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Behavioural perspectives on piglet survival

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Summary. Litters of domestic piglets show strong sibling competition, large differences among litter-mates in birth weight and rate of growth, and, in the absence of human intervention, a high mortality rate. This combination of traits suggests that pigs are using a reproductive strategy similar to that of certain bird species which produce one or more small 'spare' young whose death or survival is determined by sibling competition. Death through competition is natural in such species. Prevention of death requires the early identification and separate rearing of unsuccessful competitors.

The major behavioural pathways leading to piglet deaths are considered to be malnutrition through unsuccessful suckling behaviour, and crushing of piglets by the sow. Crushing involves two distinct behavioural sequences: posterior crushing (beneath the sow's hind quarters) and ventral crushing (beneath the udder and rib cage). Farrowing crates are designed to prevent posterior but not ventral crushing. Malnourished piglets appear to be more vulnerable to crushing, perhaps because persistent suckling attempts cause them to spend more time near the sow. Prevention of crushing thus requires a reduction in malnutrition, not merely restriction of the sow's movements. Under certain conditions, dehydration may be an important but neglected aspect of malnutrition.

Some litters of piglets have much higher death losses than others, presumably because of risk factors that apply to the litter as a whole. Early malnutrition, resulting from hypogalactia in the sow in the first days after farrowing, appears to be an important risk factor. Farrowing difficulties leading to piglet hypoxia during the birth process may be another. Risk factors that affect whole litters deserve greater emphasis in future research.

Keywords: piglet survival; behaviour; sibling competition; starvation; dehydration; trauma; hypogalactia

Introduction

Please imagine, gentle reader, that you suddenly find yourself beside a recumbent elephant in a small, locked room. The elephant seems agitated; she periodically jumps to her feet and then crashes to the floor, and may even whirl about and attack you without warning. Unfortunately, you entered the room by being squeezed through a narrow tube and perhaps partly suffocated, so you are none too steady on your feet. You ought to keep as far from the elephant as the limited space permits, but you cannot afford this luxury because you are cold, wet, unclothed, and desperately short of food; and the only source of food is the elephant's milk. Competing for this resource, however, are 10 or more individuals like yourself, some of them twice your body weight, and all murderously aggressive and armed with sharp teeth.

This Tolkienesque torture is, of course, an allegory for the trials facing a newborn piglet, but I have understated the danger considerably: a mature elephant is only about 50 times the size of an adult human, whereas many sows are 200 to 300 times larger than their smallest offspring. In the light of these odds, it hardly seems surprising that neonatal death is a major problem in pig production, and that such elementary causes as crushing by the sow and failure of the young to achieve adequate nutrition by suckling should account for many of the losses. These are, of course, behavioural problems, and in this review I want to consider how insights and ideas from the study of animal behaviour can shed new light on piglet survival.

The social context of piglet deaths

Sibling competition

Intense competition among litter-mate piglets is widely recognized as a factor contributing to piglet deaths (English & Smith, 1975; Hartsock & Graves, 1976). The competition begins in the first hours after birth (Hartsock & Graves, 1976) as the pigs attempt to displace each other from teats by vigorous pushing and sideways biting movements (Fig. 1). The behaviour involves some remarkable weaponry: the canines and third incisors are fully erupted at birth at such an angle that the typical sideways biting movements can produce significant facial lacerations (Fraser, 1975). The initial, intense competition subsides gradually as the piglets develop fidelity to one or two particular teats, but in litters with unsettled suckling positions, fighting and facial lacerations continue for several days or weeks (Fraser 1975; de Passillé *et al.*, 1988).

Fig. 1. Piglets competing for a teat in the first hours after birth.

This remarkable competition, although rare among mammals, has striking parallels in certain birds in which sibling competition plays a key role in the reproductive strategy of the species (see Mock, 1984, for an excellent review). For example, great egrets (*Casmerodius albus*) commonly lay slightly more eggs than the number of chicks that are normally reared. Because the chicks hatch over a period of several days, the older chicks are appreciably larger when the youngest hatch. The siblings are very competitive, and the small chicks, bearing the brunt of this competition, suffer high mortality. They may be killed outright by their siblings, or they may die of starvation because of the fierce competition for food (Mock *et al.*, 1987). In such species, however, even the small chicks may be raised successfully if food proves to be abundant or if one of the larger chicks should die (Mock, 1984). The small extra cost of producing an additional chick therefore provides an 'insurance policy' on the life of the better young, and allows the parents the option of raising additional young should the food supply prove to be adequate. This reproductive strategy involves three components: a small extra investment to produce one or two 'spare' young, intense sibling competition which ultimately determines the number of young raised, and a size difference which produces a competitive asymmetry and ensures that the survival of the better young will not be seriously jeopardized by the presence of the 'spare' young.

