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The Behaviour of Swine

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The pig was a forest-dwelling animal from the beginning of its history. In some parts of the world it has been domesticated for at least 7000 years. The European breeds of domestic swine were derived from the local wild pig, *Sus scrofa.* Herds ranged in pastures and forests and kept indoors only for fattening. The breeds in the Far East were derived from another wild pig, *Sus vittatus,* a smaller animal with shorter legs and a higher reproductive ability (Mohr 1960; Zeuner 1963). The two types interbred readily. The modem breeds of pig evolved from different crossings between the two original types. They form a rich diversity of genetic material and more than 200 breeds have been catalogued. Certain wild types of pig-like animals, such as the African bush pig (*Pontamochoerus larvatus*) and the wart hog (*Phacochoerus aethiopecus),* have never been domesticated.

The basis of the social structure in feral swine is the matriarchal herd: one or several females with their offspring. The males are not permanently associated to such herds, often ranging solitary or in 'bachelor' groups (Fig. 52). Under domestication the pig has been modified from a pugnacious, free-ranging, foraging beast to a more docile animal which is handled readily in large groups under conditions of confined rearing. The behavioural plasticity of swine is emphasized by the rapidity with which wild pigs have adapted to rearing in restricted conditions. Although most of our knowledge of the behaviour of swine has been gained from data collected incidentally to research on nutrition, breeding, physiology and management, a number of experimental studies have recently appeared in learning, adaptation, social, sexual and maternal behaviours, making the pig the best known species among domestic mammals, from the point of view of behaviour.

CLIMATIC EFFECTS ON THE BEHAVIOUR OF PIGS

There has been considerable interest in the effects of the physical environment, especially ambient temperature, on the physiological responses or economic productivity of pigs (for reviews see Hazen & Mangold 1960; Bianca & Blaxter 1961; Mount 1968; Stephen 1971; Ingram 1972). However, relatively little work has been done on the effects of the physical environment on the behaviour of pigs, although the subject is of increasing importance due to the development of intensive husbandry systems using controlled environments.

STUDIES UNDER NATURAL OR HUSBANDRY CONDITIONS

The behaviour of pigs under hot, dry conditions has been studied by Heitman et al. (1962), in an experiment in which the pigs were provided with different measures for relief from the heat. The results obtained indicated that, when shade was the only relief measure provided, it was used about 80% of the time between 7 a.m. and 3 p.m. Addition of a wallow reduced time spent in the shade, although the pigs preferred the shaded wallow to the unshaded one. The use of the hut was relatively low compared to other sources of shade. The air-conditioned hut was used about 60% of the time and the use of all the heat-relieving measures increased rapidly when the temperature was above 21°C. The authors stress the importance of shade and wallows to pigs kept in hot conditions.

In hot environments, pigs confined in pens without wallows will lie in areas wet with urine or faeces (Heitman & Hughes 1949), or root up the cooler subsoil and lie on it in an extended posture to facilitate heat loss. Ambient temperature also influences food intake: pigs ate less as ambient temperatures increased from 4°C to 38°C.

The behaviour of a group of young pigs living in a natural environment including both open field and woodland, and in a temperate climate, been studied by Ingram and Legge (1970). Air movement, radiant temperature, dry bulb temperature and rainfall were recorded. The pigs did not begin to shelter and huddle together in the hut until ambient temperatures were below 5°C, although their lower critical temperatures (the temperature below which metabolism increases to maintain body temperature) was estimated to be about 25°C. The pigs tended to spend most of the time in the area of lowest air movement except when food was provided ad libitum when they stayed near the food troughs. They displayed no tendency to select the highest mean radiant temperature.

Fig. 52. The evolution of the social organization of pigs.
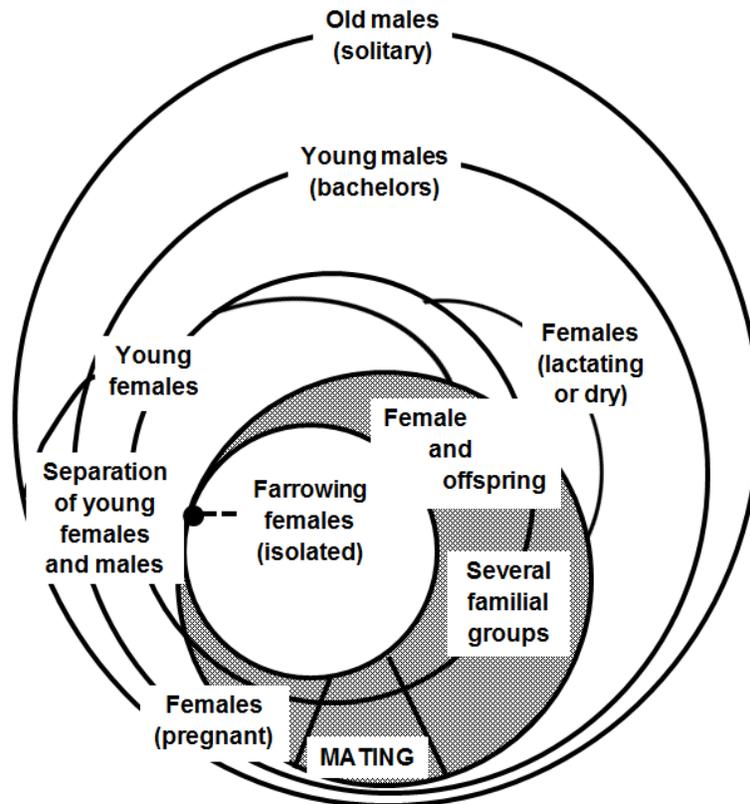
STUDIES UNDER LABORATORY CONDITIONS

In piglets, Mount (1967) has shown that postural changes can modify heat loss considerably. Conductive heat loss to the floor was reduced by 33% when the piglet changed its posture from being stretched out and relaxed, to one in which it was crouched with its limbs under the body and floor contact was minimized. Convective heat loss is influenced by changes in air movement, but Mount (1966) found that the rise in oxygen consumption in pigs exposed to increased air movement was less than would be expected on the basis of experiments with a heated cylinder. Piglets can alter their posture so as to reduce the amount of radiation from their body surface (Mount 1968).

Young pigs huddle together in the cold and Mount (1960) has measured the metabolic savings which this behaviour can effect. When ambient temperatures fell from 30°C to 10°C, the piglets exposed individually increased their oxygen consumption by about 75% while the groups (4-6) only increased their oxygen use by about 50%.

The temperature preferences of young pigs have been studied using a thermocline apparatus (Mount 1963) and it was found that piglets less than 1 day old prefer a temperature of 32°C, while between 1 and 41 days they prefer a temperature of about 30°C.

Although it possesses apocrine glands in its skin, the pig is not a sweating animal and normally loses very little water from its skin. When the skin is wetted with clean water, the effect is short-lived, but when coated with wet mud, the high rate of evaporation persists for 2 hours.

Using operant conditioning techniques, a series of experiments have been carried out to examine the factors which influence thermoregulatory behaviour in pigs (Baldwin & Ingram 1967, 1968a, b). When young pigs aged 8-14 weeks are exposed to cold, they readily learn to press panel switches with their snouts in order to obtain short bursts of

radiant heat from infrared heaters suspended above them. When a range of ambient temperatures from -10°C to +40°C was examined, it was found that the pigs rarely operated the heaters at temperatures above 25°C. It was also shown that pigs in a cold environment will learn to press panels in order to turn off a cold draught from a fan for a few seconds, but at ambient temperatures above 30°C the pigs seldom turned the fan off (Baldwin & Ingram 1967). In similar circumstances pigs aged from 8 to 14 weeks learned to operate the heaters at ambient temperatures of 20°C but not at 25°C (Baldwin & Lipton 1973).

Behavioural thermoregulation has also been studied under more natural conditions in a group of 4 pigs aged 8-14 weeks, and living outside in a small hut with an adjoining yard. A bank of heaters suspended over a portion of the yard could be turned for 6 seconds when the pigs pressed a switch panel. The animals did not operate the heater as frequently as when a single pig is tested in a temperature-conditioned room. They often preferred to huddle together in the hut, especially during the night.

The above experiments illustrate several points regarding behavioural thermoregulation in pigs and emphasize some of the limitations of operant methods. The reduction in the rate at which the heaters were operated when the pigs had access to the larger yard appears to indicate that, in a complex environment, other activities such as rooting or various social interactions take precedence over thermoregulatory behaviour. The operant method is powerful technique for the study of the physiological factors influencing the behaviour, but does not give an indication of the pig's response in a natural environment.

The territorial behaviour exhibited by feral swine may persist under the conditions of domestication. If pigs are not provided with shelters for nesting, they establish a definite area for this purpose. Some home range behaviour may be exhibited in shelter seeking: newcomers to an established group are usually segregated in a separate part of a large shelter or forced to use a separate shelter. When large numbers of pigs are brought together in stockyards, they bed down in groups according to the farms from which they originated. Littermates also tend to nest together.

Eliminative behaviour does not take place anywhere in the territory: when confined to a relatively small pen, they use one corner for this purpose.

Gates can be used in a permanent structure to restrict the size of the nesting area so that the animals are forced to eliminate elsewhere. Some buildings are constructed with a dunging alley in which the animals are trained to excrete. Patterns of elimination are influenced by the location of food and water; generally, much of the excreta is deposited near the water source.

ACTIVITY PATTERNS

Swine are not well adapted to running. In the wild pig, trotting is used for long-range displacements and galloping for short periods during emergencies. The activity pattern of adult swine is largely diurnal. But during hot weather, or in tropical environment, they are active during the night. When pigs are kept indoors and fed on concentrates, they may rest up to 80% of the time (Diousson 1965; Lips 1965); on pastures, they spend most of the day foraging, rooting and walking. The nocturnal pattern of activity in the feral pig seems to be a consequence of hunting.

