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Physiological and reproductive correlates of behavioural strategies in female domestic pigs

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Abstract. Thirty-seven pregnant primiparous domestic pigs, *Sus scrofa*, were introduced into a large indoor pen. The pigs were divided into three groups according to their ability to displace others in agonistic interactions and the behavioural characteristics of these groups were investigated. High Success pigs were able to displace at least as many individuals as displaced them. They were characterized by low levels of inactivity, high involvement in social interactions and high aggression. No Success pigs never displaced any other pig and were most inactive, least aggressive and showed low involvement in social interactions. Low Success pigs were able to displace some pigs but were more often displaced themselves. They were aggressive, despite their relative lack of success, and experienced the highest levels of aggression from and displacement by others. During the first month in the group, High Success pigs gained the most weight. Low Success pigs had the highest basal levels of salivary cortisol and showed the highest peak cortisol levels in response to an adrenocorticotrophic hormone challenge test. At the first parturition, Low Success pigs produced the lowest weight of piglets born alive. Hence there were more adverse effects associated with being aggressive and often displaced than with being aggressive and usually winning, or being unaggressive and involved in few interactions. The strategy used to cope with the social environment may be as important as the success achieved in agonistic interactions, at least in terms of consequences for physiology and reproduction.

An individual's ability to control or cope with the social environment can affect not only its priority of access to resources such as food, shelter and mates, but also its physiological state and health (Henry & Stephens 1977; Fokkema 1985; Koolhaas & van Oortmerssen 1988). A large body of work has examined the physiological correlates of social rank in male animals classified as dominant or subordinate. In general, the dominant animals have elevated sympathetic–adrenomedullary activity while the subordinates are characterized by elevated pituitary–adrenocortical function (Sassenrath 1970; Henry & Stephens 1977; Ely & Henry 1978; Eberhart et al. 1983; Mormède 1990). Prolonged elevation of sympathetic–adrenomedullary activity can lead to cardiovascular pathologies such as hypertension (Henry & Stephens 1977; Ely 1981; Fokkema 1985; Koolhaas & van Oortmerssen 1988); prolonged activation of the pituitary–adrenocortical system is more likely to result in immunosuppression (Comsa et al. 1982; Barnett et al. 1987; Martin 1988) but may also play a role in cardiovascular pathology (Henry 1983).

Recent studies have moved away from the simple dominant–subordinate classification of individuals and have focused more closely on the behavioural strategies used by animals to deal with the social environment. For example, there may be at least two different ways of responding to failure in agonistic interactions. Von Holst et al. (1983) demonstrated two alternative responses shown by male tree shrews, *Tupaia belangeri*, to dominant male cage mates. The males either remained alert and actively avoided or defended themselves against attacks, or they became very inactive and showed no self defence and little response to external stimuli. This second response resulted in increased adrenocortical function, a rapid decline in body condition and eventual death, while the first response was accompanied by increased sympathetic–adrenomedullary function and resulted in the survival of the individual. Studies of wild house mice, *Mus musculus*, and group-living rats,

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Rattus norvegicus, have also demonstrated the existence of two types of male response to defeat (Fokkema 1985; Benus 1988).

Individuals who are dominant and successful in agonistic interactions can also show different methods of achieving this position. Sapolsky & Ray (1989) demonstrated that dominant male free-living olive baboons, *Papio anubis*, can differ quite dramatically in their behavioural style and physiological profile. Low basal cortisol levels are characteristic of dominant animals who are good at differentiating between threatening and neutral actions of a rival, or who control a situation involving a threatening rival by initiating a fight. Dominant males who do not show these characteristics have elevated basal cortisol levels similar to those of subordinates. The general strategy which the animal uses to respond to the social environment is thus probably more important than the actual social status that the animal achieves, at least in terms of consequences for its physiological state and health.

Much of the work in this area has been on laboratory colonies of male rodents and primates kept in relatively small groups. Our purpose in the present study is to add to the relatively few studies of female animals (e.g. Batty et al. 1986; Schuhr 1987), to examine the responses of individuals to a large social group, and to extend the available data to include a commercially important species which is often kept in high density groups: the domestic pig, *Sus scrofa*.

On many farms, pregnant domestic pigs are kept in large all-female groups in which individuals leave the group to give birth and re-join it after having been separated from their offspring (Hunter et al. 1988). The mixing together of unfamiliar animals, or animals who have been separated for several weeks, can result in high levels of aggression. In this study, we examine the responses of 37 primiparous pregnant pigs to introduction into a new pen and mixing with unfamiliar individuals. Recent work by Lawrence et al. (1991) has shown that female pigs can be distinguished according to their behavioural responses to a series of non-social and social challenges, and that they show some cross-time consistency in their behaviour. Our aim in this study is to investigate whether different ways of responding to the stress of social mixing can be identified and whether any correlates of physiology and reproduction can be found. To this end, we measure each individual's behaviour, weight change, pituitary adrenal function, immunocompetence and reproductive performance.

We assess pituitary–adrenal function using dexamethasone (DXM) suppression and adrenocorticotrophic hormone (ACTH) challenge tests. These tests are of use in assessing the functional state of the system which may, in turn, reflect the psychological state and experiences of the individual during the preceding few weeks. Decreased sensitivity to the suppressive effects of DXM (a synthetic glucocorticoid) on ACTH and consequently on corticosteroid release appears to be related to pituitary–adrenal hyperactivity (Hanin et al. 1985). It has been observed in depressed humans (Hamm et al. 1985), in rats exposed to inescapable electric shock ('helpless' rats, Haracz et al. 1988), in young male pigs subjected to overcrowding (Meunier-Salaun et al. 1987) and in low-ranking male baboons (Sapolsky 1983). A high maximal response to ACTH is often seen in individuals who have recently been exposed to certain types of chronic stress (Dantzer et al. 1983; von Borell & Ladewig 1989; Mormède 1990). Although chronic stressors such as exercise, heat stress and confinement have varying effects (e.g. Barnett et al. 1984; Rampacek et al. 1985; Rees et al. 1985; von Borell & Ladewig 1989; Cure 1989; Ladewig & Smidt 1989), the effects of social disruption appear more consistent. Increased crowding or competition for access to food often results in an elevation in the ACTH response (calves, *Bos taurus*: Friend et al. 1977, 1979, 1985; pigs: Meunier-Salaun et al. 1987). Similarly, low-ranking animals who have received high levels of aggression from others often show an increased response to ACTH (rhesus monkeys, *Macaca mulatta*: Sassenrath 1970; mice, Ely & Henry 1978; but see Sapolsky 1990).

By studying the domestic pig, our aim is not only to add to fundamental knowledge about coping strategies in the social environment, but also to provide information that may be used to develop pig housing and management techniques that minimize any detrimental behavioural and physiological consequences of housing pigs in groups.

METHODS

Subjects, Housing and Care

The subjects were 37 Large White × Landrace (Masterbreeders, Tring, U.K.) primiparous pregnant pigs housed in a large indoor pen

(16·5 × 5·5 m). The pen was ventilated by two thermostatically controlled 900 rpm 18 inch fans, and was lit both by direct sunlight and artificial lighting with lights switched on at 0600 hours and off at 2200 hours. The pen was divided into a strawed lying area (11·4 × 5·5 m) and an unstrawed dunging area (5·1 × 5·5 m). Part of the dunging area was occupied by an electronic sow feeder unit (crate manufactured by Quality Equipment, Bury St Edmunds, U.K. and electronics by Nedap Poiesz, Hengelo, Netherlands) in which the sows were fed one at a time. Each sow wore a collar fitted with an electronic tag. On entering the feeder, the sow's tag was identified by an electronic interrogator unit and the food due to the sow was automatically dispensed. Sows were fed 2·2 kg per day throughout the experiment and each daily feed cycle started at 1500 hours. Water was provided ad libitum from four drinker points in the dunging area. The dunging area was cleaned daily and straw was added at regular intervals to the lying area. At any one time, a maximum of 30 sows were in the pen together.

