the different pig species, much of which was summarised in the proceedings of a recent meeting in Berlin (Frädrich 1991), in the IUCN status survey and conservation action plan for pigs, peccaries and hippos (Oliver 1993) and in a forthcoming book on the biology of pigs, peccaries and hippos (Macdonald and Gansloßer 2000). The updated information relevant to the sow is presented briefly here.

In equatorial regions Warthogs breed throughout the year (Vercammen & Mason 1993). However, there is a distinct farrowing season in most of eastern and southern Africa, which is related to the pattern of rainfall (Child et al. 1968, Boshie 1981, Mason 1982). Similarly, in regions of higher rainfall spread over most months of the year, farrowing is synchronised to the short dry season (Vercammen & Mason 1993). Female sows are almost always found singly together with juveniles and subadults (Mason 1982, Somers et al. 1994). By way of contrast, Forest hogs live in family groups of 6–14 individuals led by an adult male (D'Huart 1978, 1991). Two or more females are usually present, together with juveniles and subadults. Bushpigs and Red river hogs (*Potamochoerus porcus*) also live in family groups of 9–15 individuals, in which both parents play a role in the rearing and defence of the young (Seydack 1990). Bushpigs are predominantly nocturnal, although there is some evidence to suggest that diurnal activity in winter may be related to temperature regulation (Vercammen et al. 1993). The Eurasian wild pig may also become nocturnal in disturbed areas, but is usually most active in the early morning and late afternoon (Briedermann 1990). The adult female and her litter forms the basic social unit, a social grouping which is said to be the case for the Pigmy hog and the Javan warty pig (*Sus verrucosus*) also (Oliver 1980, Blouch 1993). The Sulawesi warty pig, has been seen with young, and with other males and females, but there are no detailed studies of the social grouping of this species in the wild (Macdonald et al. 1996). The Babirusa sow tends to be found alone with young, which may be subadults and/or juveniles, although groups of from one to three adult females with young have been seen together (Patry et al. 1995). Two thirds of the groups containing adult females and young had no adult males present.

Observations in zoological collections revealed that when the Babirusa sow nears the end of pregnancy she becomes more antagonistic (Leus et al. 1992). It has also been observed that adult male and female Babirusa will cannibalise the piglets from another sow (Bowles 1986, Leus et al. 1992). It is likely, therefore, that in the wild the sow separates from the other pigs during the farrowing period. The prefarrowing behaviour of the Warthog also comprised some agonistic behaviour towards other Warthogs as well as former siblings from about 6–8 weeks prior to farrowing (Cumming 1975). Pregnant Eurasian wild pig segregate themselves about 5–6 days before birth and become intolerant of other group members (Martys 1982). However, no intolerance was shown by the Bushpig or the Red river hog (Seydack 1990, Neurohr 1991).

4.2 Nests and burrows

Although not all pigs make nests in which to sleep at night, the pregnant sow will either construct a farrowing nest, or in the case of the Common warthog, use a burrow in which to deliver her young. The pre-parturient Forest hog makes a nest of tall grasses under piles of branches 1.5 m high and 4 m in diameter (D'Huart 1978), and large nests made out of grasses have also been reported for the Bushpig, although whether or not they are constructed seems to be weather-dependent (Sowls & Phelps 1966; Seydack 1990). The farrowing nests made by the Babirusa in the wild tend to be up to 3 metres long and constructed over a depression in the ground which may be up to 25 cm deep, and similar constructions (Figure 4) have been constructed within the last 48 hours by animals in zoological collections (Selmier 1978; Leus et al. 1992). The Sulawesi warty pig makes a farrowing nest which can be distinguished from that of the Babirusa in that it is smaller, and shows evidence of rooting behaviour during its construction (Selmier 1978). The Pigmy hog makes a nest about $> 160 \times 140 \times 45$ cm in the night of parturition (Figure 4) which is of a similar design but apparently somewhat larger than that used for overnight accommodation of non-pregnant animals (Oliver 1980, Oliver et al. 1997). The latter, which has been described in detail, is constructed over a circular or oval 10 cm deep depression in the ground formed first by rooting and pushing the soil outwards with the snout. The Eurasian wild pig and the domestic pig also prepare a farrowing nest shortly before delivery of the young (Frädrich 1965, Briedermann 1990, Macdonald [unpubl.]). The Warthog generally uses holes in the ground for shelter at night and for farrowing, and will sometimes bring grass into the latter, as shown in Figure 5. The effectiveness of Warthog holes in moderating daily temperature fluctuations is described by Sowls & Phelps (1966), Bradley (1971) and Radke (1991).