Pigs fit this pattern remarkably well. First, their overt neonatal competition and damaging weaponry constitute a notable parallel with the siblicidal bird species. Second, studies spanning several decades and numerous countries have shown that, in the absence of special management intervention, the pre-weaning mortality rate of domestic piglets is typically 20% or higher (e.g. Braude *et al.*, 1954; Bauman *et al.*, 1966; Sadana & Singh, 1972; Nielsen *et al.*, 1974; Bolet, 1982). While this rate can be reduced greatly by special techniques such as cross-fostering and artificial rearing, the death of one or more piglets per litter is so common that it can be viewed as normal rather than pathological. Third, many litters of piglets show a large differential in birth weights creating a competitive asymmetry strongly favouring the larger young (English & Smith, 1975; Thompson & Fraser, 1986). In addition, in a wide range of mammalian species, the energetic cost of producing newborns is small compared to the cost of raising them (Hayssen, 1984; see also Clutton-Brock *et al.*, 1989). The particularly small size of newborn piglets (relative to the sow) suggests that in this species the production of 'spare' young might be an inexpensive gamble well worth taking as long as the extra piglets have a certain probability of surviving. Obviously these ideas need to be tested with data from wild pigs for which selective breeding has not tampered with litter size and variation in birth weight.

If the parallel with siblicidal birds does hold, then we would expect to see certain piglets whose survival is jeopardized by a lack of success in sibling competition. The study by de Passillé *et al.* (1988) suggests that this may be the case. Based on a study of early suckling behaviour, de Passillé *et al.* (1988) concluded that piglets fall into two groups: a majority of "typical pigs" that establish and maintain a preferred teat pair in the first 2 or 3 days and thereafter rarely fight for their suckling positions and very rarely miss a milk ejection; and a minority of "problem pigs" that fail to establish a consistent position, continue to fight for teats, often miss milk ejections, and gain less weight. The problem pigs studied by de Passillé *et al.* (1988) were, of course, those that survived long enough to be studied, but I would speculate that the same process of exclusion from normal suckling leads to early death in many cases.

Are pigs phylogenetically adapted to over-produce young of heterogeneous size and allow sibling competition to do any necessary culling? This hypothesis, although admittedly speculative, merits study because of its implications for piglet management. It implies that when we try to keep large litters alive, we are battling not just against disease organisms, cold environments, and other external challenges, but against an evolved reproductive strategy. It imples further that we need (i) to accept as natural that certain piglets in large litters are likely to be excluded by competitive pressure from adequate milk intake, (ii) to minimize the effects of chilling, disease, starvation, etc, and thus prolong the life of the unsuccessful competitors, and (iii) to identify unsuccessful competitors and remove them to a different sow or rearing system while they are still alive.

Direct and indirect sibling competition

Having argued that competition is relevant to piglet survival, it is important to clarify the type of competition involved. In nature we can discern two broad types of competition which, for simplicity, could be termed *direct* and *indirect* (see Krebs & Davies, 1987: pp. 93–110). Resources that can be readily defended, such as the small breeding territories of many woodland birds, are likely to be the object of direct competition marked by threats and physical aggression. Other resources, such as grazing opportunities for herbivores in a large pasture, may be too difficult or uneconomical to defend. However, one grazer might still gain a competitive edge over its neighbours by finding the richest patches or by exploiting the resources more efficiently. This, too, is competition in that one animal prospers at the expense of another by 'using up' the resource (Krebs & Davies, 1987), but the competition is indirect, inconspicuous, and not overtly aggressive.

For piglets both types of competition occur and are fairly distinct (Table 1). A teat is a defendable resource and is the object of direct, aggressive competition, especially in the first hours after birth. Once lactation has become well established, however, milk is a largely undefendable resource because the piglets can obtain it only during the brief milk ejection which occurs at all teats simultaneously (Fraser, 1980; Ellendorff *et al.*, 1982). Various features of the sow's nursing behaviour also seem designed to promote a fairly even distribution of milk among all piglets that have established ownership of a teat (Fraser, 1980).

Table 1. Summary of the two proposed types of competition among litter-mate piglets

	Direct competition	Indirect competition
Objective	Possession of a functional teat	Increased milk intake
Type of resource	Defendable (teat)	Undefendable (milk)
Time of competition	Mainly first days after birth, some continuing later	Throughout lactation; especially later as milk becomes limiting
Mechanism	Overt fighting at the udder	Effective stimulation (massage and draining) of teat
Result of failure	Death or very poor weight gains	Below-average weight gains

Piglets do circumvent this egalitarian system, but only by indirect means. Figure 2 illustrates two studies showing that a piglet's weight gain when suckling is improved by having lighter litter-mates and worsened by having heavier litter-mates. The mechanism of this competition has not been defined precisely, but a strong piglet could perhaps stimulate its own teat to greater production by massaging the teat more vigorously before milk ejection (Fraser, 1984) or after (Algers & Jensen, 1985), or by draining the teat more efficiently. Since there is some upper limit on the sow's ability to produce milk, the advantage thus obtained by one piglet occurs at the expense of piglets suckling other teats (Thompson & Fraser, 1986). The result is that the gap in body weight between the better and poorer pigs increases continuously during the lactation in some litters, until the piglets begin eating solid food (Thompson & Fraser, 1986).

