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Social Stress and Welfare Problems in Agricultural Animals

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Early in its chequered history the term 'stress' generally referred to a bodily state involving the development of gastric ulcers, the heightened activity of the pituitary and adrenal cortex and a number of related physiological features. This syndrome could result from a variety of conditions including wounding, physical restraint and exposure to cold; because of this similar set of effects, such conditions were called 'stressors' (Selye, 1950). The term 'stressor' is now often used to cover a number of environmental features even though they have quite different physiological effects. In addition many agriculturalists and veterinarians use the term 'stress' even more loosely, invoking it as the supposed cause of almost any unexplained drop in production. Such a practice indicates a growing awareness that a host of environmental and other factors may have a subtle effect on an animal's well-being. In what follows, conditions will be called 'stressors' only if they have been shown to have a general physiological effect, but the discussion will touch on a wider range of factors which result in disturbed behaviour or appear to effect adversely the welfare of the animal.

Disruptions of an animal's social behaviour can, in some respects at least, mimic the effects of such classical stressors as infection and exposure to low temperatures. For example, Barnett (1958) found enlarged adrenals among wild rats which were subjected to attack by other rats in the laboratory. However, the experience of being attacked was not necessary for this physiological response, as the aggressors showed much the same changes as the victims. In fact Archer (1969) reported heightened adrenocortical activity among individually caged mice simply as a result of their being housed next to other mice, without actual physical contact. If adrenocortical activity is increased by social interaction, it seems reasonable that it should be reduced by solitary confinement. Up to a point this appears to be true for male mice (Brain & Nowell, 1970), but prolonged social isolation, lasting a month or more, may have the opposite effect (Sigg et al., 1966).

'Social stress', such as may arise from drastic changes in social behaviour and population density, can have a marked influence on growth, reproductive performance and many types of behaviour (Barnett, 1964). The implications for intensive husbandry are obvious.

GENERAL PHYSIOLOGICAL ASPECTS

The physiological reactions of animals to stressors may be divided into the 'emergency reaction' and the 'general adaptation syndrome' (GAS). The emergency reaction consists of increased activity of the sympathetic nervous system along with increased output of adrenaline or noradrenaline from the adrenal medulla. The GAS is the more long-term response to stress, involving the release from the anterior pituitary of adrenocorticotrophic hormone which stimulates the adrenal cortex to release glucocorticoids (Selye, 1950). Both the emergency reaction and the GAS result in a variety of secondary physiological changes.

Evidence for the occurrence of the emergency reaction and the GAS should ideally be based on measurements of the primary physiological responses, that is, for the former, increased sympathico-adrenal activity and for the latter increased ACTH secretion of glucocorticoid secretion. However, since these measurements are difficult to make, evidence is usually based on some of the secondary changes. If possible more than one parameter should be used and it must be remembered that there may be differences between species. For example the emergency reaction may be relatively more important than the adrenal cortical response in birds than in mammals (Draper & Lake, 1968). Also there is evidence that adrenal cortical activity is partly controlled by an extrahypophyseal hormone in the bird in contrast to the mammal (Resko et al., 1964; Frankel et al., 1967). Furthermore, the nature of glucocorticoid secretions varies considerably between species, but with either corticosterone, or cortisol, or both, constituting the major proportion of the total secretion (Chester Jones et al., 1962). Depletion of ascorbic acid from the adrenal is not such a good test in birds as in mammals, since mild stimuli may cause depletion whereas intense stimuli may cause repletion (Freeman, 1971).

The Pavlovian school of psychophysiologists has paid much attention to the development of pathological states through conditioning and, although the stimuli commonly used in their studies are not relevant to this chapter, the findings are of greater interest in the general field of psychosomatic stress (Kurtsin, 1968).

GENERAL BEHAVIOURAL ASPECTS

In addition to cases in which there is a clear physiological 'stress' response, many other social and environmental conditions have been found to be aversive to animals, or give rise to abnormal behaviour, without a proven physiological reaction. Animals may be distressed either when they are thwarted or when in conflict between two mutually incompatible tendencies. However, there is some evidence that these two categories are not distinct: if frustration is aversive, then in a food-thwarting situation the animal may be in conflict between the tendency to approach the food and to avoid the frustration (Adelman & Maatsch, 1955).