4.3 Nutrition during gestation and lactation

In Southeast Asia, the mating of the Bearded pig seems to coincide with the flowering of the trees of the Dipterocarpaceae dominated rain forests, and the offspring are born about three or four months later when the ripe, oil-rich fruits fall to the ground (Caldecott & Caldecott 1985, Dove 1993). Similarly in Europe, during a good fruiting year, acorns and/or beech nuts may comprise up to 80 % of the diet of the Eurasian wild pig from October to February, with about two thirds of the births being concentrated in the months of March and April (Stub-

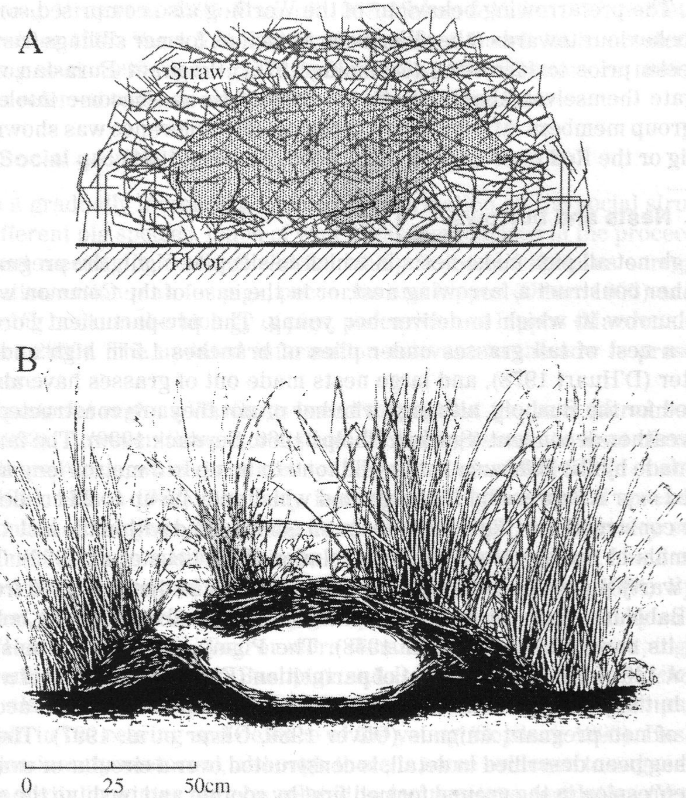

Fig. 4. The nest constructions used for farrowing by (A) the Babirusa (*Babyrousa babyrussa*) and (B) the Pigmy hog (*Sus salvanius*). (A from Leus et al., 1992 and B from Oliver, 1980)

be and Stubbe 1977, Briederman 1990). When food is abundant, such as after a plentiful fall of acorns or beech nuts, there is an increase in their reproduction (Mauget 1982, Briederman 1990). Pregnant Bushpigs appear to select a diet high in crude fibre/cellulose, if it is available, and thereby accumulated energy stores as subcutaneous and intra-abdominal fat before birth (Seydack and Bigalke 1992). However, the average size of Bushpig litters tended to be small (1.7) in sows which had become very fat (Seydack 1990). Although the pregnant and lactating females were not identified separately, adult females Warthog have been seen to spend more time feeding than adult males (Somers 1997). Warthogs sows preferentially consume the rhizomes of grass species during the dry season, when they are pregnant (Cumming 1975). During the dry sea-

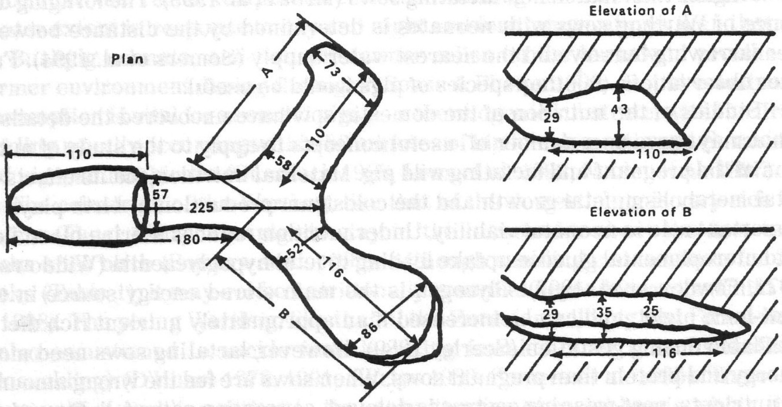

Fig. 5. Plan and elevation of a Common warthog (*Phacochoerus africanus*) burrow in which a family of piglets was born. The floor of one arm of the burrow (B) was covered with dry grass (from Bradley 1971).

son the cardiac content of the Warthog stomach has a crude protein composition of 7.1 % (Rodgers 1984).