In short, piglets exhibit early, direct competition for teats soon after birth, and indirect competition for milk throughout much of the lactation. While the indirect competition has a large influence on weight gain and may affect mortality somewhat, the early, direct competition for teats is probably much more important in determining survival.

Aggressive infanticide: social pathology or hormonal miscue?

A minor but drastic cause of piglet deaths is savaging of the newborn litter by the mother, usually during her first parturition (Van der Steen *et al.*, 1988). Killing of newborns occurs in captive animals of many species, and has often been viewed as a social pathology brought on by captivity. Eisenberg (1981: p. 398) describes various cases of captive animals killing their offspring if key requirements of the social or physical environment are not met.

Hormonal factors may play a major role in such behaviour. Female gerbils (*Meriones unguiculatus*) often kill and eat foreign young, but are maternal toward their own newborns

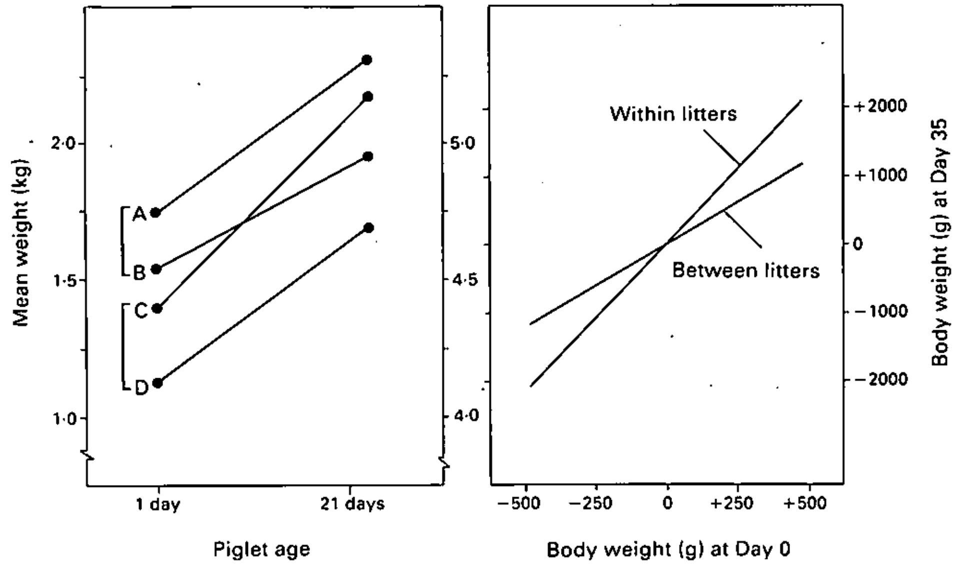

Fig. 2. Two demonstrations of competition within litters of piglets. At left, pairs of litters were born on the same day and the piglets were ranked from the A (heaviest) to the D (lightest) quartile of the combined litters. One sow raised the A and B piglets, the other the C and D piglets. The Cs thus had the advantage of being the largest piglets of the litters in which they were raised, and they out-performed the Bs by 21 days of age (from Fraser *et al.*, 1979, based on a design by Lodge & Pratt, 1963). At right, the linear regression of body weight at Day 35 *versus* body weight at Day 0, each expressed as deviations from the mean. Analysis was done between litters (based on 51 litter means expressed as deviations from the overall mean) or within litters (based on 488 piglet weights expressed as deviations from their respective litter mean). The within-litter slope is significantly greater, indicating that a piglet's birth weight relative to that of its litter-mates confers an advantage or disadvantage beyond that attributable to body weight *per se* (from Thompson & Fraser, 1986).

(Elwood & Ostermeyer, 1984). This is not because they distinguish their own from foreign young, but because the hormonal changes of late pregnancy and parturition cause a radical change in behaviour toward young in general. In the rat (Pedersen *et al.*, 1982) and the ewe (Poindron *et al.*, 1984), acceptance of young depends strongly on the endocrinological changes accompanying parturition. Savaging by sows has been little studied in this way, but one might ask whether a small abnormality in the timing of the hormonal changes at parturition, or stress-induced disruption of these hormonal changes (Hansen & Curtis, 1980), might leave the female hostile to young while her own are already being born.

In house mice, *Mus musculus*, females that developed *in utero* between 2 other female fetuses differ, as adults, from females that developed between male fetuses, both in their levels of spontaneous infanticide and in their sensitivity to the infanticide-promoting qualities of testosterone (Svare *et al.*, 1984; see also vom Saal, 1984). Here, too, in the absence of data one can only note that a similar phenomenon in pigs might help to explain the large differences between dams in aggressiveness toward newborns.

Behavioural pathways leading to death

How well do farrowing crates prevent deaths?

Much more common than aggressive infanticide is the apparently accidental crushing of young beneath the body of the mother. This problem confronts us with a paradox: that farrowing crates are used to prevent crushing, yet crushing remains probably the major cause of death when farrowing crates are used (Baxter, 1971; Glastonbury, 1977; Bolet, 1982; Spicer *et al.*, 1986; Svendsen *et al.*, 1986).