Ethologists have for long been interested in the behaviour patterns which occur in these situations, and in any study of the behavioural effects of stress it is important that these patterns should be recognized. The most important ones are as follows.

Inhibition of all but one response. For example, a flock of grazing sheep will flee when disturbed by a dog although presumably the feeding factors are still present but inhibited by the stronger fleeing factors.

Intention movements. When inhibition is not complete the behaviour in question sometimes appears in an incomplete form or 'intention movement' (Daanje, 1950). The crouching movement shown by a bird prior to the take-off leap may occur repeatedly when the bird has conflicting tendencies to fly off and remain on the ground.

Ambivalent movements and postures. These are shown when two or more tendencies are weakly activated simultaneously and they usually consist of a combination of intention movements of the introductory appetitive behaviour belonging to the tendencies concerned (Bastock et al., 1953).

Compromise behaviour. This class is similar to ambivalent behaviour but instead of a compound behaviour pattern being shown, with some components expressing one tendency and some the other, only one pattern is shown which can express both tendencies. For example, the waltz display which occurs in agonistic situations in both the junglefowl (Kruijt, 1964) and domestic fowl (Wood-Gush, 1956) appears to be a compromise of approach and withdrawal.

Overflow and vacuum activities. These are reactions to suboptimal stimuli. Hens in battery cages will occasionally perform nest-building movements as if picking up litter and depositing it round them.

Redirection activities. These occur when two or more conflicting tendencies are strongly activated by the same stimulus and the motor patterns appropriate to one of them are directed to some other subject. It is often aggressive in nature (Bastock et al., 1953). For example, in any social species, when an individual is threatened at a food source by a superior, it will often attack an inferior animal rather than retaliate.

Alternation. In conflict (usually approach/avoidance) an animal will often vacillate between the two tendencies. When food is presented to an animal in a container to which it is not accustomed, it will often alternate between approaching and avoiding the novel stimulus.

Immobility responses. Wild-caught animals will often respond to human handling by becoming completely immobile. A similar phenomenon may be the freezing postures which are often adopted by animals escaping from predators.

Displacement activities. Sometimes in a conflict or frustrating situation activities appear which are apparently irrelevant and out of context with the behaviour immediately preceding or following them. This diverse group of activities was termed 'displacement activities' by Tinbergen (1952), who suggested that the 'nervous energy' normally controlling an activity can 'spark-over' and energize another (irrelevant) activity if its normal outlet is blocked. More recent theories have suggested that, when two tendencies are mutually incompatible, other patterns which would normally be suppressed are permitted to appear through 'disinhibition' (van Iersel & Bol, 1958; Rowell, 1961; Sevenster, 1961). It has also been postulated that thwarting or conflict situations may enhance the relevant internal

stimuli for certain displacement activities (Andrew, 1956; Morris, 1956). For example, physiological arousal may cause sweating and erection of the fur or feathers, and lead to grooming. Another theory has been that pure thwarting situations lead to a switch of attention to stimuli other than those eliciting the thwarted tendency (McFarland, 1966). Displacement activities have also been explained in terms of non-specific arousal (Bindra, 1959) and de-arousal (Delius, 1967). It is probable that different displacement activities involve different mechanisms or combinations of mechanisms. It is also possible that a particular displacement activity may be motivated in different ways in different situations.

Neurotic behaviour. Conflicts arranged under laboratory conditions which may be severe and prolonged may elicit behaviour which is severely disturbed over a long period of time (Masserman, 1950; Pavlov, 1941; Liddell, 1960). Many examples of animals' neuroses show exaggerated defensive behaviour and exaggerated alarm responses (Fraser, 1968).

Aggression. Experimental psychologists, in contrast to ethologists, have tended to study the effects of frustration and conflict in relation to only one of many dependent variables. The two most important of these variables, judged by the amount of research generated, have been aggression and fixation. The original suggestion that aggression is always a consequence of frustration and always denotes its existence (Dollard et al., 1939), has been considerably modified, and now frustration is thought of as increasing the likelihood of aggressive behaviour (Miller et al., 1941). This work has dealt mainly with human subjects but there have been a few reports of frustration causing increased aggression in other species (Scott, 1948; Azrin et al., 1966; Hutchinson et al., 1968; Van Lawick-Goodall, 1968; Duncan & Wood-Gush, 1971).