Experimental Protocol

All pigs were individually identifiable by ear tatoos and tags. The pigs were introduced into the pen when they were about 9 months old and in the 7th week of their first pregnancy (gestation is usually 16·5 weeks). For practical reasons, the pigs were introduced in four batches (three batches of 10 followed by a batch of seven), each batch being separated from the next by between 4 and 6 weeks. The first batch was introduced into an empty pen and the following batches were mixed with pigs already in the pen. For every pig, including those in the first batch, introduction to the pen involved mixing with unfamiliar animals. Data collection was designed to record the behavioural and physiological responses of each pig to her first few weeks in the pen, and thus to be directly comparable in all batches. The behaviour of each batch was observed for 3 days during the 1st week following introduction and for 2 days during the 3rd week. During the 5th week, each individual was subjected to a dexamethasone suppression and adrenocorticotrophic hormone challenge test to examine pituitary-adrenal activity. Each individual's humoral immunocompetence was also studied by measuring serum IgG antibody response to the *Bordetella* bacterium component of an atrophic rhinitis vaccine. A base-line blood sample was taken 1 or 2 days prior to entry to the pen and this was immediately followed by administration of the vaccine. During the 6th week following entry, a second blood sample was taken followed by a second vaccination. A third blood sample was taken 6 weeks after this (during lactation). Pigs were weighed before entry to the pen, 1 month after entry, and just before parturition. Reproductive performance was assessed at the first parturition.

Behavioural Observations

For observation purposes, a number was sprayed on the back and flanks of each pig. On each observation day, the pigs were watched four times, once in each of the following periods: 0830–1000 hours; 1130–1300 hours; 1400–1530 hours; 1600–1730 hours. A combination of focal sampling and behaviour sampling techniques was used (Martin & Bateson 1986). All members of the batch that had most recently been introduced into the pen were focal sampled, and the order in which they were sampled was determined prior to each watch and altered from day to day.

The observer sat in an observation post 2·5 m above the pigs. At the start of each watch, the first focal animal was observed continuously for 2 min and this was followed by an instantaneous sample of that animal's behaviour. The next focal animal was then observed in the same way and so on until all focal animals had been observed. The whole procedure was then repeated a further three times so that 8 min of sampling was performed for each focal animal. Thus, for a batch of 10 animals, each watch lasted 80 min. All agonistic and non-agonistic interactions in which the current focal animal was involved were recorded. In addition, throughout the watch, all agonistic interactions, including those not involving the current focal animal, were also recorded. This was possible since nearly all of these interactions were accompanied by vocalizations or rapid locomotor movements which could be detected easily by the observer.

Interactions were recorded on a check sheet. Each line on the check sheet contained columns for the initiator's identity and behaviour, the recipient's identity and behaviour and the outcome of the interaction. The main focus of this paper is on the involvement of individuals in agonistic and non-agonistic interactions, and on their role as initiator or recipient in these interactions. Relevant behaviour patterns are defined below.

Non-agonistic interactions

These interactions comprised one or both of the following behaviour patterns and were recorded only if the initiator or recipient was the current focal animal.

Nose: the pig touches or rubs its rooting disc against any part of the head or body of another pig.

Chew: the pig grasps any part of the head, body or collar of another pig in its mouth while rhythmically opening and closing its jaws. The mouthing movement is gentle and does not cause any tissue damage.

Agonistic and avoidance interactions

These interactions included at least one of the following behaviour patterns and a note was made of any clear displacement of one individual by the other during the interaction. All interactions of this sort were recorded. The first five categories are subsequently referred to as aggressive behaviour.

Knock: the pig uses a vigorous side to side movement of its head to hit any part of the head or body of another pig. The mouth is kept closed (see Jensen 1980; head-to-head/head-to-body knock).

Bite: the pig vigorously opens and closes its mouth around any part of the head or body of another pig while rapidly moving its head sideways or forwards towards the pig (see Jensen 1980; head-to-head/head-to-body bite).

Threaten: the pig, with mouth open, makes a vigorous lunging movement of its head towards another pig without making contact.

Chase: the pig moves rapidly after another pig.

Fight: two pigs take part in an agonistic encounter involving knocking, biting, parallel and inverse parallel pressing and levering (see Jensen 1980) and lasting longer than 5 s.

Retreat: the pig moves rapidly away from a pig that is knocking, biting, threatening or chasing it.

Avoid: the pig moves rapidly away from a pig that is not directing any behaviour at it.

Using this system of behaviour recording, it was possible to build up records of the success and failure of individual pigs during agonistic encounters (success = displacement of another pig, failure = displacement by another pig), their role as initiators and recipients, and their usage of aggressive and avoidance behaviour. In addition, their participation in non-agonistic interactions was summarized.

The main purpose of instantaneous sampling of the focal animals was to determine what proportion of the observation time they spent inactive (lying still with eyes open or closed).

Test of Pituitary–Adrenal Function

These tests were carried out in situ in the pen and started at about 1330 hours. The subject animals were weighed in the morning. Saliva samples were collected throughout the tests to allow monitoring of salivary cortisol levels in response to the test procedure. The use of saliva rather than blood for cortisol sampling has been validated in the pig (Parrott et al. 1989; Parrott & Misson 1989) and alleviates the need for stressful blood collection techniques involving jugular puncture. Saliva was collected by getting the pigs to chew on a veterinary cotton bud for 15–20 s. Between 0·5 and 1 ml was obtained from most pigs. The bud was then stored in a test tube on ice and subsequently saliva was spun down from the bud at 1800 rpm for 5 min and divided into three aliquots which were stored at −20°C. Salivary cortisol was measured using an enzyme-linked immunosorbent assay (ELISA; Cooper et al. 1989).

At the start of each test, a saliva sample was collected from each pig. The pig was then restrained using a noose applied to the upper jaw, and DXM (Merck, Sharp & Dohme, Hoddesdon, U.K.) was injected at a dose of 0·02 mg/kg via an ear vein to suppress pituitary ACTH production and so to minimize circulating levels of ACTH. Saliva samples were collected 1 and 2 h after this initial injection. Immediately following the 2-h saliva sample, synthetic ACTH ('Synacthen', CIBA, Horsham, U.K.) was injected intra-muscularly at levels (4 μg/kg) that should produce a maximal stimulation of the animal's adrenal cortex (Barnett et al. 1984; Meunier-Salaün et al. 1987). Further saliva samples were collected 1 and 2 h after this injection as suggested by von Borell & Ladewig (1989).