In fact, the evidence for reduced piglet mortality in farrowing crates (Table 2) contains some significant problems of interpretation. Early survey studies generally showed lower mortality in farms using crates than in farms using farrowing pens (Robertson *et al.*, 1966; Aumaitre *et al.*, 1975; Glastonbury, 1976). However, the use of crates may have been confounded with other management differences, especially before crates came into nearly universal use. A more recent survey study by Gustafsson (1983) is less convincing.

Table 2. Summary of six studies comparing piglet losses with and without farrowing crates

Source*	Type of study	No. of litters	Total piglet losses (%)†	
			Crates	Pens
Robertson *et al.* (1966)	Comparison of two systems	150	18·7	26·6
Glastonbury (1976)	Survey-specialized pig farms	614	15·9	31·3
Gustafsson (1983)	Survey	72 507	18·7	18·7
Devilat *et al.* (1971)	Controlled experiment	46	10·2	13·5
Aherne (1982)	Controlled experiment	21	12·7	34·6
Collins *et al.* (1987)	Controlled experiment	228	12·0	12·4‡

*See also Bauman *et al.* (1966), Bäckström (1973) and Friendship *et al.* (1986) whose results do not lend themselves to being summarized in this way, Gravås (1982) who studied free and confined sows in various penning arrangements, and Aumaitre *et al.* (1975) who summarize a survey of sows farrowing with rails, crates, or tethers.
†Includes stillbirth (when available) and other deaths before weaning.
‡Stillbirths not included. Pens had sloped floors.

Results from controlled experiments have also been somewhat ambiguous. Aherne (1982) found a dramatic difference between pens and crates, Devilat *et al.* (1971) found a modest difference, while Collins *et al.* (1987) found effectively no difference in piglet losses between crates and pens with a sloped floor. However, even 'controlled' experiments of this type are rarely well controlled. For example, the use of crates was confounded with other differences in the studies of Aherne (1982) and Collins *et al.* (1987), and few studies correctly incorporate the large and well-known influence of litter size when analysing piglet deaths.

In short, although it would be foolish to suggest that crates do not prevent deaths, the degree of reduction is hard to estimate and may be considerably lower than an uncritical reading of the literature would indicate. The fact is that crushing in particular, and piglet mortality in general, remain major problems when crates are used; and this should be enough to make us question our basic assumptions.

Posterior and ventral crushing

The first assumption to be questioned is that most piglets are crushed by the uncontrolled descent of the sow's hind quarters when the sow lies down from a standing position. This is the movement that crates are designed to minimize (Baxter, 1984: p. 455) and that common revisions to crate design have been intended to impede further (English *et al.*, 1977: p. 135; Green, 1981). It is remarkable that such a fundamental and economically important point has been so little studied.

It now appears that 'posterior crushing', as just described, is only one of two major movement patterns that kill piglets (Fig. 3). The other occurs when a sow lies down from a sitting position and traps piglets beneath her thorax (Fraser, 1966; Edwards & Malkin, 1986). This 'ventral crushing' may account for many of the crushing deaths when farrowing crates are used (Edwards & Malkin, 1986). It therefore appears that while some piglets are indeed crushed beneath the sow's hind quarters, others are killed by a movement that crates have not been designed to prevent.

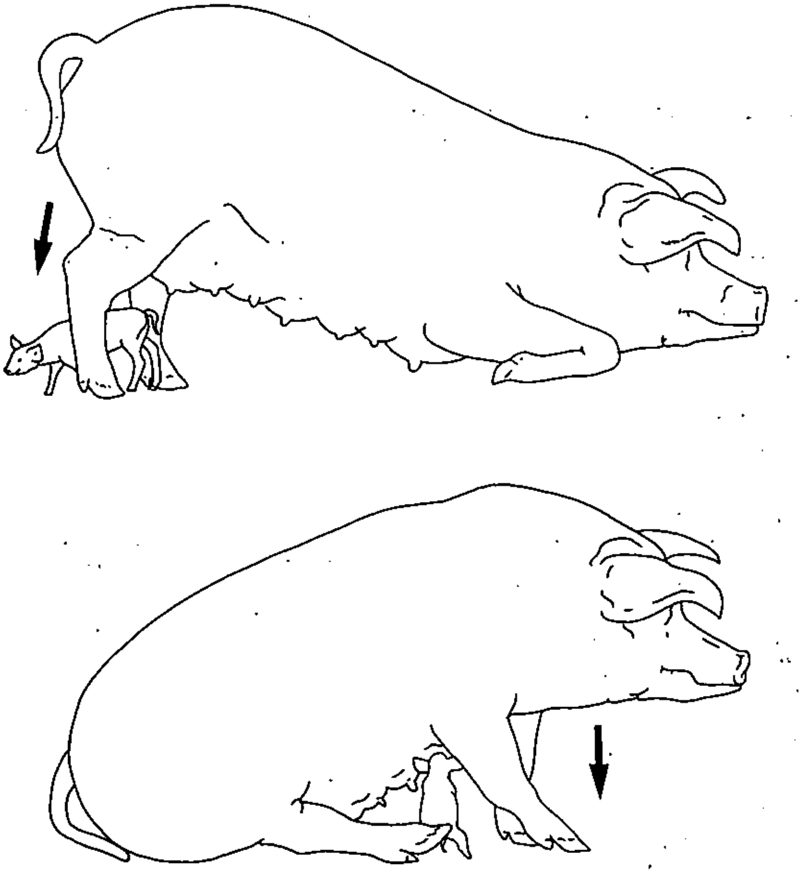

Fig. 3. The two major sequences of sow behaviour leading to crushing of piglets. In posterior crushing (above) the piglet becomes trapped beneath the sow's hind quarters when the sow lies down from a standing position. In ventral crushing (below) a piglet at or near the udder of the sow is crushed when the sow lies down from a sitting position (see Edwards & Malkin, 1986).