Fixations and stereotyped behaviour. When rats are forced to respond in an insoluble problem situation a stereotyped pattern appears which does not develop under conditions of trial and error learning (Maier, 1949). This behaviour is resistant to change when the problem is changed to a soluble one (Maier & Feldman, 1948). On account of these facts the term 'abnormal fixation' was given to the behaviour pattern. A type of behaviour which may be related to fixation is the movement, or series of movements, which is repeated regularly and which serves no apparent function in isolated or confined animals. Most famous, perhaps are the repetitive, stereotyped rituals which are commonly observed in zoos and pet shops (Holzapfel, 1939; Hediger, 1950; Morris, 1964).

MOTIVATIONAL IMPLICATIONS

In considering the thwarting or frustration of a behaviour pattern that might eventually lead to stress in agricultural animals, it is important to consider how that type of behaviour is motivated. A hen in a battery cage during the period before oviposition, when she would be nesting in extensive husbandry conditions, often shows some vacuum activities (Wood-Gush & Gilbert, 1969); performing the motions of gathering litter around herself and throwing it on her back, although none is present. Lorenz considers that such behaviour patterns are due to an accumulation of 'action specific energy' which permits the execution of the behaviour pattern in the absence of appropriate external stimuli. Although this 'psycho-hydraulic' model of motivation has been much criticized (Kennedy, 1954; Manning, 1972) it seems to fit certain types of behaviour. The desire to sleep, for example, may occur in the absence of the external stimuli that normally precede it. Many ethologists, however, prefer the type of motivational model suggested by Deutsch (1960) or by Hinde (1969). In these models external stimuli play a more important role. The argument over motivation has been very keenly debated in relation to aggression which is a central feature to any discussion of social stress and related topics. Under the psychohydraulic model aggression in animals is seen as inevitable even in the absence of appropriate external stimuli. Hinde (1969) however sees it as being dependent on internal factors which may fluctuate in strength from time to time, but which do not accumulate in strength with time. He goes on to postulate that the expression of aggression in adult animals may be kept partly under control by discovering environmental influences which tend to minimize the subsequent tendency to aggression and by understanding the ontogeny of aggressive behaviour. On the other hand if aggression inevitably finds an outlet, as assumed in the psychohydraulic model, then we need different husbandry practices to see that its outlet is harmless.

Under modern husbandry, agricultural animals, which for thousands of generations have been kept under extensive or semi-extensive conditions, are likely to be frustrated, thwarted or under conflict. The lack of appropriate external stimuli for the performance of a behaviour pattern may be one such source of distress or stress. Crowding, while seldom imposed to a degree which would endanger the health of the animals, may interfere with the normal

consummatory behaviour. At the other extreme, very bare environments may be aversive to animals (Berlyne, 1960). Other examples are discussed later.

SOCIAL ATTACHMENTS

Among many domestic species, attachments between one animal and another are important in a variety of social contexts, and management practices relating to such attachments can profoundly affect the welfare of the animals.

Formation of Parent-Offspring Bond

Of particular importance is the bond between a female mammal and its young. Among domestic birds, by contrast, the young have no contact with the dam under normal commercial practice, and contact with other young conspecifics appears to be sufficient for normal development. During the first few days after parturition, sows generally do not attack newborn piglets. At this time the sow comes to accept its own young, and fostering is usually successful if carried out within this period (Hosman, 1971). Later, however, unfamiliar young may be attacked vigorously. It is not clear why some sows savage their own piglets just after parturition; perhaps the usual suspension of hostility at this time is lacking or delayed. Cows and ewes may similarly reject young, particularly if they have been fostered, and the animals may have to be observed carefully if serious distress, and even physical damage to the young, is to be avoided.

Neathery (1971) has shown that a ewe, after a single injection of a tranquillizing drug, will often permit a foreign lamb to suckle; the ewe is then likely to accept the lamb after the tranquillizer has ceased to be effective. A similar critical period for the development of maternal-offspring interaction also applies to the behaviour of young; a calf may be unable to find the teat if it has been separated from the cow for the first 6 days of life (Finger & Brummer, 1969). Young lambs frequently die of starvation or exposure, apparently because of inadequate development of suckling behaviour and of mother-young attachment. Lambs show a progressive decline in teat-seeking activity if they are denied successful suckling experiences during the first hours of life (Alexander & Williams, 1966). The behaviour of the ewe is also important for eliciting and maintaining suckling behaviour by the young (Alexander & Williams, 1964).