The insatiable curiosity of the pig (Plate XI(a)) deserves careful study. When a person approaches a herd an alarm call, or 'woof', is given and the animals may scatter in apparent fright. If the intruder stands still or sits down, the pigs invariably return to investigate by smelling, rooting and nibbling. They are particularly apt to bite rubber boots, or roots at gates and doors that could allow them access to an unexplored area. When large groups of pigs are raised in close confinement, on concrete, they have little area to explore and a limited distance to travel for food and shelter. Rooting, nibbling and chewing are prevented. In such a situation, destructive activities like tail-biting may occur. The frequent distribution of fresh straw reduces the occurrence of this abnormal behaviour (Van Putten 1967). A play object, such as a chain or rubber hose in each pen, will also occupy the group's attention and may minimize tail biting.

TEMPERAMENT AND EMOTION

Hodgson (1935) found genetic segregation in temperament among a series of highly inbred lines. One line became aggressive, while sows of a second line were placid to the point of utter indifference towards their litters. There was a

high percentage of neonatal mortality in both lines. Sows of the former lines· were so nervous that piglets were trampled to death, whereas the latter line sows were so lethargic that they did not respond to the squeals when they. accidentally lay on their young. Susceptibility to alarm may be heritable (Dawson & Revens, 1946). Considerable individual variation occurred among 42 sows in the time taken to return to a feed trough after being frightened away by an electric sparking device. Strain, sex, season and individual variations exist in the 'open field behaviour' of pigs (Beilharz & Cox 1967b). Stress reactions may occur when pigs are transported or penned together for the first time (Cena 1965). Some breeds, such as the Belgian Pietrain, are much affected by transport stress. How temperament may affect learning ability is brought out in the next section.

SENSORY CAPACITIES AND COMM UNI CATION

Olfactory and auditory cues play a part in the feeding behaviour of feral pigs (Bobak 1957). The light wave-lengths to which pigs are maximally sensitive are slightly lower than those for humans, within the range of 465-689 nm. If strong responses to non-visual cues for food are developed early, vision will not be used later by the animals in this context.

Audition. Hearing is well developed in feral pigs. Since the ears are relatively short and immovable, localization of sounds is made by movements of the head. Marcuse and Moore (1946) trained pigs to lift a lid for food in response to the higher of two tones, 480 and 1000 cycles, respectively. The upper tone was then reduced in 3-4 cycle increments. Until the tones differed by 54 cycles, the animals' general activity was lower during the positive signal and the lid was raised appropriately. Until the tones differed by 24 cycles, the vocal response to the positive signal was a series of short grunts as the lid was raised, whereas during the negative signal it was a high-pitched squeal. There was no discrimination when the tones differed by only 22 cycles. Acoustic signals seem to be of major importance in the organization of social behaviour. Grauvogl (1958) has described more than 20 different sounds emitted during resting, social agonistic, feeding, play, maternal and sexual behaviour.

Smell. The sense of smell is well developed in both feral and domestic pigs. Rooting for buried food is accurately oriented by olfactory cues. Smell is also effective in discriminative learning. Although sows did not learn in 500 trials to discriminate among cards differing in form, colour or size (Klopfer & Wesley 1954), they learned in 10-20 trials to respond correctly to 1 of 3 neutral grey cards from odours they deposited during the trial by touching a card with their snouts. The odours were still perceptible to animals several hours after the trial and after the stimulus card had been washed.

The pig's characteristic odour is produced by various secretions. Several pheromone-producing organs have been studied. The carpal glands are well differentiated on the front leg; their secretions are not sex-related. In the male, the fluid of the preputial pouch produces a sexual pheromone. The delta-16-androstene, present is this secretion and identified by Patterson (1968), is produced in the testis, the submaxillary salivary gland and possibly the skin glands as a result of the metabolism of androgens. This steroid is responsible for the 'boar' odour in pork.

LEARNING AND INTELLIGENCE

Pigs learn easily to manipulate mechanical devices to obtain food water. This capacity is used for self-feeding. The study of learning in animals is an important part of comparative psychology and has been greatly facilitated by the development of conditioning procedures.

Classical conditioning may be considered as a method for achieving a degree of stimulus equivalence in which a previously neutral stimulus becomes capable of eliciting a conditioned response. Such techniques have not often been used in pigs, despite their interest.

Operant conditioning is a procedure which will reliably increase the frequency of any behaviour in the repertoire of an animal: animals will learn to respond in order to obtain what they want or to remove something they dislike. Such techniques were successfully used by Baldwin to study temperature and food preferences in pigs. A classically conditioned response can be superimposed upon operant responding for food; when an electric shock is paired with a tone operant responding is rapidly suppressed with tone alone (Dantzer 1972; Baldwin & Stephens 1973).

Avoidance conditioning may be considered as a form of operant conditioning, and provides a convenient method for examining the performance of a large number of animals in a relatively short time. Willham et al. (1963) concluded on

the basis of performance of the pigs, that 50% of the variance in relatively hologenous groups was due to genetic causes. The Duroc appear as superior in avoidance learning. Other learning studies were seldom used in pigs. Wiekert and Barr (1966) found that in the T-maze, females performed better than males and that breed differences could be demonstrated. Using an 'open field' test for emotionality, Beiharz and Cox (1967b) observed that the measure of exploratory activity in a strange environment has no value in predicting production traits.

INGESTIVE BEHAVIOUR

Feeding Behaviour

Swine are omnivorous and their diet may include a wide variety of foods. Feral pigs eat plants, tubers, roots, seeds, grasses, buds and leaves. They also consume earthworms, caterpillars and slugs, snakes and frogs, eggs and young birds, rodents, or any ill or dead animal (Bubenik 1959; Porzig 1967).

Domestic pigs on pasture spend 6-7 hours a day searching for food and eating. However, the eating time is often less than 10 minutes a day when they are hand-fed with concentrates. With self feeders, the feeding-time is prolonged.

Qualitative regulation diet. The presence and relative amounts of certain dietary constituents markedly affect food intake. The pig's motivation for sugar was measured by an operant conditioning technique in which the animal presses once for the first reinforcement, twice for the second, etc. The pigs went to the highest ratios for the strongest sucrose solution (Kennedy & Baldwin 1973). Saccharin has a positive effect at low concentrations and a negative one at higher doses; cyclamates are without positive action.

In practical feeding, baby pigs prefer rations to which sugar or saccharin has been added (Nelson et al. 1953; Aldinger et al. 1959). Salt and quinine reduce feed intake. The addition of 5% lard to the ration increases the feed consumption of baby pigs (Combs & Wallace 1959).

The palatability of various protein sources and cereals has been studied by Aumaitre and Salmon-Legagneur (1964). Yeast and fish meal additives increase feed acceptance, whereas meat meal depresses it. Soya cake was the only oil cake which increased feed consumption. Wheat was preferred to rye, barley, oats and corn.

The amount of cellulose in the diet also influences feeding behaviour: hulling increases the palatability of cereals, and large amounts of alfalfa meal depress consumption.

Pigs eat balanced amounts of corn and protein supplement when the two are offered in separate parts of a self-feeder.

Mixed rations can be presented in a variety of physical forms from fine meals to compressed pellets of different sizes. Baby pigs consume 6 times more pellets than meal of the same composition (Salmon-Legagneur & Fevrier 1955).

Quantitative regulation of food intake. The feeding patterns of both weanling and adult pigs are influenced by systems of management. Immediately before the usual feeding time, hand-fed pigs move to the feeding equipment or to where the herdsman enters the area. The temporal patterns of ingestion are more casual among self-fed pigs, more nearly geared to individual appetites. Pigs may be stimulated to eat by the movement of others from the nesting area to the feeder.

Group size and interaction of the sexes affect growth and feed consumption (Jonsson 1955). Among the pre-pubertal animals fed in groups of 4 (2 gilts and 2 barrows), barrows grow more rapidly than gilts; the reverse is true among individually fed animals. Daily gains do not differ significantly under the two systems of feeding, but the within-litter variance is 4 times larger under group feeding than individual feeding, suggesting influences of dominance order. Pigs also grow more rapidly when there is competition for space at a self-feeder. Rippel (1960) found that the optimum number of feeder cups was 1 for each 5 pigs. At a ratio of 1 : 7, growth rates were satisfactory for lighter weight pigs, but were sharply reduced after pigs reached 130 lb. There was simply insufficient time for each pig to eat enough feed to sustain maximum growth.

As early as 1883, Shelton reported that feed increases when pigs are kept outdoors during the winter. In a detailed study of environmental conditions Heitman and Hughes (1949) showed that the feed consumption of adult pigs decreased as the temperature increased from 40 to 100°F (4· 4 to 37· 8°C). In a cold environment the thermogenesis uses energy from feed that would be convened to meat at higher environmental temperature. Feed requirement does not increase during the winter if nest areas are provided with electrically heated floors (Barber et al. 1955a). Appetite levels can be modified by genetic selection. The Duroc, for example, has a greater appetite and grows more rapidly than the Poland China, although fewer ingested nutrients are converted to muscle (Gregory & Dickerson 1952).

Feeding equipment and management. To reduce unfavourable competition during feeding, troughs can be subdivided with crossbars or stalls and scattered over a large area. Equipment for self-feeding is designed around the rooting habits of the pig. Self-feeders hold a supply of feed in a series of feeding cups, usually protected from the weather by hinged metal lids. When a pig is *3-5* weeks old, it learns to root up the lids for feed. The generally recommended floor space requirements for maximum growth to 200 lb is 14-20 ft^2 per pig; however, pigs on 7-8 ft^2 gain as well as those with 15-16 ft^2 (Rippel 1960).