The Warthog farrowing season is mainly during October and early November in eastern Africa, about one month before the rains (Child et al. 1968, Mason 1990). A similar synchrony with the rains, somewhat earlier in the year is seen in Senegal (Guiraud 1948). The young grass produced by the rains not only provides enough food of high quality for the lactating female and her young, but also provides additional cover (Child et al. 1968, Boshie 1981). Material in the stomach of the Warthog during the wet season, had a crude protein content of 11.1 % (Rodgers 1984). However, if drought conditions, following the failure of the spring rains, coincide with farrowing, Warthog sows are in poor body condition, and neonatal mortality is particularly high (Mason 1990). The lactating Bushpig selects diets from fast-growing plant tissues, where nitrogen and minerals such as phosphorus are concentrated, and does not have to concentrate on meeting her energy requirements because of fat stores in her body (Seydack & Bigalke 1992). It is not surprising that Bushpig lactation coincides with the plant growing season. However, Bushpigs normally forage over large areas, and because of limited mobility of the piglets, this is not possible during the first two months after giving birth (Seydack 1990). The Bushpig boar assists with the rearing of the young and will guard the piglets, thereby allowing the sow to roam more widely to feed. Further studies are required to identify and further quantify the nutrients being obtained by pregnant and lactating sows of all pig species in the wild.

Water consumption by lactating domestic sows is estimated to be at least 40 % higher than that in non-lactating sows (Mroz et al. 1995). The foraging distance of Warthog sows with neonates is determined by the distance between her farrowing burrow and the nearest water supply (Somers et al. 1994). Further observations on other species of pigs would be useful.

Studies of the nutrition of the domestic sow have uncovered the details of what may serve as a number of useful concepts to apply to the study of nutrition of the pregnant and lactating wild pig. Maternal nutrition, via its effects on fetal metabolism, fetal growth and the colostrum production at birth plays an important role in neonatal viability. Undernutrition reduces uterine blood flow and uteroplacental glucose uptake leading to fetal hypoglycaemia (Widdowson 1971, Fowden et al. 1997). Glycogen is the main stored energy source in the new-born piglet, and can be increased if an appropriately nutrient rich diet is available during gestation (Seerley 1989). However, lactating sows need more energy and protein than pregnant sows. When sows are fed the wrong amounts of nutrients, post-weaning oestrus is delayed, conception rates fall, litter sizes are reduced and milk yields (and piglet weaning weights) are reduced (Foxcroft 1997, Whittemore 1998). The lactating sow will use her own body reserves to supplement dietary nutrient intake. It is advised that lactating sows should be fed to appetite, and to achieve the required intake of nutrients, a greater quantity of diet of lower nutrient density is needed (Whittemore 1998). Domestic sows have been shown to digest fibre more effectively than growing pigs (Varel and Yen 1997). Increased absorption of bacterially produced volatile fatty acids by pregnant sows elevated the fat and energy content of milk.

The role of microbial digestion of fibre by wild pigs also deserves study, from both a nutritional and a behavioural viewpoint. Studies of the pregnant domestic sow demonstrate that it is possible to feed very differently composed diets without detrimental effects on the numbers of piglets born or the weight of the piglet at weaning (Vestergaard and Danielsen 1998). Diets with a high content of soluble fibre may also increase litter size (Varel & Yen 1997), perhaps by an underlying, and as yet incompletely understood endocrinological mechanism (Robinson 1990, Foxcroft 1997). This may explain why a female Red river hog only reproduced after her high-fat, high-sugar diet was changed to a high fibre diet (Diamant 1997). Additionally and importantly, diets with a high content of soluble fibre have demonstrated advantages over concentrate diets in their large capacity to induce satiety of the pregnant sow, and to reduce or prevent stereotypic and other abnormal behaviour (Varel & Yen 1997). How these should be adapted and tested with different species of wild pigs remains to be investigated systematically.

4.4 Suckling behaviour

Neonatal piglets are poorly insulated and very susceptible to loss of heat in the first few hours after birth. Mount (1962) found with domestic pigs, and Seydack (1990) with Bushpig that neonates and juveniles would huddle or bunch together, thereby decreasing their total surface area for heat loss. There is some evidence that the rectal temperature of the Warthog neonate fluctuates to a greater extent in response to day and night ambient temperatures than that of the Bushpig neonate, and that the former relies on the burrow to provide a warmer environment during the night (Sowls & Phelps 1966). Rapid colostrum consumption is vital for neonatal pigs as a thermogenic substrate, with the first suckling usually occurring within 30 minutes of birth in domestic and Eurasian wild pigs, and Babirusa (Gundlach 1968, Leus et al. 1992, Noblet et al. 1997).

The colostrum of the Warthog, like that of the domestic pig is very rich in protein (Faust 1961). The piglets stay in the burrow for about the first two weeks after birth (Somers et al. 1995). Although suckling can continue for 21 weeks (Table 1), it may not be nutritionally essential beyond 9 weeks (Child et al. 1968). The young Warthog, like that of the Eurasian wild pig and Forest hog is also accustomed to suckle from lactating females other than its mother (allosuckling) (D'Huart 1978, 1991, Martys 1982, Somers et al. 1995). The contribution that suckling makes to the strengthening of social bonds within the post-parturient social group remains to be studied.