Test of Humoral Immunocompetence

The immune system was challenged by giving two 2-ml intra-muscular injections of an oil-based atrophic rhinitis vaccine (Intervet, Cambridge, U.K.) separated by 6 weeks. This vaccine contains two components: a *Bordetella* bacterium and a *Pasteurella* toxin. Blood samples were collected by jugular puncture into silicone-coated Vacutainer (Becton Dickinson, Meylan, France) tubes. The blood was allowed to clot and settle at room temperature and the serum was pipetted into three aliquots, frozen and stored at −20°C. An ELISA technique, based on methods described by Roitt et al. (1989, pp. 25.5–25.6), was developed to assess *Bordetella* antibody concentration. Eight concentrations of the test sample (100 μl), diluted in phosphate buffered saline (PBS) containing 0·1% of a detergent, Polyoxyethylene-sorbitan monolaurate ('Tween 20', Sigma, Poole, U.K.), were pipetted in duplicate in half log dilution steps into wells on plates coated with *Bordetella* bacteria (Intervet, Cambridge, U.K.). A positive (antibody present) and negative (antibody absent) control was included on all plates. The plates were incubated for 40 min at 37°C. The plates were then emptied and washed with PBS and 0·1% Tween 20 (washing buffer). Goat anti-pig alkaline phosphatase labelled IgG (100 μl) was added to the plates at 1:1000 dilution and incubated for 40 min. The plates were then emptied again and washed. Alkaline phosphatase tablets (Sigma, Poole, U.K.) diluted in diethylnoamine buffer were then added to each well. After 20 min of incubation, the colour reaction was read by assessing absorbance at 405 nm using a Dynatech microplate reader. The sample titres were expressed as the maximum dilution that showed an absorbance value equal to the positive control on each plate after correcting for inter-plate variation. This was taken as the maximum dilution of sample at which antibody could still be detected; the greater this dilution, the more antibody in the sample.

Measures of Reproduction

Several measures of reproduction at parturition were taken. These included the number of piglets born alive, dead or mummified, the total number of piglets produced, the sex ratio of the litters, the mean piglet birth weight, and the total weight of piglets born alive.

Data Analysis

For each individual, an index of success in agonistic interactions was calculated as follows

$$\frac{\text{no. of pigs that an individual is able to displace}}{\text{no. of pigs that an individual is able to displace + no. of pigs that are able to displace the individual}} \times 100$$

An animal's index could thus vary between 0 and 100. For example, those with an index of 50 or more were relatively successful in that they could displace at least the same number of pigs as displaced them. This index was used in preference to calculating a dominance hierarchy from the results of interactions between all pairs of individuals, because of the large number of reversals observed within dyads. The lack of a stable hierarchy calculated in this way is not surprising considering the social upheaval caused by the mixing of unfamiliar animals. In addition, owing to the large number of individuals in the group, not all possible pairs of pigs interacted in an agonistic context, thus making construction of such a hierarchy difficult. Also, female pigs often show a rather unstructured and non-linear hierarchy (Meese & Ewbank 1972; Hunter et al. 1988). In any case, the index was principally designed to reflect the experiences of individuals in agonistic encounters during the period after mixing, rather than to provide information on a clear cut dominance hierarchy.

The pigs were divided into three groups according to their relative success in agonistic interactions (see Results). A classification approach to analysis was used in view of the findings of various studies which have suggested that there is not necessarily a linear relationship between social status and physiological state or between social status and behavioural style (see Introduction). Consequently, a simple correlational approach was thought unlikely to reveal significant associations between these measures and a classification approach was chosen following the advice of Simpson (1985, 1986).

Analysis of variance was used to compare the behaviour, physiology and reproduction of the three groups. Data were transformed as appropriate when the assumption of normality was not fulfilled (Sokal & Rohlf 1981). Most data were analysed using a one-way ANOVA with group as the between-subjects factor. Multiple comparisons between means were performed using Duncan's multiple range test. Repeated measures ANOVA was used to analyse physiological data with group as the between-subjects factor and time as the within-subjects factor.

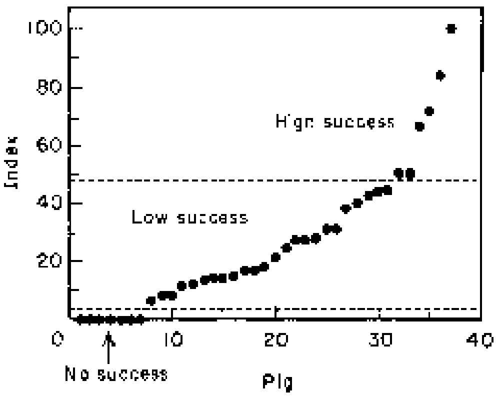


Figure 1. Indices of success in agonistic interactions for the 37 pigs. Three groups are distinguished: the High Success group (index ≥50), the No Success group (index = 0) and the Low Success group (index: 7–44).

RESULTS

Behaviour and Success in Agonistic Interactions

The success indices (see Methods) calculated for the 37 animals during the first week after introduction into the pen were highly positively correlated with those calculated for the third week (r=0·714, N=37, P<0·001) and therefore an overall index was calculated for each pig over the 3-week period. The distribution of scores on this index demonstrates the large variation in success experienced by different individuals during introduction to the pen (Fig. 1). For the purposes of further analysis, the animals were divided into three groups according to their relative success in agonistic encounters. Two small but quite distinct groups occurred at the top and bottom ends of the success index scale. Only six animals were able to displace at least as many pigs as could displace them (High Success, Index ≥ 50), while seven animals failed to displace any other individual at all (No Success, Index = 0). The majority of animals were able to displace others but were more often displaced themselves (Low Success, Index = 7–44).

Within each batch of pigs introduced into the pen, there was considerable variation in success in agonistic interactions. The first batch differed from the others in that it contributed all six of the High Success group which subsequently dominated members of incoming batches. However, all batches contributed animals to the Low Success group (batches 1–4: 4, 9, 6, 5, respectively), and all batches except the first had animals in the No Success group (batches 2–4: 1, 4, 2, respectively).

The distinction between the Low Success and No Success groups was made in the light of studies which suggest that in certain species there may be at least two ways of responding to failure in agonistic interactions (see Introduction). In relation to the current study, one possibility is that the No Success group responded to failure in agonistic encounters by showing low levels of involvement in agonistic interactions and low aggression, while the Low Success group continued to behave in a more aggressive and competitive way. To examine this possibility, the behavioural characteristics and experiences of pigs in all three groups were analysed.

The actual frequency (interactions/h) of involvement in agonistic and non-agonistic interactions did not differ between pigs from the three groups (agonistic: $F_{2,34}$=1·18, P=0·32; non-agonistic; $F_{2,34}$=0·31, P=0·74). However, when adjusted for the current group size (i.e. taking into account the number of other individuals in the pen at the time), High Success pigs were involved in significantly more agonistic ($F_{2,34}$=5·70, P=0·007, Fig. 2a) and non-agonistic ($F_{2,34}$=6·89, P=0·003, Fig. 2b) interactions than either Low Success or No Success pigs. In both cases, there was a non-significant tendency for No Success animals to be involved in the least number of interactions, as would be expected if these animals were avoiding encounters with others.

We analysed the types of behaviour that pigs from the three groups used during agonistic encounters. The percentage of each pig's agonistic encounters that she initiated using aggressive behaviour was highest in the High Success group and tended (non-significantly) to be lowest in the No Success group ($F_{2,33}$=12·76, P=0·0001, Fig. 2c). However, the percentage of a pig's interactions involving receipt of aggression from another, in which it responded with aggression, did not differ between the three groups ($F_{2,34}$=2·14, P=0·13). Overall, pigs in the High Success group were most likely to use aggression during an agonistic interaction, and pigs from the No Success group were least likely to do so ($F_{2,34}$=9·34, P=0·006, Fig. 2d). In terms of the absolute frequency of aggressive behaviour performed per hour, the same pattern emerged. No Success pigs used aggression least often and High Success pigs used it most often ($F_{2,34}$=12·60, P=0·0001, Fig. 2e).