Drinking Behaviour

Self-fed pigs alternate between eating and drinking until satisfied. When hand-fed they eat until all the feed is gone and drink water afterwards. Young pigs can learn to manipulate mechanical self-watering devices before 2 months of age. A pig will raise a protective lid with its snout, root against a pressure plate, or bite on a pressure valve inside a short length of rubber hose to obtain water.

SEXUAL BEHAVIOUR

Sequence of Sexual Behaviour

The courtship behaviour lasts only a short time when a boar is placed in a small pen with an oestrous female. The male mounts and ejaculates quickly. The latency of ejaculation is generally less than 3 minutes. However, when females are living freely in a herd, sexual behaviour begins long before the first mating and lasts several days. In this section, we shall be concerned with the detailed description of this behaviour.

Table 31. An Experimental Study of Mutual Attraction of Sexual Partners

Subject	Stimulus		Time spent near stimulus (sec)
Oestrous female	Intact boar		192
	Spayed boar		42
Oestrous female	Intact boar	{ both anaesthetized	148
	Spayed boar	and not visible	64
Anoestrous female	Intact boar		69
	Spayed boar		67
Normal boar	Oestrous female		140
	Anoestrous female		113

The subject is placed in a T-maze for 5 minutes and given a choice between 2 animals, one being a potential sexual partner.
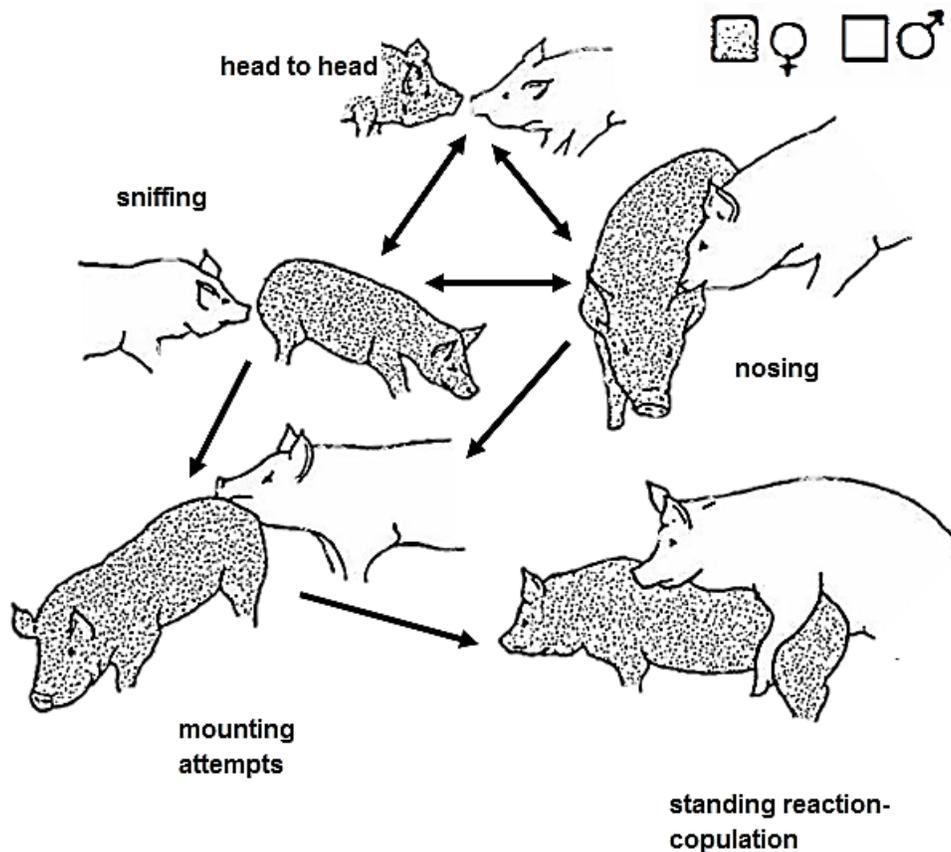
PRELIMINARY PHASE

Behavioural changes occur in the female several days before the onset of oestrus; she becomes nervous and moves about at the slightest disturbance, while her di-oestrous pen-mates continue to rest. When kept indoors, females will use any opportunity to move out of the pen. When pro-oestrous females are tested with boars at regular intervals, they often leave their sleeping quarters to await the arrival of the males as the regular time of testing approaches. Movements in an open field are more frequent. Spontaneous activity increases to about twice the normal level during

oestrus. Di-oestrous females show frequent genital control, nose the flanks of their oestrous penmates, and attempt to mount. At this time and during oestrus, the sow utters characteristic sounds, a soft rhythmic grunt (Grauvogl 1958).

Meeting of sexual partners. When placed in a group of sows, the male controls each female successively, sometimes pursuing an anoestrous one fiercely. In such a group, the oestrous sow will immediately go to the boar, sniff the anal and preputial regions, and remain close to him. T-maze experiments indicate that the male attracts the oestrous and pro-oestrous female (Signoret 1967b). The sows show a definite orientation towards the boar 1 day before oestrus. This reaction becomes more intense during oestrus and lasts for two days after oestrus (Table 31). The olfactory stimuli seem to account for such an attraction as the oestrous sow reacts in the same way towards an anesthesized boar that she cannot see. On the other hand, the male shows little preference in a similar choice experiment between an oestrous and an anoestrous sow. These results confirm the herd observations on the critical role played by the female in the meeting of sexual partners.

Fig. 53. The sequence of precopulatory behaviour in swine.

PRECOPULATORY PATTERNS

Both male and female exhibit some preliminary courtship behaviour before mating. The sequence of events which occur in precopulatory behaviour patterns is presented schematically in Fig. 53. When a male approaches an oestrous female which runs from him, he will follow her persistently and attempt to herd her to a standstill. Should the opportunity afford itself, he will nose her sides, flanks and vulva during pursuit. During this activity, and much of what follows, the boar emits 'mating song' (*chant de cour*) a regular series of soft, gutteral grunts, about 6-8 per second at an intensity of 85-95 decibels at a distance of 1 m; he pauses every 15-20 seconds to catch his breath (Signoret & Du Mesnil Du Buisson 1961). A male rarely uses the 'mating song' when he approaches a stationary oestrous female. He lightly presses his nose against her head, shoulder or flank, and as he reaches her genito-anal region, his nuzzling generally becomes more vigorous. When he sniffs her genitalia, he often pokes his snout between her hind legs and,

with a sudden jerk lifts her hindquarters into the air. During this phase of courtship, the boar grunts continuously, grinds his teeth, moves his jaws from side to side and foams at the mouth. A rhythmic emission of urine is characteristic of the boar during sexual arousal and occurs during the preliminary phase of sexual behaviour. The female shows a special interest in the male and nuzzles his scrotum, flanks and genitals. She bites his ears lightly, and the animals often remain head-to-head. The female also sometimes tries to mount the male. Mutual mounting attempts or genital sniffing lead to the parallel position frequently described in other ungulates. The characteristic response of the sow which is willing to mate is the standing reaction or mating stance. This is finally adopted by the female and ends the preliminary phase of sexual behaviour by allowing the boar to mount and copulate. The sow becomes stationary, arches her back, cocks her ears and is rigid in every limb. In this stance, she is moved only with a great effort, and cannot be herded in the ordinary way.

All elements of the courtship pattern are not displayed in all circumstances; considerable variation occurs, for example, in the frequency and duration of pursuit and nuzzling. During extremely hot weather, sex drive declines, and boars cease to mate about mid-morning and do not resume such activity until dusk.

Mate preference. Some sows seem to be more attractive to boars than others, and some females are exceptionally receptive to specific boars. A female may also occasionally display a decided aversion to a particular boar. This may be associated with the order, frequency, and/or intensity of the elements in his mating pattern.

MOUNTING

The boar mounts a female in the mating stance immediately. In records of 202 natural matings (Signoret 1968), the average mount latency was 43 seconds; during semen collection with a dummy, 3260 ejaculates were obtained in an average of 72 seconds. Only 17.4% of fully receptive females are not mounted immediately when presented to a boar (Schenk 1967). Some boars mount and dismount a female repeatedly before coitus; other boars mount once and copulate. During mounting, the boar swings his trunk upwards to a nearly vertical position and rests his forefeet on the female (Plate XII).

The frequency and duration of mountings for each mating depend on the receptivity of the female, her ability to support the weight of the male and the dominance interactions among boars. During multiple sire mating, it is not unusual to see a female being mated by one male, while one or two other boars are mounting her head or sides. The mounting of the forequarters is more common in young boars than in those with sexual experience.

INTROMISSION AND EJACULATION

The mounting boar thrusts until the tip of the partially exposed penis penetrates the vaginal orifice. Only then is the penis fully unsheathed. The penis is of fibro-elastic type, spirally shaped with a pre-scrotal sigmoid flexure, and does not enlarge during erection. When intromission is vaginal, the boar seldom withdraws or dismounts and ejaculation occurs. A series of pelvic thrusts may occur after a rectal intromission, but the penis is most often withdrawn without ejaculation.

During ejaculation the boar's haunches are clenched together and pressed forward, and a muscular wavelike movement of the perinuem is visible as anal winking. One of the testes is retracted so that a visible contraction occurs on one side of the scrotum. Two or three separate waves of semen may be ejaculated before the boar dismounts.

Among farm animals, the boar has the longest ejaculation time. Copulation is performed within 3-20 minutes with an average of 4-5 minutes (Burger 1952; Bascos 1953; Signoret 1968). The female generally remains completely immobile until the boar dismounts. The female sometimes (18% of observed cases) moves at the end of copulation, but this seldom disturbs ejaculation (Schenk 1967). After mating, the sow remains by the boar and often licks the flocculent discharge which accumulates on his penis. When Burger (1952) allowed each of the two boars free access to a female during a complete oestrous period, they mated 7 and II times respectively; the interval between matings ranged from 0.2 to 15.4 hours (Fig. 54). In similar circumstances, other boars mated 4-8 times, with an average of 6.6 times (Bascos 1953).