Throughout the suckling period, the mean time spent suckling by Warthog piglets was 77.5 seconds with the interval between bouts of suckling averaging 37.4 minutes (Somers et al. 1995). In the wild the Babirusa juvenile seems to be able to obtain milk for a relatively long time, despite the contact between mother and piglet being broken repeatedly (Patry et al. 1995). Observations in the zoo suggest that nursing lasts for about one to three minutes, with piglets feeding from two teats alternately for about 20 seconds (Selmier 1978, Bowles 1986, Macdonald 1991).

4.5 Weaning

There is a considerable range in the number of days that the young spend suckling, and the time after birth that they are weaned normally. This is indicated in Table 1. There is little detailed information available from the wild, and where it is available, shows that piglets in the wild will be weaned about one month earlier than those reared in captivity (e.g. Bushpigs, Seydack 1990). Young Warthog will eat solid food from about one month of age (Frädrich 1966, Child et al. 1968, Mason 1982). Many observations are made of the behaviour of neonatal piglets in zoos, and are recorded in the daily reports of the keepers. It would be of more than passing interest to have this material published as it would assist an appreciation of the changing nutrient requirements of the piglet in the first few weeks after birth.

5. Zoo and field-based studies of nutrition during pregnancy

In a number of recent reviews of the influence of nutrition on the reproduction of farm animals, attention has been drawn to the very small numbers of experiments which consider the implications of a nutritional effect applied at one point in the reproductive cycle to events later on in the same cycle, and to the fewer studies still which consider the overall reproductive lifespan of the animal (Robinson 1990, Foxcroft 1997, Whittemore 1998, Peet-Schwering et al. 1998). There is convincing evidence that nutrition and metabolic state have an effect on embryo survival, and that the clearest responses to changing nutritional state occur when nutrition is limiting. For those working with animals in the wild and in zoological collections, the overall reproductive lifespan of the animal has been an obvious consideration, even though the information of how nutrient availability might affect it is still quite lacking. However, some attention to this topic with respect to the Bushpig may be found in the studies by Seydack and Bigalke (1992). They demonstrated that sows from the nutrient-poor Southern Cape had large body sizes, small litter sizes and high energy storage levels, whereas Bushpig sows from the nutrient-rich Eastern Cape had small body sizes, large litters and low energy storage levels.

It is important therefore to learn from the studies of the domestic pig, and to recognise that apparently beneficial effects of enhanced nutrition at or before ovulation may result in counter-productive effects later in gestation when the demands for nutrient from the gravid uterus may not be supplied by the digestive tract. Until adequately designed and co-ordinated studies have been carried out within zoos and in the field, it may be wise for zoo nutritionists to establish simple, sufficient and specific diets for the different species of pigs held in zoological collections, and for individual zoos to train their keepers to feed their pregnant animals individually to maintain their body condition prior to lactation. The amounts of nutrients fed to the pregnant animal should provide for the maintenance of the sow, the tissue products of conception (fetuses, uterine development, placental tissues, mammary growth), the growth of maternal body protein and lipid, and the deposition of protein and lipid reserves which will be available to support the forthcoming lactation (Whittemore 1998). Likewise, the amounts which should be fed to the lactating animal should correspond to the demands being made on her at that time. It is natural that the sow will mobilise body lipid and protein for milk synthesis, and lose body weight, but it is essential that adequate food supply is given to her to prevent that loss from being excessive, which might compromise subsequent reproductive performance (Whittemore 1998, Peet-Schwering et al. 1998). Zoological collections should monitor these changes, in part by routinely weighing their animals. It is also important to recognise that because of normal variation, it is essential to have good experimental design, and particularly to ensure the individual study of large enough numbers of individual animals, when seeking to uncover the effects of nutritional treatments.

The problems of quantifying the food intake of wild animals, in terms of amount of specific food items eaten and their chemical composition has been acknowledged for some time (see reviews by Dierenfeld 1997 and Chivers 1998). Nevertheless, it is the detailed information on the nutrient composition of the plant or animal species consumed in the wild which will ultimately provide information necessary to the compilation of dietary guidelines for application to captive populations of animals. Although all pig species are omnivores, there are significant differences in the proportions occupied by each of the dietary constituents, when differences in habitat preferences and foraging methods are taken into consideration (Leus & Macdonald 1997). The additional impact of pregnancy and lactation on dietary intake has largely been unexplored in studies of wild pigs. In order to effectively manage, and where necessary conserve, wild pig populations in the wild and in captivity, quantitative data must be gathered on the species (plant and animal) and biochemical composition of the animals' diets, during the pregnant and lactating states.

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