Agonistic interactions either involved aggressive behaviour by one or both individuals or they

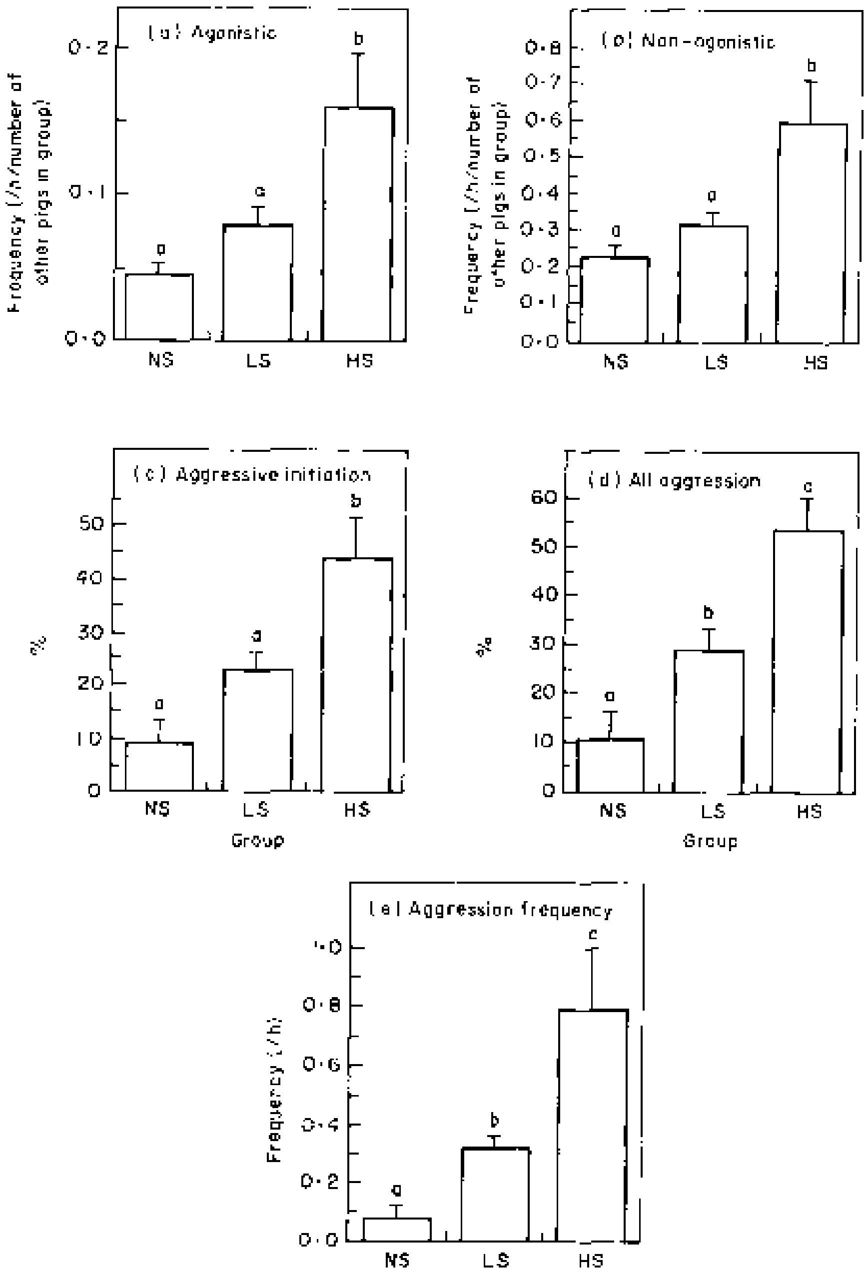


Figure 2. Number of (a) agonistic and (b) non-agonistic interactions in which each pig is involved (/h/number of other pigs in pen). Percentage of a pig's agonistic interactions in which it (c) initiates the interaction using aggression and (d) performs aggressive behaviour at any time during the interaction. Frequency of (e) aggressive behaviour performed by pig/h. NS = No Success group, LS = Low Success group, HS = High Success group. Group means are plotted with error bars denoting 1 SE. Bars with different letters represent means that are significantly different.

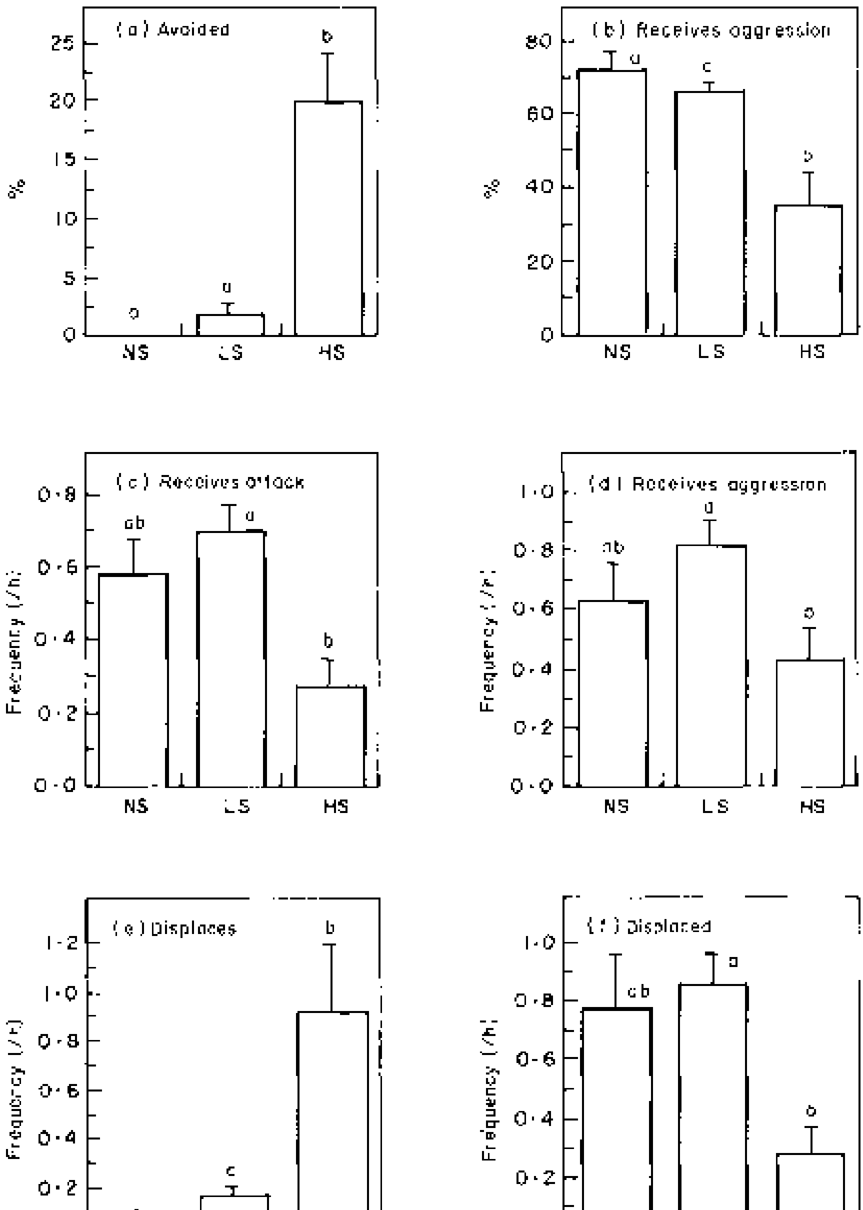


Figure 3. Percentage of a pig's agonistic interactions in which it is (a) avoided and (b) the recipient of aggression. Frequency/h at which a pig (c) is the recipient of an attack, (d) receives aggression during an agonistic encounter, (e) displaces others and (f) is displaced by others. Details as for Fig. 2.

involved no aggression but active avoidance of one individual by the other. The percentage of agonistic interactions in which the pig actively avoided another did not differ between the groups ($F_{2,14}$= 1·17, P=0·32), and nor did the percentage of encounters in which the pig was displaced and used active avoidance ($F_{2,14}$=1·36, P=0·27). Similarly, the absolute frequency/h of active avoidance did

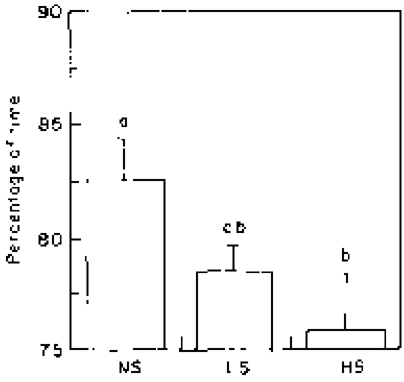


Figure 4. Percentage of observation time during which the pig is inactive. Details as for Fig. 2.

not differ between the three groups ($F_{2,34}=0.52$, $P=0.59$).