Fig. 54. Frequency and duration of copulation of a Large White boar when allowed free access to a single sow during one oestrous period. Data from Burger (1952).

Presentation of a new oestrous sow was the most successful stimulus in eliciting repeated ejaculation. During 40-minute observations, sexual activity was not renewed after arousal or physical activity if the boar remained with the same female. The boar ejaculated immediately when a new female was presented. An attempt was made to find out how often this response could be elicited by presenting a new sow to boars immediately after each ejaculation, or after 30 minutes, whichever occurred first. Up to 5 successive ejaculations took place; the latency of ejaculation, but not the duration, was prolonged with successive ejaculations.

Sexual Functions in the Male

STIMULI RELEASING THE MALE SEXUAL RESPONSE

All the patterns of courtship behaviour may be released in the boar by a di-oestrous female, another male or a variety of inanimate objects ranging from dummy sows to oversimplified devices for semen collection looking more like a table than an artificial female (Ito et al. 1948; Aamdal et al. 1958; Paredis 1961) (Fig. 55). According to Buchlman's (1950) hypothesis for cattle the main stimulus which releases mounting behaviour in the boar is a visual one: an immobile structure looking more or less like a conspecific animal. This mechanism seems to have an innate basis: young boars reared in groups of males will readily mount a simplified dummy at the first opportunity. If ejaculation is achieved, i.e. if semen is collected in an artificial vagina, the response will be retained. However, visual stimuli from the shape of the body, head and ears are increasing the value of dummies (Rothe 1963). A young pig tethered under the dummy has the same effect (Smidt 1965).

ABNORMALITIES IN SEXUAL BEHAVIOUR

The mounting reactions of the male, released by a simple visual stimulus, may explain the abnormal mounting (Plate XII (c)) and homosexuality which are frequently observed in swine.

Boars reared in pairs of all-male groups often form stable homosexual relationships.

The so-called bizarre sexual objects may take their origin in the same mechanism: if the sex drive is sufficiently high, an oversimplified schema may release the sexual response. Some boars for example, will mount a watering device, a straw pack, etc.

Fig. 55. Various artificial devices for semen collection in the boar.
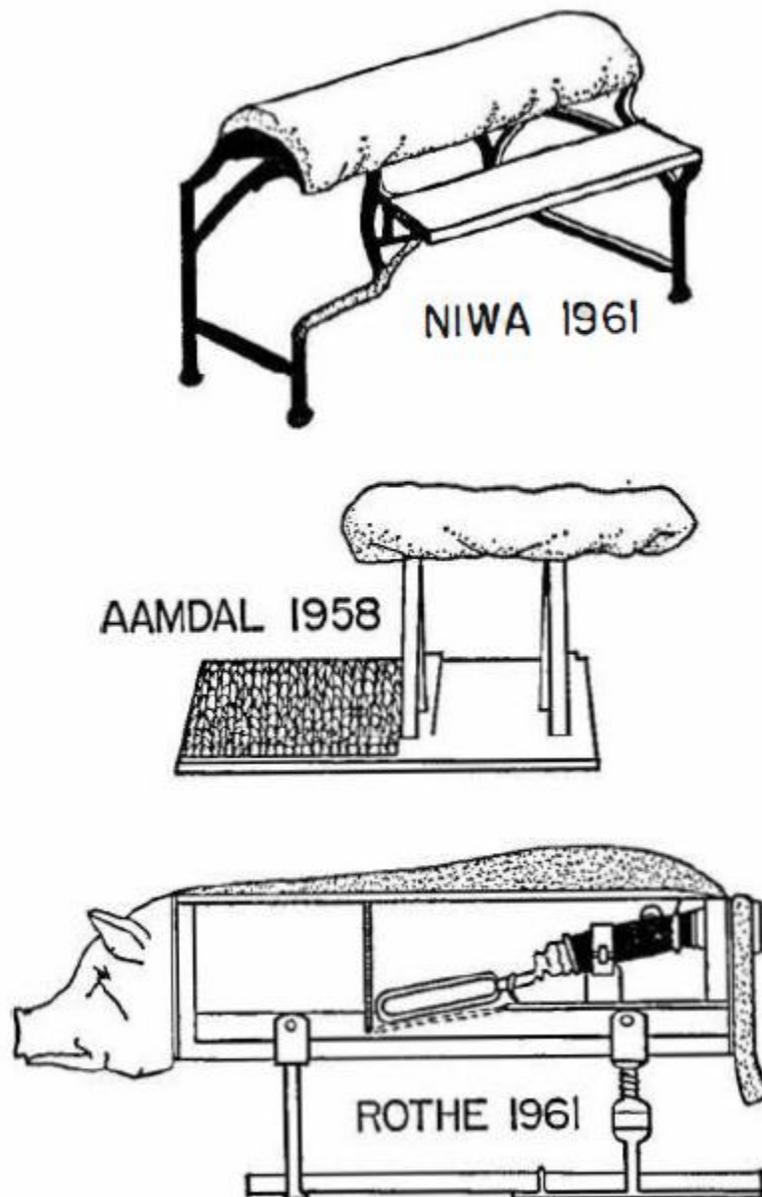
PHYSIOLOGICAL ASPECTS OF THE BOAR'S SEXUAL FUNCTION

The boar generally reaches puberty before 7 months of age but the age of physiological maturity (presence of spermatozoa) may differ from the time of appearance of mating behaviour. A coordinated behavioural response is seldom evident before 130-150 days of age. However, testis weight and sperm output increase until the age of 1 year. The stimuli which cause ejaculation appear to be essentially tactile. The fixation of the spiral-shaped penis in the cervix seems to have major importance. This is obtained in an artificial vagina with increasing pressure. Thermal stimuli are unnecessary (Table 32). Boar semen is characterized by its large volume, relatively low concentration and

high total number of spermatoza. The presence of a gel-like material should also be noted. Semen is ejaculated in different fractions : a preliminary one; one rich in sperm; and a third with the largest volume but a low concentration of sperm. Gel-like material is emitted throughout ejaculation. Sperm emission through a fistula in the vas deferens occurs only during collection of the rich fraction (Wierzbowski & Wierzchos 1968).

Table 32. Sexual Functions in the Boar.

Patterns	Values
Age at first meeting	5-8 months
Mounting latency	30-70 seconds
Duration of ejaculation	5 minutes
Semen volume*	300 ml
Gel volume*	40 ml
Number of sperm/ejaculate*	1×10^{11}

Highly variable depending on how often semen is collected.
These figures are for 1 collection per week.

GENETIC FACTORS

The inheritance of patterns and intensity of sexual behaviour is evident when clear-cut differences between breeds are demonstrated. The broader differences between breeds are brought out clearly when experimental and environmental factors remain constant, and individual variations are consequently minimal. Even when both environment and experience are carefully controlled, variation within any one breed is considerable.

Sexual Functions in Females

PUBERTY AND CYCLE

Puberty. Most gilts reach puberty at 6-18 months of age; breeds differ in this respect and heterosis is expressed by earlier maturity of some breed crosses (Foote et al. 1956).

The length of the normal oestrous cycle is 21 days, with some variation according to breed (reviewed by Boda 1959; Signoret 1967a). Once the oestrous cycle begins it continues to occur regularly, unless the sow becomes pregnant. 'Abnormal' cycles longer than 30 days represent only 5% of the 1800 cycles observed by Signoret (1967a).

There is no evidence of seasonal changes in the female sexual cycles of domestic breeds (Burger 1952; Signoret 1967a). Feral swine reportedly have a breeding season in November-December, although this may begin as early as July and continue until February. No detailed study of this surprising difference between domestic and feral swine has apparently been made.

Fragmentary evidence suggests that a sudden alteration in management such as feeding regimen or movement of females from one pasture or one farm to another, may cause a change in the oestrous cycle. Thirty per cent of prepubertal gilts exhibit their first oestrus on the fourth, fifth and sixth days after transport (Du Mesnil Du Buisson & Signoret 1962).

Oestrus. Burger (1952) found no diurnal pattern in the onset of heat. Oestrus normally lasts 40-80 hours (Signoret 1967a), its length varying with breed, reproductive cycle and season.

The duration of heat is reduced by continuous presence of the male, even in ovariectomized females injected with oestrogen. However, one or two matings without further contact with the boar are ineffective. Ovulation takes place earlier and in a shorter time after copulation (Table 33). In the ovariectomized sow one oestrogen injection induces normal sexual behaviour. The response is unaltered after cyclic treatment for 1 year. The duration of oestrus increases logarithmically with the doses of oestrogen (Table 33), but the delay between injection and the onset of oestrous behaviour is unchanged (about 70 hours). A dose of 0.6-0.7 mg of oestradiol benzoate induces an oestrous

period of normal length in gilts weighing approximately 120 kg. Individual and seasonal variations also occur in the duration of heat.

Synergistic action of progesterone and oestrogen does not exist in the sow but sexual behaviour can be inhibited by progesterone injected after oestrogen.

Table 33. The Effect of the Presence of the Male and the Occurrence of Copulation on the Duration of Oestrus and Ovulation in the Sow

Parameter	Duration (hours)
Duration of oestrus in intact gilts not mated	55
Duration of oestrus in intact gilts mated twice (6 hour interval)	55.8
Duration of oestrus in intact gilts artificially inseminated	55.9
Duration of oestrus in ovariectomized gilts injected with 1 mg of oestradiol benzoate:	
oestrus detection at 6 hour interval	75
duration of oestrus in permanent presence of a boar	65
Average end of ovulation after the onset of oestrus, sow isolated	42
Average end of ovulation after the onset of oestrus in the presence of a boar	35
Average duration of ovulation, sow isolated	4
Average duration of ovulation in the presence of a boar	1

SIGNS OF OESTRUS

Restlessness, capricious appetite, mounting of other females, and frequent attempts to urinate, particularly in the presence of a boar, are characteristic behavioural signs of oestrus. Spontaneous activity reaches about twice the normal level during late oestrus.