Crushing and malnutrition: end points of a common process?

A second debatable assumption is that a piglet saved from crushing will not simply die later from some other cause. Post-mortem examinations have typically identified trauma (usually crushing) and starvation as the two leading causes of piglet deaths. Most studies cite trauma as the more prevalent cause (Veterinary Investigation Service, 1959; Sharpe, 1966; Bauman *et al.*, 1966; Nielsen *et al.*, 1974; Bille *et al.*, 1974; Svendsen *et al.*, 1986; VIDO Swine Technical Group, 1986; Kunz & Ernst, 1987), but some make it clear that crushing can be a secondary factor claiming the life of a piglet that is already debilitated by a failure to achieve adequate nutrition (Veterinary Investigation

Service, 1959; Fraser, 1966). This implies that some piglets may be crushed because of a behavioural difference or deficiency related to malnutrition, but, alas, a post-mortem examination is not the ideal time to study an animal's behaviour.

To remedy this, English & Smith (1975) collected case history data on 236 piglets that subsequently died. Although crushing and trampling were involved in 34·7% of deaths, nearly half of these animals had already been weakened by malnutrition or other factors. Judging the primary cause of death to be the initial factor in the fatal sequence, English & Smith (1975) blamed starvation for 43% of deaths, while crushing of healthy piglets accounted for an additional 18%. The combined toll attributed to starvation and crushing together was similar to that seen in studies using post-mortem examination alone, but the proportions attributed to the two factors were roughly the reverse of those seen in some other studies.

This suggests that crushing and starvation may often serve as alternative end-points of a single process. A piglet that is debilitated by being excluded from teat ownership or by otherwise failing to establish adequate milk intake is likely to be crushed, but if crushing is prevented, the animal may die from malnutrition some time later.

Why are starving piglets crushed?

Why are starving piglets so often crushed? The conventional wisdom has been that malnourished piglets are less vigorous and less able to escape from dangerous movements by the sow. Doubtless this is true, but I suspect that there is an additional reason.

In many animal species the young have some behavioural means—such as the begging calls of nestling birds—to stimulate the parent to provide more food (Hussell, 1988). It is a common observation that certain litters and certain individual piglets remain at the udder after a nursing, or return to the udder between nursings, and massage and suck the teats for long periods of time. Algers & Jensen (1985) suggest that this behaviour causes greater production of milk by the teats that are stimulated, and thus constitutes a mechanism whereby the piglets can 'ask' for more food. This implies that undernourished piglets or undernourished litters should be more persistent in stimulating the udder and, hence, spend more time close to the sow and in danger of being crushed.

When crushing involves starving piglets, prevention of crushing may simply delay death but not prevent death in the long run. In such cases, further restriction of the sow is unlikely to be of much benefit unless the primary malnutrition is also rectified.

Malnutrition: starvation or dehydration?

The 'forgotten nutrient' may also contribute to early malnutrition of piglets. Table 3 summarizes findings on water intake by very young piglets from studies covering the past 25 years, and shows an obvious progression toward greater water use in the recent studies.

Why this trend? In recent decades, much emphasis has been placed on the piglet's need for warmth (e.g. Morrill, 1952; Curtis, 1970; Le Dividich & Noblet, 1981). The resulting improvements in the farrowing environment have undoubtedly lessened the incidence of piglet deaths through chilling and hypoglycaemia. However, as the effective environmental temperature approaches body temperature, increased evaporative moisture loss from the body can be expected (Curtis, 1983). Under very warm conditions, fasting piglets lose weight rapidly unless drinking water is provided (Morrill & Sampson, 1952). Piglets in a warm commercial environment could conceivably become short of body fluids if their intake of milk is impaired by poor competitive ability or by hypogalactia in the sow (see Ehlert *et al.*, 1981; Svendsen & Andréasson, 1981).