The way in which pigs were treated by others varied between the groups. Pigs from the High Success group were actively avoided more often during agonistic encounters than pigs from the other groups ($F_{2,34}=30.32$, $P<0.0001$, Fig. 3a). In addition, these pigs received less aggression per agonistic encounter than did pigs from the other groups ($F_{2,34}=16.46$, $P<0.0001$, Fig. 3b).

In addition to the differences in how pigs behaved during agonistic encounters, there were also differences in their actual experience of aggression from others. The absolute frequency/h of being attacked by others (i.e. being the recipient of aggression) was highest in the Low Success group ($F_{2,34}=4.71$, $P=0.016$, Fig. 3c). The same was found for the absolute frequency of aggression received from others, either as initiator or recipient in an interaction, although this was not quite significant ($F_{2,34}=2.83$, $P=0.07$, Fig. 3d). The absolute frequency/h of displacing others was highest in the High Success group ($F_{2,34}=19.50$, $P<0.0001$, Fig. 3e), while the absolute frequency/h of being displaced was highest in the Low Success group ($F_{2,34}=12.60$, $P=0.0001$, Fig. 3f).

The percentage of a pig's non-agonistic encounters that she initiated did not differ between the three groups ($F_{2,34}=1.52$, $P=0.23$), while the proportion of time spent inactive by pigs tended to be highest in the No Success group and lowest in the High Success group although not significantly so ($F_{2,34}=2.42$, $P=0.10$, Fig. 4).

In summary, the analysis suggested some clear differences between the behavioural characteristics and experiences of pigs in the three groups. The High Success group were least inactive and were involved in relatively more agonistic and non-agonistic interactions than the others. They were most aggressive, they received least aggression from others and they were most often actively avoided. The No Success group were the most inactive, tended to be involved in the fewest agonistic and non-agonistic encounters and, during agonistic encounters, used aggressive behaviour least often. The Low Success group were intermediate in their inactivity and use of aggression during agonistic encounters. Most notable was their overall experience of the highest levels of attack and aggression from other individuals, and the greatest number of displacements by others.

Weight Gain

Weight prior to introduction to the pen did not differ between the three groups ($F_{2,34}=0.06$, $P=0.94$). However, the amount of weight gained per pig during the first month in the pen was significantly higher in the High Success group than in the other groups ($F_{2,31}=4.06$, $P=0.02$, Fig. 5a). The mean weight of the groups at the 1-month point was not significantly different, probably owing to large within-group variance ($F_{2,31}=1.41$, $P=0.26$). Just before parturition, there was again no difference in weight between the groups ($F_{2,30}=0.44$, $P=0.65$), and between the 1-month point and parturition, there was a non-significant tendency for pigs in the Low Success and No Success groups to gain more weight than those in the High Success group ($F_{2,27}=2.42$, $P=0.10$, Fig. 5b).

Pituitary–adrenal Function

Pigs from both the High Success and No Success groups had significantly lower levels of salivary cortisol throughout the pituitary–adrenal function test than pigs from the Low Success group ($F_{2,12}=3.96$, $P=0.029$, Fig. 6a). The Low Success group had a high baseline cortisol level and showed the strongest suppression response to DXM and the highest peak level of cortisol in response to the ACTH.

Humoral Immunocompetence

The test of humoral immunocompetence failed to demonstrate any difference between the three

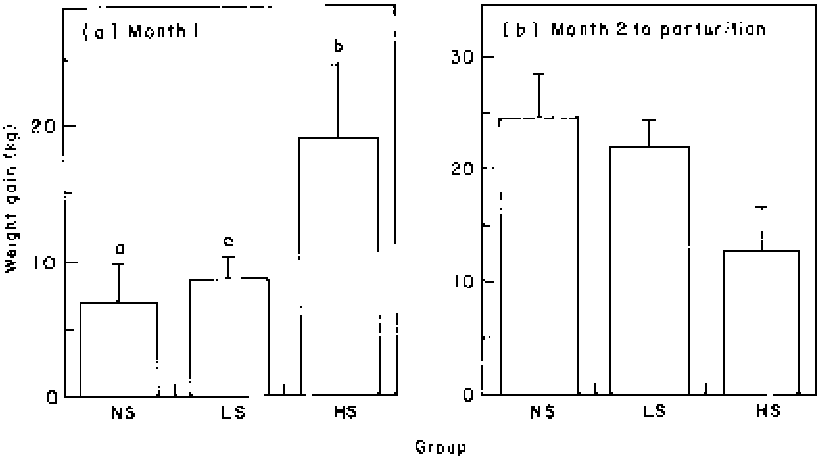
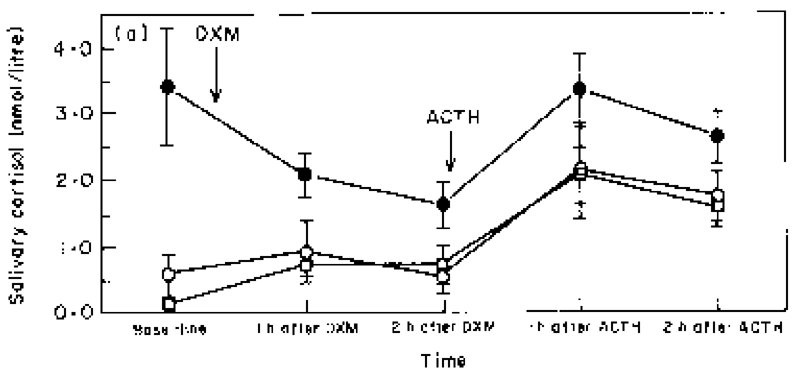


Figure 5. Weight (kg) gained by pig during (a) first month in pen and (b) the period between the end of the first month and parturition. Details as for Fig. 2.



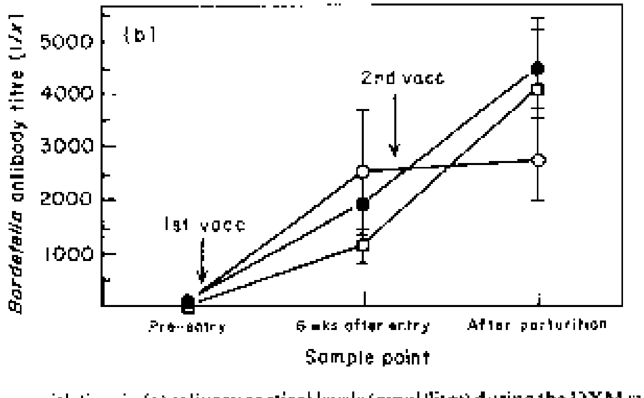


Figure 6. Changes with time in (a) salivary cortisol levels (nmol/litre) during the DXM suppression and ACTH challenge experiment and (b) the serum dilution (1/*x*) at which *Bordetella* antibody can be detected. Group means are plotted for the NS (○), LS (●) and HS (□) groups. Error bars denote 1 se. Arrows indicate the timing of injections.