The vulva begins to enlarge 2-8 days before the onset of heat. It becomes red and a mucous discharge appears. Aborization of cervical mucus (Betteridge & Raeside 1962) and changes in vaginal pH (Schilling & Rostel 1964) are reportedly good physiological indicators of oestrus.

SEARCHING FOR THE MALE

A tendency to go to a male in a T-maze appears in oestrogen-injected spayed females (see Table 31) and the attraction of the male increases with the dose of hormone (Signoret 1967b).

The response persists in gilts reared in isolation from birth. When they are presented to a boar after hormone treatment, they go to him immediately. On the other hand, if females are spayed, but not injected with hormone, they react identically towards a male or female at first contact. The attraction for the male is apparently endogenous and not acquired by social experience.

IMMOBILITY REACTION

When an oestrous female is touched on the back by a boar or by a handler, she assumes a stationary position (the mating stance or immobility response). Every oestrous female assumes this stance more or less quickly when presented to a boar; however, only 48% of the oestrous gilts tested by the herdsmen do so in the absence of a male. The frequency of response increases from 40% before the tenth hour of oestrus to 60% between the twenty-fourth and thirty-sixth hours.

Gilts reared in isolation from birth react in the same way as do normal females when tested after ovariectomy and hormonal treatment; some become immobile immediately, whereas others do so only when presented to a boar. Schenk (1967) was unable to demonstrate any difference between gilts and sows.

Signoret and Du Mesnil Du Buisson (1961) have determined the stimuli which initiate the immobility response. Olfactory and auditory stimuli appear to be most important; 90% of the oestrous gilts tested responded in the

presence of these stimuli only (Table 34). The addition of visual and tactile stimuli increased the number responding by 7 and 3% respectively.

When a recording of the mating grunts was broadcast during the test, 50-60% of the females assumed the mating stance. The odour of a pen from which a boar has been recently removed also elicits the immobility response in 62 % of oestrous gilts. The odour of preputial secretion has the same effect. The fluid can be easily collected from the preputial pouch, but must be warmed to body temperature: it is not effective below 20-25°C (Signoret 1965). 5α-androst 16 ene-3-one isolated by Patterson (1968) is apparently responsible for 'boar' odour and for this olfactory stimulation.

Table 34. Effectiveness of Various Stimuli in Releasing the Postural Standing Reaction of Oestrous Sow

Stimulation	Postural standing reaction (%)
Pressure on back only	48
Broadcasting boar's courting grunts	70
Odour of preputial secretion at 40°C	80
Smell and sound of boar	90
Smell, sound and sight of boar	97

MATERNAL-NEONATAL BEHAVIOUR

During the last month of pregnancy females may show a reduction in activity, and feral sows restrict themselves to smaller home ranges which include the farrowing nest (Kurz & Marchinton 1972). Vulval swelling and enlargment of the mammary glands are often apparent several days prepartum, but the time of their onset is quite variable (Jones 1966). More reliably a serous secretion can be detected when the teats are squeezed up to 48 hours before parturition; the secretion generally turns milky 24 hours or less pre-partum.

Nest-building and Parturition

During the last 24 hours or more before farrowing, sows typically show a great increase in restlessness (Jones 1966). In farrowing crates the animals may grind their teeth, bite and root at the rails and change position frequently between standing and lying. Experienced mothers may be more placid than primiparae.

Nest-building is most common during the 6 hours before parturition but may persist for a day or more (Jones 1966). If a domestic sow is on pasture during this time, it will often choose a nest site, hollow a depression in the ground, and line the depression with straw, grass and other material which may be carried for some distance. The sow resists most human attempts to re-locate the nest, but will move the nest away from air currents (Hosman 1971a). Farrowing crates and concrete floors prevent much of the nest building behaviour, but many of the motor elements are still present. Periods of nest-building typically alternate with quiet intervals when the sow lies on its side and may show mild abdominal straining.

Farrowing appears to follow a diurnal pattern: parturition is rare during the morning and early afternoon, more common in the late afternoon, and most common during the night (Grauvogl 1958; Friend et al. 1962).

About 10-90 minutes before the birth of the first piglet, the sow's nest-making and other restless activities cease, and the animal settles, lying on one side. Abdominal straining then becomes more apparent and movements of the legs are common. A small amount of viscous fluid, perhaps slightly blood-stained, escapes from the vulva, and the first piglet is typically born no more than 20 minutes later. Between the birth of successive piglets the sow may shiver and show more abdominal straining and further vaginal discharges. The tail is often swished vigorously seconds before a birth (Jones 1966; Randall 1972).

Sows usually remain lying on one side throughout most of parturition, but piglets are sometimes born when the sow is standing or lying on its belly (Randall 1972). Restless females may stand or change position after the birth of individual piglets, and this increases the likelihood that the sow will damage the piglets by lying on them. Primiparae in particular may become disturbed when the piglets approach the female's head for the first time (Randall 1972).

Occasionally, females will attack their own young under these circumstances, but damage can usually be prevented if the young are removed as soon as they are born and returned a few hours later.

Most piglets are freed from the drying fetal membranes soon after they begin to move about, but weak animals may not escape. The umbilical cord is commonly intact when the piglet is born (Plate XIII), but it is usually detached within 15 minutes. Some sows eat all or part of the placenta.

Table 35. Typical Farrowing Statistics for Swine

Feature	Value
Vulvar swelling	1-7 days before parturition
Milky secretions on udder	6-48 hours before parturition
Sow settles, lying on one side	10-90 minutes before parturition
Vulvar discharge	1-20 minutes before birth of first piglet
Time to farrow entire litter	3½ hours (½ to 16 hours)
Additional time to expel membranes	4½ hours (0 to 12 hours)
Interval time between piglets	16 minutes (1 minute to several hours)
Piglets in posterior presentation	25-45%
Piglets in dorsosacral presentation	95%
Piglets with umbilical cord intact	60-70%
Perinatal mortality	6%
Time for piglets to suck on teats	10-35 minutes

Data from Grauvogel (1958), Friend et al. (1962), Friend and Cunningham (1966), Jones (1966) and Randall (1962).

About 6% of piglets die within an hour or two of birth (Friend et al. 1962; Randall 1972). The still-birth rate is particularly high in long farrowings and toward the end of farrowings.

In many quantitative measures the sow's farrowing behaviour is highly variable. Some typical statistics are shown in Table 35 which is based on a number of different studies using different breeds and procedures; not all observers have reported similar findings.

Nursing and Suckling

Compared to other mammals, swine display rather complex nursing and suckling behaviour. Nursing is very frequent, occurring every 50-60 minutes on average (Barber et al. 1955b; Niwa et al. 1951). The sow requires considerable stimulation from the piglets before milk is ejected. Accordingly, nursing episode often lasts from 2 to 6 minutes with milk ejection lasting only 10-25 seconds toward the end of this period. Throughout this time the piglets progress through a succession of different types of behaviour and the sow vocalizes continuously.

Pattern of nursing behaviour. At the beginning of a nursing episode the sow usually lies on one side with its head back, its udder turned to expose both rows of teats, and with the uppermost legs often held in the air. When the piglets are on the udder the sow gives rhythmic grunts. Typically, the rate of grunting is fairly constant for a minute or more, and then increases, sometimes abruptly (Fraser 1973). Milk flow normally begins 25-35 seconds after the beginning of the period of rapid grunts. During milk flow, or even before it has started, the sow's grunting declines in frequency and eventually stops. Some sows show a second peak in grunt rate near the time of the beginning of milk flow (Whittemore & Fraser 1974).

Phases of suckling. The behaviour of the piglets generally progresses through 5 phases during a single suckling, although the divisions among them are not always clear-cut. Initially the piglets collect at the udder and jostle for position. This behaviour gradually merges into the second phase in which the animals nose the udder vigorously with their snouts. In the third phase the piglets hold the teats in their mouths, usually sucking with slow mouth movements of about 1 per second. When milk flow begins the piglets suddenly draw back slightly from the udder and commence sucking with rapid mouth movements of about 3 per second (Phase 4). Finally milk flow ends, and the piglets may dart from teat to teat, and recommence sucking with slow movements or nosing the udder.

The phases of suckling arc related in a systematic way to the behaviour and rate of vocalization of the sow (Fig. 56). The phases of competition for teats and of nosing the udder (Phases 1 and 2) generally last for r or more minutes and occur during the early period when the sow's rate of grunting is fairly constant. Phase 3 (slow sucking) typically begins at the time when the rate of grunting increases and lasts for about 20 seconds. Phase 4 coincides with the period of the main milk flow, usually lasting 10-20 seconds; and the heterogeneous Phase 5 begins when the flow has ended and may continue for several seconds or several minutes (Plate XIII).