Simple studies of water intake provide suggestive data. With water provided in an open bowl, litters with very poor weight gains in the first 2 days after birth, presumably caused by early hypogalactia in the sow, drank considerably more water during these days than did litters with rapid gains in body weight (Fraser *et al.*, 1988b). In addition, water intake by young piglets is much

Table 3. Average water use per piglet in the first week (or part thereof) after birth in 7 studies

Water use per piglet (ml/day)	Period covered	No. of litters	Reference
9	Days 1–7	33	Aumaitre (1964)
12	Days 1–7	9	Friend & Cunningham (1966)*
0	Days 1–7	14	Bekaert & Daelemans (1970)
0	Days 1–5	20	Wojcik *et al.* (1978)
12	Days 5–10		Wojcik *et al.* (1978)
~40	Days 1–7	36	Svendsen & Andréasson (1981)
35	Days 1–4	51	Fraser *et al.* (1988b)†
~90	Days 1–2	32	Phillips & Fraser (1989)†‡

*Water provided 9 h/day.
†After correction for evaporation and estimated spillage.
‡Two water dispensers (one conventional and one modified) provided per pen.

higher at a room temperature of 28°C than at 20°C (D. Fraser, P. A. Phillips & B. K. Thompson, unpublished data).

Physiological studies are needed to determine the importance of dehydration in piglet deaths, and the conditions that give rise to dehydration. In the meantime, provision of a water bowl from the time of birth (e.g. Phillips & Fraser, 1989) would seem a sensible precaution in warm environments.

Death-prone piglets and death-prone litters

High-mortality litters

Several studies argue that some litters are more prone to death losses than others (Bel Isle & England, 1978; de Passillé & Rushen, 1989). Table 4 shows frequency distributions of deaths per litter from these and other studies. If deaths were distributed randomly among litters, then the frequencies should conform to a Poisson distribution (Sokal & Rohlf, 1981). However, all 6 distributions are flatter than predicted on the assumption of randomness; that is, there are too many litters with many deaths, too many with no deaths, and too few with a moderate number. The fact that all the distributions depart from the expected values in the same way (although the difference reaches statistical significance in only some of the cases) strongly suggests that some litters are indeed more mortality-prone than others.

In the light of this, I think it helps to conceptualize risk factors in two categories, as shown in Fig. 4: individual risk factors that apply to specific piglets, and litter risk factors that apply to litters as a whole. If the litter risk factors are high (e.g. lactation failure by the sow), then the entire litter may be lost, regardless of the viability of the individual piglets. If an individual piglet is at high risk (e.g. very low birth weight), then this individual is likely to be lost, even though the rest of its litter may thrive. These extremes have been well recognized as two alternative pathways leading to death (English & Wilkinson, 1982). More interesting are those cases in which a moderate level of litter risk might combine with a moderate level of individual risk to produce a number of deaths in a litter in which there is no obvious reason why several piglets should have died.

To identify litter risk factors, a simple but imperfect starting point is to look for features that distinguish litters with many deaths from those with few or none. The study by de Passillé & Rushen (1989) followed this approach deliberately and several other studies (summarized in Table 5) have presented comparable data. The studies confirm, as expected, that high-mortality litters tend to have more piglets per litter at birth, somewhat lower average birth weights, and slightly

Table 4. Number of litters classified according to the number of deaths per litter in 5 studies

Deaths per litter	Study*					
	A	B	C	D-Y	D-C	E
0	8	80	14	39	31	51
1	11	43	9	33	32	12
2	10	31	6	21	14	3
3	3	16	4	8	7	1
4	4	7	2	7	4	0
5	1	8	1	1	4	0
6	1	3	0	1	1	0
7	1	2	0	0	0	1
8	0	0	1	0	0	0
9	0	0	0	0	0	0
10	0	0	0	0	0	0
11	0	1	0	0	0	0
Total litters	39	191	37	110	93	68
Goodness of fit†	n.s.	$P < 0{\cdot}001$	$P \sim 0{\cdot}13$	$P \sim 0{\cdot}05$	$P \sim 0{\cdot}03$	n.s.

*Sources: A, Bel Isle & England (1978); B, Maddock (1980); C, de Passillé & Rushen (1989); D-Y, Dyck & Swierstra (1987), Yorkshire litters; D-C, Dyck & Swierstra (1987), crossbred litters; E, Fraser *et al.* (1988a).
†Departure from a Poisson distribution determined by a χ^2 goodness-of-fit test.

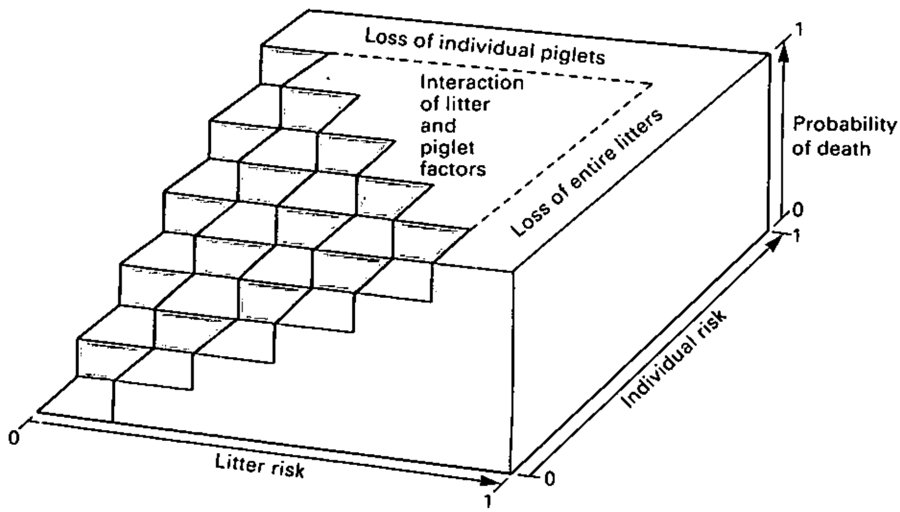

Fig. 4. Conceptual scheme showing the probability of death of a piglet as the combined effect of risk factors that apply to the individual and those that apply to the litter as a whole.

greater within-litter variation in birth weights. However, the one really striking feature of the high-mortality litters is the very poor rate of weight gain by the survivors in the first few days after birth.

