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STRESS, WELFARE AND THE STATE OF EQUILIBRIUM

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Equilibrium and motivation

In order to recognise and evaluate the responses of animals to adversity it is necessary to know something about the systems which enable animals to regulate their internal state. Some aspects of internal state, such as body temperature or the osmotic pressure of blood can be measured directly so that it is possible to see the effects of functional systems which maintain the body state between identifiable upper and lower limits. Other aspects of internal state may be very difficult to measure because the variable which is regulated is within cells or in the brain. For example, it seems that animals act so as to prevent total sensory input from remaining at a very low level for a long period or rising to a high level. The existence of this system and many others, can be recognised only by seeing the regulators in action. It is likely that our knowledge of systems which have the effect of avoiding more or less extreme states, is incomplete, especially where those systems are confined to the nervous system.

Many functional systems include both behavioural and physiological components whose function may be to rectify divergence from the tolerable state range or to achieve an end such as predator avoidance or mate finding. In order to lower body temperature an individual might sweat, pant or go somewhere cooler so that identification of displacement of body temperature would necessitate physiological and behavioural monitoring. Maintenance of state within the tolerable range might be done by negative feedback control, in which a displacement of state is detected and the regulatory action is carried out, or by feedforward control in which a predicted change in state is prevented by regulatory action. Much of the behaviour which has a regulatory function is initiated well before the state of the individual approaches the limits of the tolerable range so feedforward control is frequent. Whether the function of behaviour is regulation of body temperature, maintenance of food intake, minimising the risk of predation, or any other, it is essential that decisions be taken so that the appropriate action takes place at the appropriate time (7,p.79). These decisions are based on the levels of a wide variety of causal factors, each of which is affected by a sensory input after processing in the brain, or a monitor of internal state such as blood glucose or hormones, or an output from an internal clock. Many causal factors will affect the likelihood that a decision will be taken to carry out a particular behaviour so the motivational state of an animal is the state of all causal factors. If many of the causal factors which promote preening are at high levels then preening is likely to occur but its occurrence will depend upon all other causal factors as well. If causal factors promoting feeding, drinking, escape from a predator or courtship are high then these activities, rather

than preening will occur. Some behaviours, such as escape from a predator or obtaining food when food is scarce, are more urgent than preening and take precedence on most occasions. Natural selection has led to the existence in each animal of a decision making system which increases fitness, meaning individual survival and hence reproductive potential. Predator avoidance would normally take precedence over other activities but a balance amongst all essential functions must be achieved so that on some occasions feeding or even preening must occur in conditions where there is danger of predation. The motivational systems of domestic animals must be very similar to those of their wild ancestors.

When a decision to carry out a behaviour is taken, one possible consequence is that the behaviour occurs and there is the required effect on the state of the animal which leads to changes in causal factor levels and the termination of the behaviour. Such a sequence of events is very frequent and animals clearly have an expectation of the result of an action. If a hen carries out a preening movement it expects a change in the sensory input from that region of the skin and feathers which it intended to preen. The actual input can be matched with the expected input. In a similar way, the characteristics of its surroundings are recognised and there are expectations about repeated fluctuations in the surroundings which allow the recognition of subtle changes in the surroundings by comparison of input with a model in the brain (6). The actual input has been referred to by Wiepkema (36) and others as istwert and the expected input as the sollwert. The comparison between istwert and sollwert allows rapid recognition of a second possible consequence of a decision: where a behaviour occurs but the state of the animal does not change in the expected way. A mismatch may occur because the response is not adequate to correct the change or because something unpredicted has happened. In these circumstances, the behaviour may continue for a long period or some other physiological mechanism or behaviour may be initiated. A third possible consequence of a decision is that, due to environmental constraints the animal is unable to carry out the behaviour at all or is restricted in the extent to which the behaviour can be shown. Welfare problems may arise from (i) the effects of inability to rectify a divergence from tolerable state range or to prevent an imposed aversive stimulus; (ii) the effects of unpredictable events or unpredictable consequences of actions; and (iii) the effects of frustration in which an action is prevented wholly or partly. Another situation which is often discussed in motivational terms as being aversive is that in which "conflict" occurs. The argument put forward is that levels of causal factors promoting two different actions are both high and there is conflict concerning which to carry out. Since motivational state at all times will involve several causal factor levels being high it seems unlikely that the situation per se would be aversive. Many examples of conflict do, however, involve some frustration in that one or both actions are prevented or made difficult by environmental constraints. Hence such situations can be considered when frustration is discussed. Alternatively the necessity to encounter aversive stimuli is present so it is the effects of these which should be assessed.