Fig. 56. Suckling behaviour is related to the nursing grunts of the sow. The broken vertical line shows the beginning of milk flow, at which time all litters change from Phase 3 (sucking with slow movements) to Phase 4 (sucking with rapid mouth movements or 'true sucking'). The heavy line shows the mean number of grunts given by the sow, averaged round the beginning of milk flow. The broken sigmoid curves indicate the times at which the various litters made the transition from each phase to the next. Phase 1: competing for teats; Phase 2: nosing the udder; Phase 5: return to nosing or slow sucking after the end of milk flow. Averaged over 85 nursings by 15 sows. *(After Whittemore & Fraser 1974)*
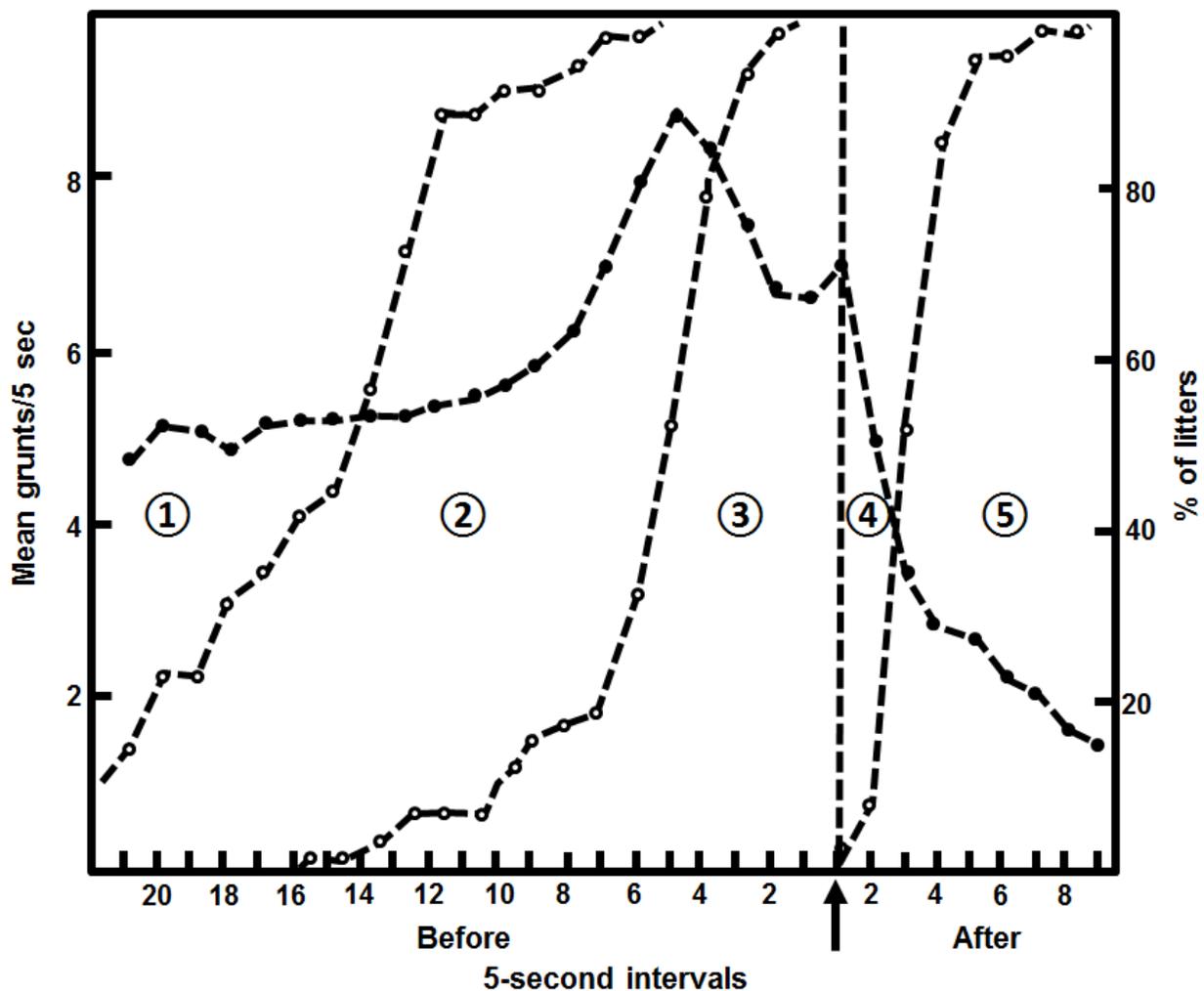
Development of the behaviour. The nursing vocalizations of the sow do not take on the pattern shown in Fig. 56 until about one day after farrowing. During this day milk is generally available to the piglets for passive withdrawal, and the piglets do little more than suck on the teats. Thereafter, however, a concerted effort by the piglets is required if the

sow is to eject milk; but still the distinct phases of nosing and sucking may not be apparent for several more days. Barber et al. (1955b) observed no distinction between Phases *3* and 4 until their piglets were 6 weeks of age; some other investigators have not observed this distincti:on at all (Donald 1937; Gill & Thomson 1956). Niwa et al. (1951) recorded changes from birth to weaning in various quantitative aspects of nursing and suckling behaviour (Fig. 57).

Fig. *57.* Qualitative changes in nursing and suckling behaviour during an entire lactation, based on 5 Middle White sows. *(After Niwa et al. 1951)*
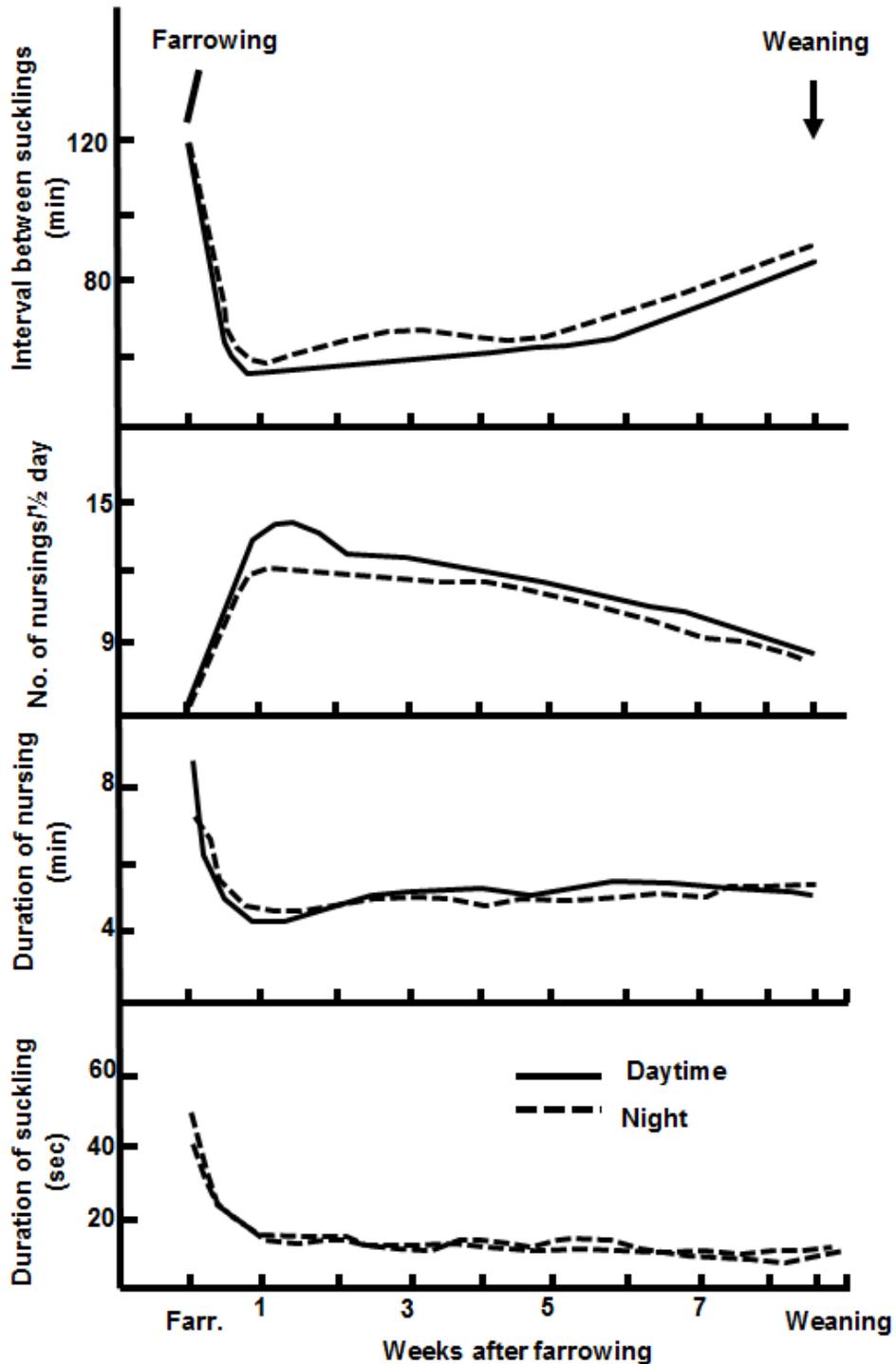
On intensive units sows may give a certain proportion of unsuccessful nursings in which no milk is ejected (Whittemore & Fraser 1974). The cause of these unsuccessful nursings is not clear, but fright or adrenaline injections can inhibit milk ejection (Braude & Mitchell 1952).

Initiation of the behaviour. It is frequently impossible to distmguish whether a nursing episode has been initiated by the sow or the piglets: the sow may begin to grunt and expose its udder, and the piglets may rise and begin to squeal almost simultaneously. At other times, however, the sow may rouse the piglets by grunting or nudging them; alternatively some of the piglets may stimulate the sow to expose its udder by squealing and nosing at her side. Since almost any disturbance may cause the piglets to rise and squeal, nursing can commonly be provoked by commotion in the piggery. This is particularly true on intensive units where the sounds of one litter nursing seem commonly to initiate nursing among other litters (Hosman 1970).

Nursing position. A sow usually lies in one particular part of the pen fornursing. Many animals nurse about equally often lying on the right and left sides (Hopler 1943); but the variation is enormous. For sows which consistently lie on the same side, the teats of the bottom row may give less milk, presumably because they are less available for stimulation by the piglets (Gill & Thomson 1956). Feral and phacochoerus pigs frequently nurse in a standing position (Fradrich 1965). This is also common among some domestic sows, particularly, it appears, if the litter is large and engages in noisy fighting on the udder.