Early malnutrition as a litter risk factor

The first days after birth are marked by exceptionally large variation between litters in piglet weight gains (Thompson & Fraser, 1988). Some litters enjoy large, steady gains in the first days after birth, others gain very little, and some lose weight for 1 or more days.

Table 5. Characteristics of litters with high and low mortality in several studies

	Mortality class		
Variable	High	Low	Source
No. of piglets per litter	14·1	10·1	A
	13·5	9·9[a]	B
	12·5	10·5[b]	C
	10·6	8·6[a,b]	D-Y
	12·2	10·0[a,b]	D-C
Birth weight (kg)	1·06	1·23	A
	1·31	1·48	B
	1·40	1·37[b]	C
	1·05	1·22[b]	D-Y
	1·35	1·51[b]	D-C
	1·25	1·36	E
Standard deviation of birth weight (mean of litter values)	—	—[c]	A
	0·269	0·243	B
	0·21	0·17[b]	C
	0·22	0·19[b,d]	D-Y
	0·25	0·23[b,d]	D-C
	0·213	0·206	E
Early weight gains (g/day per piglet)	38	136[e]	B
	13	130[b,f]	C
	75	131[f]	E

Sources: A, Bel Isle & England (1978), the 7 high-mortality litters (out of 39) had ≥4 deaths; B, Pettigrew *et al.* (1986), the 20 high-mortality litters (out of 182) had ≥4 deaths; C, de Passillé & Rushen (1989), the 8 high-mortality litters (out of 37) had ≥3 deaths; D-Y, Dyck & Swierstra (1987), Yorkshire litters only; the 17 high-mortality litters (out of 110) had ≥3 deaths; D-C, Dyck & Swierstra (1987), cross-bred litters only; the 16 high-mortality litters (out of 93) had ≥3 deaths; E, Fraser *et al.* (1988a), re-analysed from the original data; the 5 high-mortality litters (out of 68) had ≥2 deaths.

Explanatory notes:

[a]Piglets born alive.

[b]Values for low-mortality litters were calculated as weighted means of 0-, 1- and 2-death litters.

[c]Values not shown because s.d. values in original paper do not appear to be means of litter values.

[d]Approximate s.d. were calculated from mean values of standard error and litter size.

[e]Daily gain for Days 0–7 calculated from mean weights at birth and 7 days.

[f]Daily gains for Days 0–3, based on piglets that survived to weaning.

The reasons for these large between-litter differences in early gain are not entirely clear, but differences between sows in initial milk production are undoubtedly involved. The sow's lactation is notoriously fragile in its first few days. Various disease conditions (Martin & McDowell, 1975) and hormonal abnormalities (Gooneratne *et al.*, 1982) may be involved, but the line between normal and abnormal is often difficult to draw (Thompson & Fraser, 1988). Whatever the reasons, a sow's milk production in the first days of lactation can vary from excellent to disastrous, and many litters of piglets experience mild to severe malnutrition soon after birth.

The involvement of infectious disease in this problem brings us to a paradox: post-mortem studies indicate that few piglets die from infectious disease compared to the many that die from crushing and starvation (English & Wilkinson, 1982), yet high standards of hygiene and disease prevention are recognized as ways of reducing piglet mortality. The resolution of the paradox may be that disease organisms rarely kill piglets directly, but rather increase the incidence or severity of early hypogalactia in the sow. This in turn exposes the piglets to early malnutrition with the result that more piglets die from the major killers such as starvation and crushing. The obvious implication is that attention to the health of the sow at farrowing is a major avenue for reducing piglet mortality.

Attention to the sow's water intake may be another approach. Water intake varies greatly among sows in the first days after farrowing. One of our studies showed that sows with low water intake on the first 3 days of lactation (<6 l/day) tended to be inactive, had litters with low average weight gain, and accounted for many of the piglet deaths (Fig. 5).