Weaning

The separation of mother and young at weaning is probably a source of considerable distress. If young are weaned after they have learned to take solid food they may display only a slight temporary upset. Earlier weaning may have more prolonged effects. Lambs taken from their dams and allowed free access to artificial teats spend time sucking the scrotum, navel and ears of other lambs (Stephens & Baldwin, 1970). The same is true of calves; and piglets weaned as late as 3 weeks frequently perform a sustained rubbing of the bellies of their penmates, sometimes interfering with feeding, elimination and other behaviour. In some systems of management, piglets weaned a few days after birth may consume little food for several days. Abnormal aggression and hyperactivity may develop under these conditions. Since piglets show an adrenocortical response to starvation from as early as one day of age (Dvorak, 1971), it seems likely that very early weaning brings about a classical physiological state of stress.

Separation

Disruption of normal mother-offspring interaction can have other complex effects on behaviour. Calves kept with their dams but muzzled between meals have higher immune globulin concentrations than calves allowed to suckle for the same time but separated from their dams between sucklings (Selman et al., 1970).

Moore and Amstey (1962) found that lambs and kids which had been fostered were less likely to become immobile when handled than normally mothered lambs and kids. Separation of kids has also been reported to lead to a deficit in the acquisition of a conditioned response (Hersher et al., 1963). Separation of an animal from its usual herd or pen-mates generally leads to distress. A suckling piglet, removed for a few minutes from its mother and litter-mates, frequently defaecates, becomes extremely active and gives a distinctive pattern of loud repeated vocalizations. A similar response is often given by a pig several months of age when separated from its habitual group for only a few minutes. Attachments to members of a peer group may effectively replace the bond of a young animal to its mother. Ratcliffe et al. (1969) housed weanling pigs in individual pens with solid walls affording only auditory and olfactory contact among the animals. Under this type of social isolation the pigs showed abnormal 'withdrawn' behaviour and

had a high incidence of coronary arteriosclerosis. Other evidence suggests that visual contact is important for pigs if physical contact is prevented. Indeed it is generally considered necessary to allow individually housed pregnant sows to see other animals, although this may not be necessary just before parturition. Furthermore, some of the behaviour of obstreperous boars may be a result of the partial social isolation to which these animals are sometimes subjected.

GROUP INTERACTIONS

With the increasing tendency to house commercial livestock indoors in groups, it is important to understand more about the effects of such potential · sources of distress as high population density, large group size, the introduction of strange animals during the formation of new groups and competition among animals within a group for limited resources.

Group Size and Density

Group size and density have been shown to influence social behaviour in different species, and to have a variety of physiological effects on the heart, adrenal glands and gastric ulceration. Ideally the size of the group and the stocking density should be treated as separate factors, but they have often been confused in experimental studies (cf. Bryant, 1972).

Peripheral plasma corticosterone and adrenal corticosterone levels increased in a linear fashion as the number of laying hens in a cage was changed from one to five (Lei et al., 1972). Group size and density were thus being increased simultaneously. Increased density has been reported to lead to higher adrenal weights in fowls (Siegel, 1959, 1960) but this was not substantiated by Bolton et al. (1972) and Bareham (1972). However, the use of adrenal mass as a criterion of function in these experiments requires caution. In a survey of studies on domestic fowl in which adrenal weights were given, the standard errors of the means were often large (Wells & Wight, 1971); this may reflect experimental difficulties in the removal of the glands. Wells and Wight also suggest that the evidence for increased adrenal secretion due to increased population density is much weaker with fowls than with small mammals where it is well documented. The incidence of coronary arterial disease with myocardial infarction in fowls is affected by the size and sexual composition of the groups (Ratcliffe & Synder, 1964). However, it is not clear how these coronary changes are related to other aspects of physiological stress.

Although the incidence of gastric ulceration in pigs appears to be increasing, it is not clear what part social factors and intensive husbandry play in this trend (Kowalczyk, 1969) as several studies have been contradictory (Reese et al., 1966; Muggenburg et al., 1967; Pickett et al., 1969). Behavioural studies have rarely found a simple relationship between density and social behaviour in fowls (Banks & Allee, 1957; Craig et al., 1969; Craig & Guhl, 1969) or pigs (Bryant & Ewbank, 1972).