Orientation of the piglets on the udder. Within the first day of life most litters demonstrate a strong tendency to occupy the anterior teats preferentially (Wyeth & McBride 1964). This apparent preference soon becomes fixed since the piglets, during the first few days, show increasing consistency in returning to the same part of the udder at each suckling (Van Loen Molennar 1967). The consistent position which the piglets occupy & on the udder is generally called the 'teat order' but this should not be confused with any form of dominance order or with leader-follower relations.

There is a tendency for the piglets on the more anterior teats to become particularly heavy (reviewed by Barber et al. 1955b). It is frequently suggested that the anterior teats have greater potential for milk production, but there are many other possibilities. Some of the superior growth of anterior-suckling piglets may reflect an advantage possessed at birth, as there is a weak tendency for piglets with high birth weight to occupy the anterior teats (Wyeth & McBride 1964; McBride et al. 1965). However, this relationship has not been detected in all studies (Navratil 1959).

The tendency of the piglets to occupy the anterior teats preferentially, and the weak correlation between birth weight and teat number, have sometimes given rise to the belief that the piglets actively fight for the anterior teats, the heaviest animals generally being the victors. While such competition may occur, the great majority of the noisy fighting which is often observed during suckling appears to be simply a result of a breakdown of stable teat order (McBride 1963). Donald (1937) describes one litter which normally suckled successfully if the sow was lying on the right side; but when it lay on the left there was much confusion among the piglets.

The piglets at either end of the udder are particularly consistent in their choice of teat, while those occupying teats in the middle of the udder are likely to make 'errors' (Donald 1937). Accordingly, facial wounds which littermates inflict on each other during disputes over teats are more common among middle-suckling piglets.

Other Maternal Behaviour

Apart from elaborate nursing and nest-building, the maternal activities of the sow are generally quite simple. The piglets typically shed their fetal membranes and find a teat without assistance except that the mother tends to lie with the udder well exposed during and just after farrowing. This tendency may persist for several days post partum when it can serve a second function: the skin temperature of the udder is particularly high, and piglets can keep warm during the critical early days of life by huddling around the exposed udder. Among domestic pigs this behaviour is dangerous, however, since piglets so positioned are likely to be crushed by the sow. Accordingly, creep heaters and farrowing crates are generally used to restrain the sow in one part of the pen while encouraging the piglets to lie elsewhere.

The danger of piglets being crushed by the sow may be due in part to the fact that artificial selection has altered the basic body shape of the animals. Behaviourally the sow is well equipped to avoid damaging her young. Sows

generally lie down very cautiously, and only after ploughing through the bedding with the snout. Furthermore many sows are very responsive to the squeals of their young and will rise in response to the vocalizations of a trapped piglet. However, some placid females appear to have lost much of this tendency.

Compared to other domestic species, sows are very tolerant of foreign young. This is particularly true during the first two days post partum, and fostering can usually be done successfully at this time (Hosman 1971b). Thereafter the sow shows an increasing tendency to distinguish her own young, probably on the basis of smell; a foreign piglet which strays into the wrong pen is likely to be bitten. Interestingly, however, sows are more tolerant of strange piglets if a large number are introduced at once, particularly if the environment is changed at the same time. Accordingly, litters can be placed together in large pens for community rearing, and the sows tolerate the cross-suckling which often occurs under these conditions.

A few sows, particularly primiparae, do not show the usual suspension of hostility to young during the first 2 days of the lactation. These animals will bite even their own young, especially when the piglets first venture near the mother's snout. Randall (1972) observed that such behaviour generally ceases after one or two piglets have found a teat and commenced suckling.
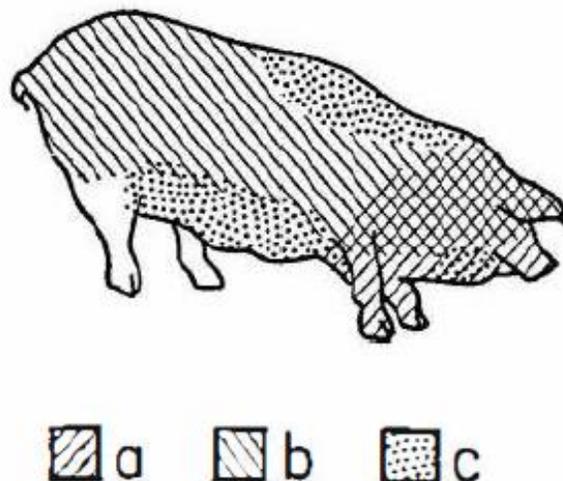
SOCIAL BEHAVIOUR

Feral pigs typically live in herds of less than 10 individuals but groups with up to 80 animals sometimes form. The groups generally consist entirely of females and their young, but boars join the groups particularly during the reproductive season (Snethlage 1934; Heck 1950; Kurz & Marchinton 1972). Under commercial conditions litters are frequently kept together throughout their lives, or they may be formed into larger groups by the sudden introduction of totally unfamiliar animals.

Tactile stimuli are important to pigs, and Hediger (1954) considers them to be 'contact animals', which usually have bodily contact with other members of the group when resting. However, social grooming rarely occurs among pigs (Fig. 58).

There have been few recent studies on the behaviour of domesticated pigs which have been allowed to forage for themselves in the wild (Hanson & Karstad 1959) and the following account of social behaviour is based upon studies using domesticated pigs, usually kept under confined conditions. There is a need for studies on the behaviour of domesticated pigs kept under 'free range' conditions.

Fig. 58. Grooming behaviour. a, The area scratched by the hindlegs; b, The area rubbed on vertical objects; c, The area licked and nosed by other pigs.

The Dominance Order

Social behaviour in pigs has been reviewed by Hafez and Signoret (1969), Bryant (1970), Ewbank (1972) and Meese (1972). Two types of social organization have been described in the domestic pig.

1. The teat order which is established among the litter when the piglets compete for the preferred anterior teats (McBride 1963). This social order has been discussed elsewhere in this chapter.
2. The dominance hierarchy which is established after weaning. According to Meese and Ewbank (1973a) the relationship between these two types of social organization is not yet clear.

It is well known that, when a number of unacquainted pigs are put together, they fight and establish a linear type of dominance hierarchy and, when this has been established, the top ranking pig will, often without fighting, take precedence over all the others in a competitive situation for food. The second ranking pig will be submissive to the first, but will take precedence over all the others, while the third ranking animal will submit to the first and second pigs, but will dominate the rest; the lowest ranking pig will submit to all others in a competitive situation. As Ewbank (1969a, 1972) mentions, occasionally two pigs will occupy the same social rank and be equal, i.e. A > B > C = D > E > F, and sometimes 'special relationships' develop, in which a pig may dominate an animal which, in relation to the rest of the group, is above it in social rank, i.e. A > B > C > D > E > F > G, but F dominates D. Such relationships are sometimes termed 'triangular'.

The experimental determination of a pig's position in the social hierarchy has usually depended upon the observation of the outcome of agonistic encounters to decide which pig took precedence in a competitive situation for food. McBride et al. (1964) considered a social encounter between two individuals with a dominance-subordination relationship as consisting of three components.

1. Intraspecific aggression.
2. Submission signals.
3. The acceptance of submission.

For example, when two unacquainted pigs are placed in a competitive situation for food they will fight and eventually one will win and the loser will retreat. On subsequent occasions, the process will be repeated, usually with the same result, and eventually the habitual loser responds to the mere threat of attack with an act of submission. In pigs the threat may vary from a slight nudge or tap to a bite or slash and submission may vary in intensity from a single backward step to a rapid retreat which may be accompanied by squealing.

However, the subordinate pig may retaliate to the threat and this can occur before, during or after the act of submission. According to McBride et al. (1964), in a well-established social order, communication of threat or submission is formalized and submission may simply be indicated by a lowering of the direction of the eyes. However, Bryant (1970) has observed that retaliation is more common in established groups and may represent 'habituation' of the relationship. Such commonly observed retaliatory behaviour in pigs led Beilharz and Cox (1967a) to classify the dominance-subordination relationship in pigs as 'bidirectional' as opposed to 'unidirectional', in which subordinates never retaliate.

In a bidirectional dominance hierarchy, individuals of different social rank may indulge in aggressive behaviour, but one member of the pair maintains its dominant position by winning more often.

Social dominance in groups of young female pigs has been described by Rasmussen et al. (1962) who determined a linear dominance hierarchy when inadequate feeder space was available. McBride et al. (1964) observed dominance orders in pigs and concluded that growth rate was related to social rank and estimated that at 16 weeks some 13% of the variance in growth was due to social rank. In another study, McBride et al. (1965) partitioned 17% of the within litter variation in weight at 8 weeks old as due to social rank and demonstrated that pigs of high rank were heavier. Beilharz and Cox (1967) examined dominance hierarchies in groups of pigs raised together as complete litters from birth, and observed that the relationships tended to be bidirectional and that males tended to dominate females.

In experiments in which they removed pigs of varying social rank from established groups, and then observed the behaviour which occurred when they were returned after various periods, Ewbank and Meese (1971) examined how

long an isolated pig apparently retained an awareness of the identity and rank of the rest of the group and how well the remainder remembered the identity and rank of the isolate. Removal of pigs of any rank in the social order altered neither the basic hierarchy nor the amount of aggression within the rest of the group. The duration of time that an animal could be removed, isolated and returned varied with its social rank. Top-ranking pigs could be returned safely after 25 days, but low status pigs were severely attacked after only 3 days' absence.