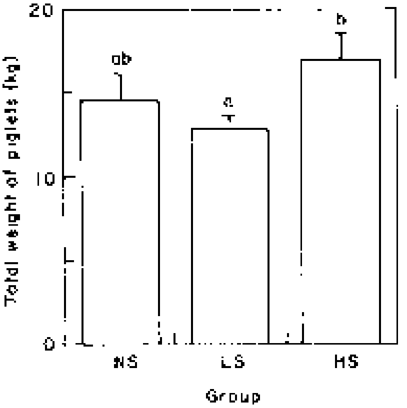


Figure 7. Total weight of piglets born alive after the first pregnancy. Details as for Fig. 2.

groups in IgG response to the *Bordetella* bacterium component of the vaccine ($F_{2,27}=0.22$, $P=0.81$). Large variation within groups was evident (Fig. 6b).

Reproduction

Pigs in the High Success group gave birth to heavier total weights of live-born piglets than did pigs in the Low Success group, with the No Success group being intermediate ($F_{2,30}=3.66$, $P=0.03$, Fig. 7). No other differences were found.

DISCUSSION

Recent studies of the effects of social interactions on an animal's physiological state have moved away from a simple distinction between dominant and subordinate individuals to examine more closely the behavioural characteristics and strategies of the individuals involved (see Introduction). The idea of individuals using alternative tactics to tackle a particular problem has also been well developed in the behavioural ecology literature (Dunbar 1982; Dominey 1984) and emphasizes the possibility that different behavioural approaches to a problem may be equally successful.

In the present study, we followed this line of thought in our analysis of how female pigs responded to being mixed into a group of unfamiliar individuals. We identified three broad categories. A small group (High Success) who were relatively successful in agonistic interactions, in the sense that they could displace at least as many pigs as displaced them, were characterized by the lowest level of inactivity, high levels of involvement in social interactions, and high levels of aggression. Another small group (No Success) were never able to displace another pig and were characterized by the highest levels of inactivity, low involvement in social interactions and the lowest use of aggressive behaviour. The third and largest group of pigs (Low Success) were relatively unsuccessful in agonistic encounters, in the sense that they were able to displace other pigs but were more often displaced themselves, and were intermediate in their inactivity, involvement in social interactions and use of aggression. However, perhaps owing to this group's persistence in using aggression, they experienced the highest levels of attack and aggression from others and were displaced by others most often.

The distinction between the Low Success and No Success groups is similar to that noted by Fokkema (1985) in his study of a population of rats in which the subordinates either maintained their aggressive and competitive behaviour or appeared to opt out of competition and decrease their involvement in agonistic interactions. Similarly, in wild house mice, Benus (1988) observed that some individuals responded to defeat by becoming immobile and thus decreasing the stimulus for further attack by the victor, while other individuals continued to show active offensive and defensive behaviour and, as a result, received more sustained attacks. A parallel may also be drawn with the Type A/Type B classification of certain human individuals (Friedman & Rosenman 1974). Type A individuals are ambitious, competitive, aggressive and respond actively to challenges. Type B individuals, on the other hand, have a more relaxed attitude, a lack of time urgency and a willingness to accept challenges and restrictions of the environment cheerfully and without agitation (Henry & Stephens 1977).

Our classification of pigs thus has parallels with other findings but remains an essentially simple division of animals into groups. We do not claim that each group is a collection of identical animals or that every animal has been correctly assigned to the appropriate group. Nevertheless, we feel that the groups of pigs were behaviourally distinct in a number of important ways and, therefore, that our groupings allow a more meaningful analysis than does a straightforward dominant–subordinate classification of animals. This assertion is supported by our finding of a non-linear relationship between pituitary–adrenal function and our index of success in agonistic interactions. The most striking feature is the similarity between the physiological responses shown by the High Success and No Success groups which lie at opposite extremes of our index. The lack of a linear relationship emphasizes the potential inadequacies of a simple correlational analysis, and the usefulness of classification approaches (Simpson 1985, 1986).

High Success and No Success pigs had a lower level of salivary cortisol throughout the tests than did Low Success pigs. In general, levels were low and probably represented less than 10% of total plasma cortisol (Parrott et al. 1989). The salivary cortisol levels observed in our primiparous pigs were very similar to those seen in prepuberal pigs subjected to an ACTH challenge (Parrott et al. 1989; Parrott & Misson 1989), although there is evidence of higher responsiveness in multiparous pigs (Cooper et al. 1989).

The results of the DXM suppression test were not easy to interpret, principally because the low basal levels of salivary cortisol in the High Success and No Success groups made further suppression virtually impossible. Consequently, the test turned out to be of limited use in differentiating between different types of individual in the present study. However, it is clear that DXM did cause suppression in the one group where this was possible, the Low Success group. Thus, there was no evidence of a lack of response to DXM which is often characteristic of depressed or helpless individuals (humans: Hanin et al. 1985; rats, Haracz et al. 1988).

The effect of a chronic stressor on an individual's responsiveness to ACTH challenge is still a matter of debate because of conflicting findings (Ladewig & Smidt 1989; Rushen 1991; see Introduction). The species under study, the type of stressor experienced by the individual, and the time between the occurrence of the stressor and measurement of the ACTH response are all likely to contribute to the variability of findings between studies. However, there appears to be some consistency in the response shown to social disruption, with groups of animals exposed to social upheaval or subjected to high levels of aggression from others showing elevated responses to ACTH (Sassenrath 1970; Friend et al. 1977, 1979, 1985; Ely & Henry 1978; Meunier-Salaün et al. 1987). Elevations in basal cortisol levels are also characteristic of low-ranking individuals and those receiving high levels of aggression (rodents: Louch & Higgenbotham 1967; Popova & Naumenko 1972; Schuhr 1987; Sachser & Lick 1989; pigs: Arnone & Dantzer 1980; cheetah, *Acinonyx jubatus*: Caro et al. 1989; primates: Bowman et al. 1978; Scallett et al. 1981; Keverne et al. 1982; Eberhart et al. 1983; but see Coe et al. 1979).

In view of these findings, one interpretation of the present results is that the experience of high levels of attack and defeat by Low Success animals, resulting from their persistent use of aggression despite relative lack of success, was more stressful than the consequences of the behavioural strategies employed by animals in the High Success and No Success groups. High success in agonistic interactions (High Success pigs) and apparent acceptance of low success, as evidenced by low involvement in social encounters and low use of aggressive behaviour (No Success pigs), appeared to have lower physiological and fitness costs. These results have close parallels with those of Fokkema (1985) on male rats. They provide further support for the notion that the strategy used to cope with the social environment may be as important as the success achieved in agonistic interactions, at least in terms of consequences for physiological state, and potentially for health and fitness.

It is also possible, however, that the behavioural and physiological characteristics of the pigs were not causally related but were influenced by some unknown common causal factor. Although a causal relationship between the experience of high levels of social stress and subsequent elevated responsiveness to ACTH is suggested by much research (see above), and would seem to be a plausible interpretation of the current study, the possible existence of such a factor cannot be entirely ruled out here.

In the present study, no long-term consequences for health, in terms of immunosuppression, were found in relation to the groupings of pigs. Stress and elevated pituitary–adrenal function are known to have suppressive effects on immune system function (Comsa et al. 1982; Martin 1988) but in the present study there was no evidence of depressed IgG antibody response in the Low Success group. It appears that stress depresses cell-mediated immunity to a greater extent than humoral (antibody) immunity (Okimura et al. 1986), and therefore the use of measures of cell-mediated immunity might have proved more fruitful in the present study. In addition, the increased levels of pituitary–adrenal function observed in the Low Success group may have been too small or short-lived to result in marked immunosuppression.