Regulation and stress

When physiological and behavioural responses within a functional system

are insufficient to maintain the state of an animal within the tolerable range, the individual needs more available energy so that actions which are more expensive energetically can be utilised. If danger of predation, or of attack by conspecifics or of physical damage is present, a large amount of extra energy is required for a short period of a few seconds or minutes. In many situations also, a lower level of increased energy availablity is necessary for some minutes or hours. A rapid, largely short-term increase in energy availability is provided by the activation of the sympathetic nervous system and adrenal medullary system which results in the secretion of adrenaline and noradrenaline into the blood. The more long lasting increase in energy store utilisation is initiated by corticotrophin releasing factor travelling from the hypothalamus to the adenohypophysis where adrenocorticotrophic hormone (ACTH) is secreted into the blood. This ACTH travels to the adrenal cortex where glucocorticoids, principally corticosterone in poultry, are produced. Brief activation of these two systems involving adrenal hormone production need have no adverse effect on the animal. The extra energy made available may result in more efficient food acquisition, and hence, perhaps, improved individual survival, or more effective courtship and hence greater reproductive success. If increased glucocorticoid levels in the blood result in an individual maintaining its body temperature within the tolerable range rather than dying of hypothermia, then the value of the adrenal response to the individual is obvious. The response might last for a few minutes only and the net cost to the animal might be restricted to the energy only. Behavioural and physiological responses within functional systems and short-term adrenal activation with no adverse effects on the individual are, as Dantzer, Mormède and Henry (14) pointed out, part of the adaptation of individuals to the range of environmental conditions encountered in everyday life.

Prolonged hyperactivity of the adrenal cortex can have effects on individuals which impair survival chances and ultimate reproductive success. Freeman (23, 24) and Stephens (33) list the following changes in domestic fowl which were correlated with adrenal hyperactivity: reduced food consumption, protein synthesis, growth, body weight, lymphocyte counts, immunological activity, gonadal activity; changes in cardiovascular functioning and increased susceptibility to certain diseases. Hence it would seem useful to distinguish between adrenal activity which helps animals to cope with their environment and adrenal or other responses which harm the individual.

The term "stress" normally implies that some situation is causing prolonged adverse effects on an individual. Hence it is clearly undesirable to equate stress with adrenal cortex activity as Selye (30) did and many others have done since, e.g. Banks (3). The activity may be beneficial, as explained above, and in addition,blood corticosterone levels in poultry show fluctuations during early development, see review by Freeman (24), and also show a diurnal rhythm (20). Fraser et al (22) emphasise that the implication that stress refers to some single physiological phenomenon is undesirable. Selye divided his "general adaptation syndrome" into a stage of resistance and a stage of exhaustion but then used stress for both of these. It is scientifically most useful to restrict the term to the overtaxing of regulatory systems so that the individual "shows a prolonged inability to cope" (2,p.3). The environmental factors which lead to such overtaxing are

widely referred to as stressors and stress is best used as a dynamic term. Stress is therefore defined as follows (8). Stress is the process by which environmental factors over-tax control systems in an individual thus activating responses whose effects are prolonged and ultimately detrimental to that individual in that they reduce its fitness. Individual fitness here means reproductive potential which would usually be measured by: probability of mortality, rate and quality of growth if still growing, ability to reproduce, and quality of offspring. Since it is reproductive potential which must be assessed, some estimation is necessary if management prevents either survival to reproductive age or reproduction itself.

An early indicator of stress often involves signs that some regulatory system has been stretched to a point beyond which a return to normality is impossible. After this has happened, the system may function less efficiently so that long-lasting adverse effects accrue and fitness is reduced. Indicators of stress in poultry would include increased mortality rates, increased frequency of injury, ulceration, greater susceptibility to disease, e.g. work by Gross and Siegel (25,26), some abnormal behaviour, signs of adrenal hyperactivity, perhaps high brain analgesic levels, reduced growth rate and reduced egg production. Injury, disease susceptibility, abnormal behaviour, etc which would impair fitness if the individual had to compete with other birds for resources, such as food or a mate, should be regarded as indicators of stress even if the husbandry of the birds is such that these birds do not have to compete for resources.