Group Formation

Although a certain level of aggression may be maintained in permanent groups, some of the most intense fighting is observed when strange animals are placed together (Guhl, 1968; Craig et al., 1969). A variety of studies have shown loss of economic performance among pigs, poultry and cattle when group membership is altered (cf. Bryant, 1972). However in pigs the use of tranquillizers may obviate aggression when mixing strange animals (Callear & van Gestel, 1971; Symoens & van den Brande, 1969). Furthermore the introduction of unfamiliar animals may have a variety of physiological effects.

Siegel and Siegel (1961) reported that groups of male chickens kept as a minority in pens of strangers have significantly heavier adrenals than birds remaining in their own flocks. This technique of social mixing has also been shown to increase levels of plasma corticosterone and to increase the birds' resistance to certain bacterial diseases while decreasing resistance to certain viral and mycoplasmal diseases (Gross & Siegel, 1965; Gross & Colmano, 1969).

During paired competitions the heart rate of cockerels has been shown to increase sharply. Paradoxically it increases more in winners and birds that anticipate losing a fight (Candland et al., 1969).

Group Structure and Competition

Interactions among members of a social group are frequently varied and complex. Flickinger (1961) showed that after sexual maturity the adrenal weights of cockerels were negatively correlated with rank, whereas Siegel and Siegel (1961) found no such effect. Heifers at the bottom of the bunt order may be more prone to show quiet ovulation (Hafez & Lindsay, 1965). It is in feeding situations that dominance orders have some of their most striking implications. Birds low in the peck order may spend less time feeding during the day (Guhl, 1953; Tindell & Craig, 1959) and possibly show more displacement activity (Wood-Gush, 1959). Decreasing the accessibility of food in three stable flocks of domestic cockerels resulted in increased pecking between birds (King, 1965). Similarly, dominant goats in a small flock became more aggressive when competing for food, and the subordinate animals were more likely to accept punishment repeatedly than to retreat when competing and under frustration (Scott, 1948). Hafez and Lindsay (1965) have reported that cattle under 'social stress' and high competition for food space tend to eat very rapidly; this may affect proper digestion and feeding efficiency. In the light of such findings it is not surprising that social precedence has been observed to correlate with a number of aspects of commercial productivity (Bryant, 1972).

ANIMAL-ENVIRONMENT INTERACTIONS

The design of animal housing which is both humane and productive is a major task of modern agriculture, and it is widely recognized that a poor environment can disturb physiological and behavioural patterns to the point of lowering production and increasing the likelihood of disease. Examples in cattle have been given by Ekesbo (1966, 1973).

In addition, the environment can cause serious disruptions in the behaviour of domestic species. These may be considered as falling into three basic categories. First, normal activities may be 'frustrated' or prevented by some aspect of the physical or social environment. Second, artificial surroundings may lack some key releasing stimulus so that an important activity is not elicited. Third, an environment may be so barren or, alternatively, so complex and changing, that an animal receives too little or too much general stimulation.

Frustration

Frustration has been studied experimentally using domestic fowls in a feeding situation. A food-thwarting situation can be made more severe by depriving the birds of food for a longer period of time or by giving them more training so that their expectancy of food is greater when they come to be tested. Duncan and Wood-Gush (1972a) have shown with adult domestic hens that when hunger and expectancy of food are low there is an increase in preening in a thwarting compared to a control test in which the birds are not hungry and no food is present. The preening is faster and qualitatively different from normal preening and is probably a displacement activity (Duncan & Wood-Gush, 1972b). On the other hand, when hunger and expectancy of food are high, preening is depressed and there is an increase in stereotyped back-and-forward pacing movements. In the first few tests these movements look like attempts to escape but they quickly become very stereotyped in nature and difficult to eliminate from the birds' behavioural repertoire. A tranquillizer, which reduces fear of aversive stimuli, will prevent the onset of pacing if given from the start of testing but has little effect once the movements are established, suggesting that at this later stage they are motivated by something other than fear (Duncan, 1970).

When two birds are frustrated simultaneously the dominant bird shows an increase in aggressive responses towards the submissive bird (Duncan & Wood-Gush, 1971).

In addition to the feeding tendency the nesting, incubating, brooding and sexual tendencies have been thwarted experimentally in various ways and the most common responses are stereotyped back-and-forward pacing, displacement preening and increased aggression (Duncan, 1970). However, hens which are chronically frustrated in a food-thwarting situation and which show a stereotyped behaviour pattern do not show any change in plasma corticosterone level.