The potentially transient nature of the effects of social mixing is suggested by the weight changes observed in the three groups of pigs. During the first month, High Success pigs gained significantly more weight than pigs from the other two groups but, subsequent to this, No Success and Low Success pigs tended to put on more weight, although not significantly so. Consequently, no maternal weight differences were observed at parturition. Decreases in weight gain by animals subjected to aggression from others is a commonly observed phenomenon (mice: Mendl & Paul 1991a; guinea pigs, *Cavia porcellus*: Sachser & Lick 1989; pigs: Tan & Shackleton 1990). In the present study, each pig was fed individually in an enclosed electronic sow feeder and, for management reasons, it was necessary to ensure that all pigs used the feeder each day. It is possible that, owing to intimidation from pigs waiting outside the feeder, Low Success and No Success pigs did not always consume all of the food that was dropped into the trough by the electronic feeder, and consequently gained less weight than High Success pigs. Alternatively, or additionally, fear and anxiety of attack by High Success pigs may have resulted in elevated basal metabolic rates and expenditure of energy by the other pigs.

The lack of persistence of higher weight gain by the High Success group during the latter part of pregnancy is one indication that individuals in the other groups adjusted successfully to the social environment after the initial trauma of mixing. However, the differences in the total weight of live-born piglets between the three groups suggest that some long-term effects of mixing did occur. They are of particular interest because of their similarity to the differences in the measures of physiological stress, with Low Success pigs having both the highest pituitary adrenal activity and the lowest total weight of piglets born alive. This suggests a link between socially induced physiological stress and reproductive suppression in female pigs, a relationship which has been observed in other species (Bowman et al. 1978; Abbott et al. 1988).

The reasons why different individuals behaved in different ways are not clear. Pigs from all three groups were of a similar weight when introduced into the pen and so weight differences are unlikely to have been responsible for the different behavioural profiles observed. On the other hand, order of introduction into the pen did have an effect. All High Success pigs were from the first batch to be introduced. Since all pigs were the same age at the time of their introduction into the pen, these High Success pigs were older than pigs introduced in subsequent batches. This combination of age and order of introduction allowed them to establish themselves in the pen and subsequently dominate other newly introduced individuals. Thus, the method of introducing pigs in batches gave an advantage to pigs in the first batch and probably resulted in some of these individuals becoming High Success animals. However, Low Success and No Success pigs came from all three of the following batches. Thus, order effects and relative age cannot explain the existence of these distinct behavioural profiles and their different physiological correlates. Factors such as genetic differences (e.g. van Oortmerssen et al. 1985; Benus 1988) and developmental experience (e.g. Mendl & Paul 1991b) are known to underlie subsequent variation in behavioural strategy and almost certainly played a prominent role in the present study. An understanding of the developmental bases of variation in the responses shown by the pigs is an aim of current research and data analysis.

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REFERENCES

Abbott, D. M., Hodges, J. K. & George, L. M. 1988. Social status controls LH secretion and ovulation in female marmoset monkeys (*Callithrix jacchus*). *J. Endocrinol.*, **117**, 329–339.

Arnone, M. & Dantzer, R. 1980. Does frustration induce aggression in pigs? *Appl. Anim. Ethol.*, **6**, 351–362.

Batty, K. A., Herbert, J., Keverne, E. B. & Vellucci, S. V. 1986. Differences in blood levels of androgens in female talapoin monkeys related to their social status. *Neuroendocrinology*, **44**, 347–354.

Barnett, J. L., Cronin, G. M., Winfield, C. G. & Dewar, A. M. 1984. The welfare of adult pigs: the effects of five housing treatments on behaviour, plasma corticosteroids and injuries. *Appl. Anim. Behav. Sci.*, **12**, 209–232.

Barnett, J. L., Hemsworth, P. H., Winfield, C. G. & Fahy, V. A. 1987. The effects of pregnancy and parity number on behavioural and physiological responses related to the welfare status of individual and group-housed pigs. *Appl. Anim. Behav. Sci.*, **17**, 229–243.

Benus, I. 1988. Aggression and coping. Differences in behavioural strategies between aggressive and non-aggressive male mice. Ph.D. thesis, University of Groningen.

von Borell, E. & Ladewig, J. 1989. Altered adrenocortical response to acute stressors or ACTH (1–24) in intensively housed pigs. *Dom. Anim. Endocrinol.*, **6**, 299–309.

Bowman, L. A., Dilley, S. R. & Keverne, E. B. 1978. Suppression of oestrogen induced LH surges by social subordination in talapoin monkeys. *Nature, Lond.*, **275**, 56–58.

Caro, T. M., FitzGibbon, C. D. & Holt, M. E. 1989. Physiological costs of behavioural strategies for male cheetahs. *Anim. Behav.*, **38**, 309–317.

Coe, C. L., Mendoza, S. P. & Levine, S. 1979. Social status constrains the stress response in the squirrel monkey. *Physiol. Behav.*, **23**, 633–638.

Comsa, J., Leonhardt, H. & Wekerle, W. 1982. Hormonal coordination of the immune response. *Rev. Physiol. Biochem. Pharmacol.*, **92**, 115–191.

Cooper, T. R., Trunkfield, H. R., Zanella, A. J. & Booth, W. D. 1989. An enzyme-linked immunosorbent assay for cortisol in the saliva of man and domestic farm animals. *J. Endocrinol.*, **123**, R13–R16.

Cure, M. 1989. Plasma corticosterone responses in continuous versus discontinuous chronic heat exposure in rat. *Physiol. Behav.*, **45**, 1117–1122.

Dantzer, R., Mormède, P. & Henry, J. P. 1983. Physiological assessment of adaptation in farm animals. In: *Farm Animal Housing and Welfare* (Ed. by S. H. Baxter, M. R. Baxter & J. A. C. MacCormack), pp. 8–19. The Hague: Martinus Nijhoff.

Dominey, W. J. 1984. Alternative tactics and evolutionarily stable strategies. *Am. Zool.*, **24**, 385–396.

Dunbar, R. I. M. 1982. Intraspecific variations in mating strategy. In: *Perspectives in Ethology, Vol. 5* (Ed. by P. P. G. Bateson & P. H. Klopfer), pp. 385–431. New York: Plenum Press.

Eberhart, J. A., Keverne, E. B. & Meller, R. E. 1983. Social influences on circulating levels of cortisol and prolactin in male talapoin monkeys. *Physiol. Behav.*, **30**, 361–369.

Ely, D. L. 1981. Hypertension, social rank and aortic atherosclerosis in CBA/J mice. *Physiol. Behav.*, **26**, 655–662.

Ely, D. L. & Henry, J. P. 1978. Neuroendocrine response patterns in dominant and subordinate mice. *Horm. Behav.*, **10**, 156–169.

Fokkema, D. S. 1985. Social behaviour and blood pressure: a study of rats. Ph.D. thesis, University of Groningen.

Friedman, M. & Rosenman, R. H. 1974. *Type A Behavior and Your Heart*. New York: Alfred A. Knopf.

Friend, T. H., Dellmeier, G. R. & Gbur, E. E. 1985. Comparison of four methods of calf confinement. I. Physiology. *J. Anim. Sci.*, **60**, 1095–1101.

Friend, T. H., Gwazdauskas, F. C. & Polan, C. E. 1979. Changes in adrenal response from free stall competition. *J. Dairy Sci.*, **62**, 769–771.

Friend, T. H., Polan, C. E., Gwazdauskas, F. C. & Heald, C. W. 1977. Adrenal glucocorticoid response to exogenous adrenocorticotrophin mediated by density and social disruption in lactating cows. *J. Dairy Sci.*, **60**, 1958–1963.