Meese and Ewbank (1972) obtained evidence that the dominance hierarchy can show signs of instability and spontaneous changes in rank can occur without warning and are commonest in middle or lower ranking pigs. It was rare for the top animal to change its position. The establishment and nature of the dominance hierarchy has been studied by Meese and Ewbank (1973a) who formed groups from 8 previously unacquainted pigs. They found that the top pig was identifiable in 30-60 minutes and within 48 hours a dominance order had formed in the group. Most of the agonistic behaviour occurred in the first 24 hours. Social rank was not correlated with sex or weight and the dominant pigs directed most of their aggression to the rank immediately below. They concluded that the basic structure of the hierarchy resulted from summation of the strong relationships which developed between animals adjacent to each other in the hierarchy. They found a tendency towards a bidirectional hierarchy but mentioned considerable variation between different groups in the nature of their hierarchies.

James (1967) has reviewed the value of social status in pigs and concluded that it affected growth rate significantly during the suckling and post-weaning periods. High-ranking pigs have a significant advantage and he considered that body weight and social status were associated in a positive feedback system so that differences in body weight and social status were continually reinforced.

The dominance hierarchy has received considerable attention from research workers and is probably the main mechanism the group uses to regulate its social behaviour although, as Ewbank (1972) has pointed out, this may be due to the fact that most studies on social behaviour in pigs have used groups kept in confinement, which may prevent the occurrence of other forms of social organization. An indication that this may be so comes from observations on exploratory behaviour and leadership-followership relations in groups of pigs living outdoors (Meese & Ewbank 1973b). These workers found no correlation between social rank and exploratory behaviour and leadership with social rank, sex or exploratory activity.

Agonistic Behaviour

IN PIGLETS

Piglets are born with sharp temporary canine teeth and some fighting occurs very early in their lives, particularly during the establishment of the suckling order. Once this is established, there is usually much less agonistic behaviour. Play activities may include fighting but seldom involve prolonged, vicious attacks on litter mates.

IN ADULT BOARS

Agonistic behaviour in adult boars has been described in detail by Hafez and Signoret (1969) and they consider that it is probably related to the establishment of social dominance. When 2 strange boars are first penned together, they smell one another and begin to circle as they prepare to fight. There is an initial period of strutting shoulder to shoulder, with the hair on their backs bristling, and their heads raised in an alert threatening attitude. Some boars paw the ground and, in a serious encounter, the opponents utter deep-throated barking grunts and grind their teeth and snap their jaws (champing) producing large amounts of foaming saliva. Champing continues during the fight and, during typical fighting, the boars assume the shoulder-to-shoulder position and apply side pressure. They circle continuously, always pushing and attempting to slash their opponents by thrusting their heads sideways and upwards with mouth open and teeth bared. These slashes can inflict considerable damage if the boar has its tusks intact and severe lacerations of the shoulder can be caused. Experienced boars often manoeuvre the point of contact forward to their neck region so that they can swing their bodies away from their opponent and offer him a decreased target area. They may also take advantage of opportunities to bite at their opponents' front legs, neck or ears. Boars may also charge their adversaries' sides with mouth wide open to bite. Dominant, experienced boars often resolve a conflict with 2 or 3 quick attacks. However, fighting may continue for 3o-60 minutes and the dominant boar is seldom satisfied until he has pursued the loser and will continue to bite and slash the retreating animal. The loser backs away with

mouth open and head held high, squealing loudly and, if pursued, will turn and run. On subsequent meetings, the victor need only emit a warning glance, or a short grunt in order to induce submission. Fighting between newly mixed boars is less intense if both are in a strange environment.

In adult sows, fighting does not usually include the jaw clicking and salivation seen in boars and, lacking tusks, the sow only tries to bite its opponent.

IN GROUPS OF FATTENING PIGS

The development of intensive husbandry systems, in which groups of growing pigs are kept at high stocking densities, has stimulated some research on the factors influencing agonistic behaviour in such groups. Useful reviews of the effects of intensive systems on social behaviour have been published by Ewbank (I969a, b) and Bryant (1972), and the relation between animal welfare and intensive husbandry has been studied by Brambell (1965) in a comprehensive report.

Ewbank and Bryant (1972) studied aggressive behaviour among groups of pigs kept at various stocking rates. They kept groups of 8 pigs at 0.56, 0.77 and 1.19 m^2 per pig with the feeding and dunging facilities equal for all treatments. They pointed out that the usual growing pig group represents what is effectively a monocaste society, the males being castrated and the females sexually immature for the majority of their lives. In their groups, the usual social organization was a linear hierarchy, with occasional triangular relationships between some pigs.

As the stocking rate increased, the total number of aggressive interactions per unit time went up, but fewer of these interactions were clearly decided in outcome, and there was a greater proportion of retaliation. It appeared that local areas of very high population density, such as occurred around the feeder, often prevented the normal dominance-subordinate relationships from operating. For example, a challenged pig, due to the proximity of other pigs, was often unable to retreat as a submission signal and this apparent lack of submission resulted in the dominant pig reinforcing its attack and often the subordinate would retaliate. Ewbank and Bryant (1972) stress the importance of allowing sufficient space for manoeuvring and indicate that insufficient space predisposes towards a breakdown in communications and resulting increased social strife and weakening of the dominance-subordination relationships.

In another study, Bryant and Ewbank (1972) examined the effects of stocking rate and group size upon agonistic behaviour in young pigs. They used groups of 6, 12 and 18 pigs housed as 0.94 and 0.56 m^2 per pig. It was found that fewer agonistic encounters occurred in the smallest groups with the largest space allowance, but that there was an increase in the proportion of retaliations to threat (i.e. an increase in the intensity of aggression) in the smaller groups compared with the larger. The authors consider that part of the degree of retaliation may have been due to 'habituation' of the dominance-subordination relationships. They emphasize the complexity of the situation and stress the need for more research.

Aggression as a result of mixing groups of unacquainted pigs has been described by Symoens and Van den Brande (1969), who suggested that the initial fighting occurring when intruders were added to residents, was due to territorial defence by residents, and that more prolonged aggression was due to establishment of a new dominance order. Dantzer (1970) studied the aggression following mixing groups of pigs and noted that the dominant pigs were not necessarily the heaviest. The day-to-day variations in the level of aggression in groups of pigs were studied by Meese and Ewbank (1972), who found no correlations with the occurrence of sexual cycles in the females, or variations in the general level of activity in the group.

Several studies have been made on the effect of various stocking rates and group size upon the weight gain of fattening pigs (Heitman et al. 1961; Gehlbach et al. 1966) and the general conclusion is that, as the stocking rate or the group size increases, the average daily weight gain decreases. Ewbank (1972) considers that one of the more important factors involved may be changes in the social environment of the pigs.

TAIL-BITING

Ewbank (1973) states that tail-biting in intensively kept groups of fattening pigs is a disease complex of fairly common occurrence, of widespread distribution, of some economic importance, but of obscure aetiology. Although some general discussions of the problem have been published (Helms 1961; Colyer 1970; and see Van Putten 1968 and

Bowden 1973 for comprehensive reviews) there have been few experimental studies to elucidate the causes of the condition.

The damage due to tail biting can be considered as follows (Van Putten 1969):

1. Restlessness and poor growth rate.
2. Possibly fatal bullying during the tail biting episode.
3. Paralysis and death of bitten animals due to infection of the wounds.
4. Rejection of the pig's carcass during meat inspection at the slaughterhouse.

Ewbank (1973) classifies the possible causes into 6 main sections: *(a)* Genetical factors; *(b)* intercurrent disease; *(c)* physical environmental conditions; *(d)* social environmental factors; (e) teething problems; and (*f*) dietary factors. It is likely that, in any particular outbreak of tail biting, more than one of the above factors may be present. Ewbank (1973) points out that it appears that only two experimental studies on tail-biting have been published and it is obvious that more work needs to be done on this problem.

Van Putten (1969) argued that the pig will sleep for 80% of the day if the environment is satisfactory (Haugse et al. 1965) but, if the pig is not comfortable it becomes restless and, in the absence of straw bedding, will seek something to gnaw. In a typical 'barren' pig pen the ears and tails of other pigs in the group provide possible 'targets'. The ears are sensitive and bites there will provoke retaliation while, in contrast, the tail may be played with and taken sideways into the mouth. Van Putten (1969) states that it becomes bitten, probably by accident, and a small bleeding wound is produced which irritates the bitten animal, causing it to slash its tail around. This encourages further biting and several pigs may chase the wounded animal whose tail may now be gripped violently lengthwise with the incisor or canine teeth and tissue is wrenched off until only the bleeding stump is left.

On the basis of experiments in which he changed the ventilation rate and the concentration of carbon dioxide and ammonia in the atmosphere, Van Putten (1969) concluded that tail-biting was produced by bad atmospheric conditions and mentions outbreaks occurring at carbon dioxide levels of about 0.30% and an 'irritating' level of ammonia at an ambient temperature of 23°C and RH of 80%. He found that the provision of fresh straw bedding reduced the chances of tail-biting even when the climate in the fattening house was unsatisfactory. It is likely that straw bedding not only provides comfort for pigs, but also provides something to chew and play with, thus reducing the 'boredom' which may occur in their relatively barren environment. It seems unlikely that poor ventilation, accompanied by high levels of carbon dioxide and ammonia are the sole factors producing tail biting, as Bowden (1972) mentions outbreaks occurring in the absence of high levels of these gases.

Ewbank (1973) attempted to determine whether tail-biting could be induced by feeding pigs on a high energy, low fibre, vegetable protein diet, in order to test a hypothesis, put forward after an extensive survey of outbreaks of tail biting, by Gadd (1967). Ewbank (1973) was unable to produce tail-biting in groups of pigs kept without straw bedding on such a diet, even when two groups of 16 pigs were inadvertently exposed to relatively high levels of atmospheric ammonia and carbon dioxide.

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