There has been little systematic study of frustration of other farm animals. A number of workers have, however, described behaviour patterns which appear to occur during frustration or 'distress'. Calves, when frustrated during suckling, may butt the udder and perform vigorous tail-wagging (Selman et al., 1967, 1970). In adult cattle high rates of eye-blinking are correlated with high pulse rates and may be an indication of 'nervousness' (Wittke & Bartsch, 1967). Defaecation and urination may be similar indicators under some circumstances (Brantas, 1968). When pigs

are required to wait for food they may vocalize, become extremely active and bite the bars of their pens In addition to these reactions, Kiley (1969) noticed an increase in such other activities as movements of the ears and tail when pigs were thwarted experimentally in a feeding situation. In contrast, some domestic animals display abnormal immobility when distressed (Fraser, 1960). Some sheep, having to learn to negotiate a closed field apparatus alone, were reluctant to move through the area and showed displacement grazing, 'feigned lameness' and immobility (Kilgour & De Langen, 1970).

Lack of Key Stimuli

Before one can recognize that a key releasing stimulus is lacking from an animal's environment, the behaviour in question must be fairly well understood. In a study of neonatal suckling behaviour, Selman et al. (1967, 1970) observed that the calf first seeks the teat in the highest part of the cow's underbelly. Among beef cattle this reaction generally leads to a prompt locating of the teat, but in dairy cattle, with the udder extremely low, the calf may spend hours pushing at the xiphoid, brisket and flanks. In this case genetic selection appears to have upset the normal stimulus situation.

Hens of one commercial strain show an excessive amount of pacing during the pre-laying period, while those of another strain spend significantly more time sitting (Wood-Gush, 1969). Wood-Gush (1972) suggested that this difference between the strains is due to differences in responsiveness to releasers for sitting behaviour and not to differences in the strength of the nesting tendency. If the sitting component of nesting behaviour depends on the presence of key stimuli then either the non-sitting strain has lost the ability to respond to the relevant stimuli or the other (sitting) strain is generalizing to sub-optimal stimuli.

It is not clear to what extent sows, at the time of parturition, are disturbed by a lack of suitable bedding material. The extreme restlessness of some sows, which may cause damage to both the piglets and the pen, might be reduced if more normal nest-building were permitted. Pregnant sows in tether stalls perform less chewing and biting of the stalls and the neighbouring animals if they are provided with straw (Fraser, 1972).

General Stimulation

It is frequently suggested that barren environments, such as battery cages and individual stalls, subject animals to 'boredom', but this is a difficult matter to study systematically. Bareham (1972) looked for differences in behaviour in two strains of domestic hens kept in individual battery cages and in groups in deep litter pens. Certain activities were less common in cages. These behavioural differences were considered to be due to the lack of relevant stimuli rather than to physical restriction in the cages. The battery birds spent more time feeding and 'head flicked' more. Food intake was no higher in the battery birds so the increased feeding activity was probably a compensation for the lack of other pecking activity. The causation and function of the head flick are more difficult to understand. Bareham thought that it was similar to the head tic suggested by Levy (1944) to be due to movement restraint. Bareham, on the other hand, regarded head flicking as a repetitive stereotypy caused by social isolation, movement restraint and monotony, individually or together, leading to reduced sensory input. Among domestic mammals, a great many 'vices' are often attributed to 'boredom' (or for examples in the horse see Summerhays, 1959); and studies of electro-encephalogram patterns and cycles of general activity may eventually put such suggestions on a more firm basis (Ruckebusch, 1972). In contrast, parturient mammals often seek to isolate themselves from sources of disturbance, and the noise and activity on some intensive farms may constitute too much general stimulation at this particular time.