Hanin, I., Frazer, A., Groughan, J., Davis, J. M., Katz, M. M., Koslow, S. H., Maas, J. W. & Stokes, P. E. 1985. Depression: implications of clinical studies for basic research. *Fed. Proc.*, **44**, 85–90.

Haracz, J., Minor, T. R., Wilkins, J. N. & Zimmermann, E. G. 1988. Learned helplessness: an experimental model of the DST in rats. *Biol. Psychiatr.*, **23**, 388–396.

Henry, J. P. 1983. Coronary heart disease and arousal of the adrenal cortex axis. In: *Biobehavioral Bases of Coronary Heart Disease* (Ed. by T. M. Dembroski, T. H. Schmidt & G. Blümchen), pp. 365–381. Basel: Karger.

Henry, J. P. & Stephens, P. M. 1977. *Stress Health and the Social Environment: a Sociobiologic Approach to Medicine*. New York: Springer-Verlag.

von Holst, D. Fuchs, E. & Stohr, W. 1983. Physiological changes in male *Tupaia belangeri* under different types of social stress. In: *Biobehavioral Bases of Coronary Heart Disease* (Ed. by T. M. Dembroski, T. H. Schmidt & G. Blümchen), pp. 382–390. Basel: Karger.

Hunter, E. J., Broom, D. M., Edwards, S. A. & Sibly, R. M. 1988. Social hierarchy and feeder access in a group of twenty sows using a computer-controlled feeder. *Anim. Prod.*, **47**, 139–148.

Jensen, P. 1980. An ethogram of social interaction patterns in group-housed dry sows. *Appl. Anim. Ethol.*, **6**, 341–350.

Keverne, E. B., Meller, R. E. & Eberhart, A. 1982. Dominance and subordination: concepts or physiological states? In: *Advanced Views in Primate Biology* (Ed. by A. B. Chiarelli & R. S. Corruccini), pp. 81–94. Berlin: Springer-Verlag.

Koolhaas, J. M. & van Oortmerssen, G. A. 1988. Individual differences in disease susceptibility as a possible factor in the population dynamics of rats and mice. *Neth. J. Zool.*, **38**, 111–122.

Ladewig, J. & Smidt, D. 1989. Behavior, episodic secretion of cortisol and adrenocortical reactivity in bulls subjected to tethering. *Horm. Behav.*, **23**, 344–360.

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

Louch, C. D. & Higgenbotham, M. 1967. The relation between social rank and plasma corticosterone levels in mice. *Gen. comp. Endocrinol.*, **8**, 441–444.

Martin, P. 1988. Psychoimmunology: relations between brain, behaviour and immune function. In: *Perspectives in Ethology, Vol. 8* (Ed. by P. P. G. Bateson & P. H. Klopfer), pp. 173–214. New York: Plenum Press.

Martin, P. & Bateson, P. 1986. *Measuring Behaviour*. Cambridge: Cambridge University Press.

Meese, G. B. & Ewbank, R. 1972. A note on the instability of the dominance hierarchy and variations in levels of aggression within groups of fattening pigs. *Anim. Prod.*, **14**, 359–362.

Mendl, M. & Paul, E. S. 1991a. Parental care, sibling relationships and the development of aggressive behaviour in two lines of wild house mice. *Behaviour*, **116**, 11–41.

Mendl, M. & Paul, E. S. 1991b. Litter composition affects parental care, offspring growth and the development of aggressive behaviour in wild house mice. *Behaviour*, **116**, 90–108.

Meunier-Salaün, M. C., Vantrimponte, M. N., Raab, A. & Dantzer, R. 1987. Effect of floor area restriction upon performance, behaviour and physiology of growing-finishing pigs. *J. Anim. Sci.*, **64**, 1371–1377.

Mormède, P. 1990. Neuroendocrine responses to social stress. In: *Social Stress in Domestic Animals* (Ed. by R. Zayan & R. Dantzer), pp. 203–211. Dordrecht: Kluwer Academic Publishers.

Okimura, T., Ogawa, M., Yamauchi, T. & Sasaki, Y. 1986. Stress and immune responses. 4. adrenal involvement in the alternation of antibody responses to restraint-stressed mice. *Jap. J. Pharmacol.*, **41**, 237–245.

van Oortmerssen, G. A., Benus, I. & Dijk, D. J. 1985. Studies in wild house mice: genotype–environment interactions for attack latency. *Neth. J. Zool.*, **35**, 155–169.

Parrott, R. F. & Misson, B. H. 1989. Changes in pig salivary cortisol in response to transport simulation, food and water deprivation, and mixing. *Br. vet. J.*, **145**, 501–505.

Parrott, R. F., Misson, B. H. & Baldwin, B. A. 1989. Salivary cortisol in pigs following adrenocorticotrophic hormone stimulation: comparison with plasma levels. *Br. vet. J.*, **145**, 362–366.

Popova, N. K. & Naumenko, E. V. 1972. Dominance relations and the pituitary–adrenal system in rats. *Anim. Behav.*, **20**, 108–111.

Rampacek, G. B., Kraeling, R. R., Fonda, E. S. & Barb, C. R. 1985. Comparison of physiological indicators of chronic stress in confined and non-confined gilts. *J. Anim. Sci.*, **58**, 401–408.

Rees, A., Harvey, S. & Phillips, J. G. 1985. Transitory responses of ducks (*Anas platyrhynchos*) to exercise. *Gen. comp. Endocrinol.*, **59**, 100–104.

Roitt, I. M., Brostoff, J. & Male, D. K. 1989. *Immunology*. London: Gower Medical Publishing.

Rushen, J. 1991. Problems associated with the interpretation of physiological data in the assessment of animal welfare. *Appl. Anim. Behav. Sci.*, **28**, 381–386.

Sachser, N. & Lick, C. 1989. Social stress in guinea pigs. *Physiol. Behav.*, **46**, 137–144.

Sapolsky, R. M. 1983. Individual differences in cortisol secretory patterns in the wild baboon: role of negative feedback sensitivity. *Endocrinology*, **113**, 2263–2267.

Sapolsky, R. M. 1990. Stress in the wild. *Scient. Am.*, **262**, 106–113.

Sapolsky, R. M. & Ray, J. C. 1989. Styles of dominance and their endocrine correlates among wild olive baboons (*Papio anubis*). *Am. J. Primatol.*, **18**, 1–13.

Sassenrath, E. N. 1970. Increased adrenal responsiveness related to social stress in rhesus monkeys. *Horm. Behav.*, **1**, 283–298.

Scallett, A. C., Suomi, S. J. & Bowman, R. E. 1981. Sex differences in adrenocortical responses to controlled agonistic encounters in rhesus monkeys. *Physiol. Behav.*, **26**, 385–390.

Schuhr, B. 1987. Social structure and plasma corticosterone levels in female albino mice. *Physiol. Behav.*, **40**, 689–693.

Simpson, M. J. A. 1985. Effects of early experience on the behaviour of yearling rhesus monkeys (*Macaca mulatta*) in the presence of a strange object: classification and correlation approaches. *Primates*, **26**, 57–72.

Simpson, M. J. A. 1986. What is the value of a correlation coefficient? *Anim. Behav.*, **34**, 605–606.

Sokal, R. R. & Rohlf, F. J. 1981. *Biometry*. San Francisco: W. H. Freeman.

Tan, S. S. L. & Shackleton, D. M. 1990. Effects of mixing unfamiliar individuals and of azaperone on the social behaviour of finishing pigs. *Appl. Anim. Behav. Sci.*, **26**, 157–168.