Predictability

Animals subjected to physical damage or other imposed aversive stimuli such as very low temperature or electric shock will, if these are extreme enough or frequent enough, show high adrenal responses and reduced fitness. Less extreme aversive stimuli are more likely to be stressful if they are unpredictable than if the animal can predict the timing and nature of the stimulus. Work by Bourne (4) on soldiers showed that adrenal cortex activity was higher when they were unsure of when they would be required to engage in battle than when an attack was planned precisely. Rats subjected to electric shocks had many gastric ulcers if these were unpredictable but few ulcers if the shock could be predicted (34). In such studies the fact that the individual can reduce the effects of the aversive stimulus is of major importance. Unpredictability in an important event such as feeding can also lead to adrenal responses. Levine, Coover and Goldman (10, 28) found that rats which had been fed regularly but did not receive food when it was expected showed increases in plasma corticosterone. If they were trained on a fixed interval reinforcement regime and then changed to a variable interval regime so that the arrival of food was unpredictable, plasma corticosterone increased but if they were trained on variable interval then changed to fixed interval reinforcement there was no adrenal response. Unpredictable input or the absence of expected input means that the animal is not regulating its life adequately and hence such unpredictability can be disturbing. Since animals recognise discrepancies by comparing actual inputs or outcomes of action with expectancies or sollwerte based upon previous experience, in order for us to appreciate what might be stressful it is necessary to understand something of information processing and the functioning of the matching mechanisms in the limbic system and cortex of

the brain (35,27).

Animals which can predict the occurrence of events in their environment can prepare for them by modifying their behaviour and hence, to some extent, their physiological state. Some preparation can also be made for less predictable, intermittent events. Animals can also increase the average predictability of input by carrying out stereotypies (7, p.99). These might also help to regulate motivational state and reduce the necessity to respond to inputs from unpleasant stimuli (21). Dantzer and Mormède (12) found that confined hungry pigs, which were fed intermittently, manipulated a chain if it was available. Those pigs which had been able to manipulate a chain had lower cortisol levels than those not provided with a chain. The possibility, for animals encountering aversive stimuli, to show behaviour which reduces energetically expensive and possibly harmful physiological responses has some obvious advantages. Further evidence for such possibilities comes from work on behaviour in relation to the endorphin system. Beta endorphin is sometimes produced when ACTH is secreted and it has some effects on adrenal function but this opioid peptide and the enkephalins, which are shorter peptides with the same amino acid sequence as part of the beta endorphin peptide chain, have effects in the brain. Some of these effects are analgesic in that they reduce responses to pain or other aversive stimuli. The work of Wiepkema, Cronin and van Ree (37) showed that whilst confined sows spent long periods carrying out stereotyped movements, such movements were much reduced by the injection of naloxone which blocks opioid receptor sites in the brain. An interpretation of this result is that the animals show stereotypies because these increase brain analgesic levels and hence reduce the aversive effects of the housing situation.

Frustration

If the levels of most of the causal factors which promote a behaviour are high enough for the occurrence of the behaviour to be very likely, but because of the absence of a key stimulus or the presence of some physical or social barrier, the behaviour cannot occur, the animal may be said to be frustrated. A hen which is about to lay will build a nest if materials are available but if there are none, an indication of the hen's frustration is the pacing behaviour or excessive prolonged sitting which is often observed (5,38,39). Duncan and Wood-Gush (18,19) reported on experiments in which hens were trained to feed from a dish in a certain position and then prevented from reaching the food because a perspex cover was put on the dish. In such situations where frustration is caused by some agency actively preventing an action, the animal is often said to be thwarted. Hens housed singly responded to this situation by stereotyped pacing behaviour and changes in various other activities according to the duration of the period of training in that situation. Hens in pairs were more likely to attack one another when frustrated. A cock would even attack a hen with which he normally copulated. Increased escape attempts and stereotypies when alone and increased fighting when in pairs also occurred in pigs prevented from obtaining food by the presence of a barrier, or by its non-appearance when expected. There was also an increase in plasma cortisol (11). As Archer (1) has pointed out, situations where animals are not able to obtain food because of the presence of conspecifics competing with them for that food may also be categorised as frustration or thwarting. This situation often

obtains on farms and intensively housed animals are often in conditions where key stimuli are absent or some barrier prevents a behaviour from occurring so that they are frustrated (40).

When frustration occurs it might be of trivial importance in the life of the animal or it might be so frequent and involve so fundamental an activity that the fitness of the individual is impaired. It is clearly possible for frustration to be stressful or for it to result in one individual injuring another. We know little about how often such frustration occurs.