MAN-ANIMAL INTERACTIONS

Restraint

Commercial livestock are frequently subjected to restraint of movement of two different types. First, individual animals are often held briefly during routine husbandry practices such as branding, clipping wool and weighing. Second, some animals are housed for long periods in restrictive quarters such as dry sow stalls and battery cages. Brief periods of restraint have a variety of physiological effects. Pigs, like rats, display gastric ulceration and changes in the adrenal cortex during immobilization (Tournut et al., 1966), and at least some of the effects of this treatment are reduced by neuroleptic drugs (Tournut et al., 1969). Ewes which had been restrained in cages for 3 hours showed symptoms of stress as measured by increased concentrations of protein-bound iodine (Falconer & Hetzel, 1964). Stress from

restraint was also reported by Kilgour and De Langen (1970) as judged by levels of cortisol in the plasma. However, in all these experiments the element of social isolation was compounded with restraint. Prolonged restraint may involve similar physiological changes, but some behavioural effects have been noted. A sow, when first placed in a tether stall, may vocalize and struggle, but this reaction generally subsides within an hour. Thereafter the animal may spend up to 80% of the time lying down (Robertson et al., 1972), and may develop repetitive activities such as biting the tether chain or the bars of the pen (Fraser, 1972). Brantas (1968) noted that cows tied up in stalls were much more reactive to sudden noises than cows in a cafeteria court, and the tied cows tended to defaecate and urinate more frequently.

Handling and Herding

Routine handling and herding techniques may have a number of physiological effects, but at least some of these are short-lived. Wolford and Ringer (1962) have shown that handling of mature domestic hens results in a stress response as indicated by a differential leucocyte count. Similarly Freeman (1967) has demonstrated a response in 3-week-old domestic chicks as indicated by depletion of adrenal ascorbic acid. However, in an experiment by Candland et al. (1969) handling led to increased heart rate but this subsided when the birds were returned to their home cages.

Stimulation of the vulva and cervix during artificial insemination causes increased intramammary pressure and mobility of the uterus in cows; but the effect is smaller in nervous cows than in quiet ones, possibly because adrenaline counteracts the effect of oxytocin (Hays & Vandemark, 1953).

The use of a dog for moving animals may affect their physiological reaction. Caged experimental ewes showed physiological signs of stress to the presence of a barking dog nearby (Falconer & Hetzel, 1 964). In contrast Kilgour and De Langen (1970) found no significant increases in cortisol levels in ewes which had been chased by a dog for 5 minutes, but ewes which had been bitten showed increased levels. However, such variation in response to what might be a normal husbandry practice may reflect differences in experience of the ewes as well as possible individual physiological variation, and it is very likely that these differences will apply to many other practices. Similarly, cows differed in their response to being chased by a dog, some appearing to be stressed (Whittlestone et al., 1970).

Mutilation

Such routine husbandry practices as debeaking, dehorning and castration may act as stressors, but little systematic work has been carried out. Domestic cocks show depletion of adrenal ascorbic acid if they are debeaked at 7 weeks of age (Perek & Bedrak, 1 962). In some countries legislation requires that castration of certain species be done only during the early days of life.

Transportation

Transporting animals may introduce many possible stressors including exposure to a strange environment and to unfamiliar animals, crowding, noise, hunger, thirst, fatigue and unfavourable temperatures. In any given instance it is extremely difficult to determine which of these and other factors is having the most profound effect. It is, however, clear that transportation can result in a variety of physiological changes of considerable economic importance.

In beef cattle there is evidence that a high incidence of quiet ovulations occurs after transportation (Hafez & Lindsay, 1965). Meschaks (1953) found impotence developing in 20 out of 24 bulls soon after transport. Early oestrus can be induced in young gilts by transportation (Du Mesnil du Buisson & Signoret, 1962).

Rail or road transportation affected the oestrus cycles and morphology of the corpora lutea of Merino ewes out of the breeding season in Australia; a high proportion of ewes ovulated (Branden & Moule, 1964). However, the ovulation might have been due not to any stressor but to synchronization of the cycles which Hafez and Sugie (1963) suggest may occur in ewes as it does in mice.

Stress associated with transportation is thought to affect problems of disease in several ways. 'Shipping fever' of cattle may be due in large part to some of the potential stressors encountered during transport, but experimentation is needed (Sinha & Si Abinati, 1962). Transport may trigger a number of clinical conditions in horses. When pigs are transported they may defaecate an abnormally large amount ; the caecum may be evacuated in such cases, and this

can aid the spread of certain harmful micro-organisms (Williams & Newell, 1967). Also weight loss in pigs may be positively correlated with length of journey (Cuthbertson & Pomeroy, 1970). Climatic conditions can also influence the decrease in weight (Dantzer, 1970). Tranquillizers might ameliorate the effect although the evidence from cattle is equivocal (England & Taylor, 1960 ; Kercher, 1960).