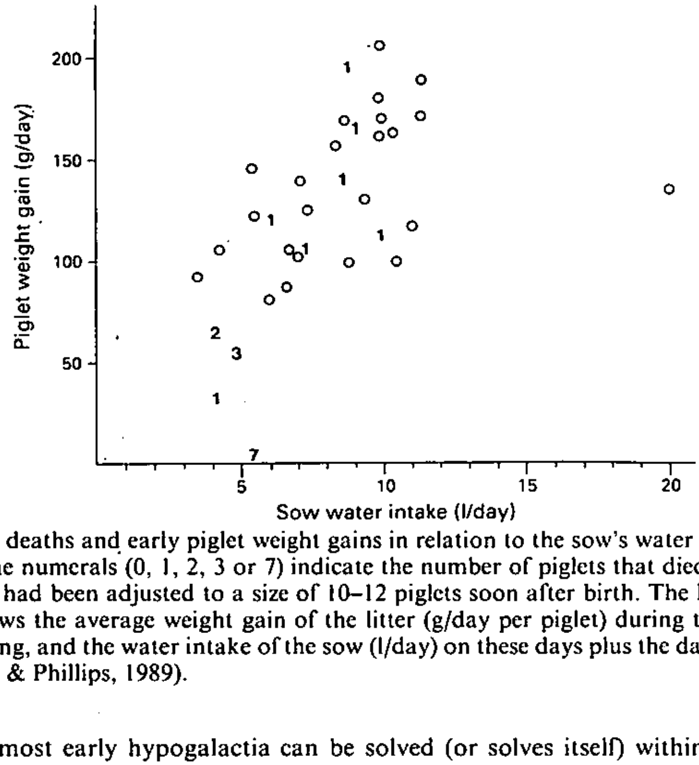

Fig. 5. Piglet deaths and early piglet weight gains in relation to the sow's water intake in early lactation. The numerals (0, 1, 2, 3 or 7) indicate the number of piglets that died in each of 34 litters which had been adjusted to a size of 10–12 piglets soon after birth. The location of the numeral shows the average weight gain of the litter (g/day per piglet) during the first 3 days after farrowing, and the water intake of the sow (l/day) on these days plus the day of farrowing (from Fraser & Phillips, 1989).

Fortunately most early hypogalactia can be solved (or solves itself) within a few days after birth. A useful strategy, therefore, is to minimize the risks from chilling, crushing and dehydration and thus prolong the lives of piglets at risk until the milk supply is restored.

The hormonal state of the sow as a litter risk factor

Studies of stillborn piglets have shown that asphyxiation is a significant danger during the birth process (Randall, 1972), and that partial asphyxiation can lead to poor survival prospects of live-born piglets (Randall, 1971). This is now recognized as an individual risk factor (Curtis, 1974), applying especially to piglets born late in the farrowing sequence. However, some tantalizing evidence suggests that hormonal differences between sows at parturition may lead to differences in the farrowing process with the result that some litters have a high incidence of stillbirths and oxygen-deprived piglets (Hacker *et al.*, 1979). The hormonal state of the sow may also cause differences between litters in circulating concentrations of hormones in the newborns which may in turn influence their vitality and early suckling behaviour (Bate *et al.*, 1985; Farmer *et al.*, 1987).

Is variation in birth weight a risk factor?

Several studies have concluded that, in addition to the known effect of low birth weight, a lack of uniformity in birth weight is itself an important risk factor for piglet survival. In particular, English & Smith (1975), Fahmy *et al.* (1978) and Pettigrew *et al.* (1986) showed a relationship between mortality rate and the standard deviation of the litter's birth weight. However, at a given mean birth weight, litters with a large standard deviation are likely to contain low-birth-weight piglets. Hence, the analyses to date have not completely separated the effects of uniformity from the well-known high mortality rate of piglets that are light at birth.

Concluding remarks

I have introduced the conceptual framework in Fig. 4, simplistic though it is, partly to argue that a change of emphasis is needed in research on piglet mortality.

We now know a great deal about individual piglet risk factors. We know about the new-born piglet's poor thermal insulation, its limited ability to regulate body temperature, its propensity to hypoglycaemia, and the need for warmth, especially for low-birth-weight animals (Mount, 1968; Curtis, 1970; Edwards, 1972; English & Morrison, 1984). We recognize fetal oxygen deprivation as the major cause of intrapartum death, and milder hypoxia as a cause of reduced viability (Randall, 1971). We recognize the immune incompetence of the newborn piglet, its requirement for colostrum, and the beneficial effect of continued colostrum intake as a protection against absorption of bacterial toxins (Lecce, 1975; Aumaitre & Seve, 1978). In these respects, as English & Wilkinson (1982) point out, many current management problems stem from a failure to apply existing knowledge, not from a lack of knowledge itself.

Much less satisfactory, however, is our understanding of litter risk factors. Research on early hypogalactia in the sow comprises little more than a porridge of individual studies identifying various hormonal, nutritional, environmental, toxic, and bacteriological factors in particular cases. We know remarkably little about how the farrowing environment and the hormonal state of the sow at parturition influence the farrowing process and, hence, the oxygen status, hormonal status, and vigour of the litter. Savaging of piglets by the sow remains a mystery.

Traditionally, piglet mortality has been studied because of its economic importance, but our growing sensitivity to farm animal welfare provides another impetus for research and improved management. Fate is not kind to the millions of less competitive piglets which, without well-designed environments and skilful handling, will die in such unappealing ways as starvation and traumatic injury. In my view, piglet mortality deserves to be viewed as an animal welfare issue of high priority, and it represents one of the many areas where animal welfare and commercial interests coincide.

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