Other evidence suggests that transportation may bring about a classical physiological state of stress. Cortisol and blood glucose levels of ewes were found to increase in one study after transportation (Reid & Mills, 1962). But in another study a 90-minute journey resulted in only moderate increases of cortisol levels (Kilgour & De Langen, 1970). Again the difference could be due to a number of features of the two studies. Starvation may be important as a stressor in transportation. Ewes starved for 4 days before a 4-hour road journey showed increased cortisol levels and all had higher blood glucose scores compared to ewes that had been fed up to the time of the journey (Reid & Mills, 1962).

Among 'stress-susceptible' strains of pigs, some animals may die for no apparent reason during transportation, while many others may display extreme physiological reactions which lead to undesirable changes in the quality of the carcass after slaughter. Much research on this topic is linked to problems of management at the abattoir, and the matter is discussed below.

Abattoir Management

During the hours before an animal is slaughtered it may be transported from the farm, placed in a strange holding pen (often with unfamiliar animals), left without food and handled or herded several times. Traditional physiological features of stress are often detected at this time. The degree of gastric ulceration in pigs increased with the time the animals were kept at the abattoir before killing (Muggenburg et al., 1967). Kilgour and De Langen (1970) compared the cortisol levels of lambs killed at two different abattoirs, one noisy and crowded and reached only after a long journey, the other quiet and not necessarily requiring so much transportation. The levels were significantly higher at the former.

The treatment of the animals before slaughter can have important effects on the quality of the carcass. Adverse conditions during transportation or at the abattoir can lead to a depletion of muscle glycogen, which, in turn, can lead to an abnormally rapid fall in pH and a more rapid beginning and cessation of rigor mortis. Among pigs this condition can cause the flesh to be pale, soft and exudative (PSE), and of reduced commercial value. In a related condition the ultimate pH may be abnormally high, causing the meat to be dark, firm and dry (DFD). Sybesma (1969) states that both these problems can be reduced by transporting and slaughtering susceptible animals under ideal conditions. It is not entirely clear what the important management factors are. Lendfers (1969) noticed differences in meat temperature, pH and rigor mortis depending on whether or not the pigs had been delayed at the abattoir before slaughter, and whether or not they had been transported at low densities and with good ventilation.

In a further study Lendfers (1971) analysed records of deaths during transportation to the abattoir of more than 200 ooo pigs. Temperature emerged as a crucial factor: the death rate was particularly high if the temperature exceeded 15°C, and in the summer months the death rate was highest among pigs transported around mid-day. The loading density, number of pigs per vehicle and the distance to the abattoir were all significant factors when temperature was high. Other work indicates that pigs sedated before transportation to the abattoir show a lowered incidence of sudden death and of undesirable changes in the carcass after slaughter (Devloo et al., 1971; Oldigs & Unshelm, 1971).

Stress before slaughter is of particular importance with pigs because selection for a lean carcass has apparently altered some of the basic endocrine functions of the animals (Unshelm, 1971) rendering some breeds liable to dire effects of stress. Still, the basic physiological reactions to conditions at the abattoir appear to be shown by cattle as well. Thornton (1971) reported a more rapid onset of rigor mortis in the heart muscle of cattle slaughtered on a busy day than on a day with fewer killings, and suggested that rigor mortis sets in more rapidly as the day progresses.

CONCLUDING REMARKS

Most of the research described above has reported relationships between aspects of animal management and behavioural or physiological changes in the animals. However, very few studies have looked at changes of both types in the same situation. This is unfortunate because scientists and practitioners alike often appear to assume that some

simple relationship must exist between 'abnormal' behaviour and the traditional physiological 'stress' responses. Several studies on pigs point out how unwarranted such an assumption may be. For example, loud vocalizations and violent struggling in restrained sows bore no simple relationship to heart rate (Marcuse & Moore, 1944). Likewise, Baldwin and Stephens (1973) found that pigs gave a number of behavioural responses, suggesting a high level of distress, in a learning situation which involved exposing the animals to electric shock; but these procedures elicited only a feeble increase in the levels of plasmacorticosteroids.

For the present these findings are somewhat puzzling. They emphasize, however, that questions of 'stress' involve a variety of rather disparate reactions by animals, and that an understanding of both physiology and behaviour will be important for the design of husbandry practices which are efficient while humane.

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