Welfare

The systems for regulating body state and coping with adversity, which are described above, have many components, some of which can be observed and measured by those attempting to assess the suitability of a method of farm animal husbandry. The mechanisms used by individuals which help them to cope with adverse conditions are often complex and many of them are not at all well understood. It is apparent that many animals use behaviour preferentially when trying to cope so that behaviour is often a sensitive indicator of adversity. A variety of physiological changes are also used to fulfil similar functions. Heart-rate may be increased, adrenal activity may occur and brain analgesics may be utilised to modify physiological and motivational state. Each of these responses can be occurring on such a small scale or for such a short time that no conclusion as to whether the husbandry method is unsuitable could be reached. If the long term effect of some environmental factors on an individual are to reduce fitness, i.e. the animal has been under stress, then most people would say that these factors are bad for the welfare of the animal. But stress, as defined here, is a relatively precise term in comparison with welfare. This is so because most people would also consider welfare to be bad if an individual had to spend much of its time correcting some deviation from the tolerable range so that stress did not occur. The correction might involve carrying out stereotyped behaviour, maintaining a very high or a very low level of responsiveness, or frequently showing behaviour which was harmful to other individuals. Welfare might also be considered to be bad if an individual continually suffered from minor injuries or disease or if it could cope with life only if it maintained itself for long periods in a self-narcotised state using natural opioids.

Some of the conditions described above could occur on farms without impairing fitness. They might, however, result in rapid death in the wild where the animal needed to be active and responsive all the time in order to survive. When people make a judgement about whether the welfare of an animal, which for example spends 20% of its waking life carrying out stereotyped behaviour, is bad they may be considering biological function and deciding that an animal which behaved in that way in the wild would not survive. Some consideration of biological mechanisms is of value when considering welfare, but it is not practicable to define welfare in terms of what would happen if an animal behaved in that way in the wild. If a decision has to be taken about what types of, or frequencies of, abnormal behaviour or physiology should be classed as indicators of bad welfare, some moral judgement is needed. The scientific evidence upon which this judgement may be based concerns what constitutes an extreme response in the species,

whether the individual is able to return to normality and indications of motivational priorities including the importance which the individual animal attaches to resources, stimuli or actions. This last point requires further explanation.

It is possible to discover something about how motivational state changes and on what basis an animal decides to switch from one behaviour to another by watching behaviour, monitoring physiology and by carrying out experiments (7,p 89). Sibly and McFarland (31,32) and others have described experiments in which motivational state can be investigated and priorities assessed by monitoring behaviour closely in controlled situations. Some indication of the importance of environmental characteristics to hens has been obtained in the preference experiments of Dawkins (15,16,17) and the preferences of pigs have also been investigated (29). As Dawkins appreciates (17) if a hen shows a preference for a condition or stimulus, the question of the priority ascribed to that condition or stimulus still remains. How hard will the animal work in order to achieve it and how important is it in comparison with other stimuli? This is very much a question about motivation and requires rigorous experimentation in order that it can be answered. The answer is difficult to interpret for, just as it is difficult to judge the importance to welfare of deprivation of the opportunity to carry out an infrequent behaviour pattern, so it is difficult to decide whether an opportunity which the animal rates as less important than, say feeding should or should not be denied to that animal. These preference experiments could provide some additional information about what husbandry methods are bad for welfare but they do not provide general answers.

Stress or bad welfare situations in which animals must frequently carry out responses in order to cope with adversity can be recognised by measuring behaviour, physiology or production in individuals but a clear sign evident from any of these alone is sufficient for a husbandry method to be judged unacceptable. As Dantzer and Mormède (13) emphasise, we have much to learn about the attempts of animals to regulate their state during chronic adversity. With more work on motivation and on stress responses it is likely that we shall discover more ways of recognising that an animal's welfare is bad so we should err on the side of the animal when deciding what to accept as adequate indicators now.

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Summary

Stress, Welfare and the State of Equilibrium

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Animals regulate their internal state by means of functional systems whose behavioural and physiological components act so as to rectify divergence from the tolerable state range. The occurrence of behaviour, whether its function is body temperature regulation, predator avoidance, or any other, depends upon decisions about what to do and when. Such decisions are based upon the levels of a variety of causal factors and, once taken, an action may occur with the required effect, or the animal may be unable to achieve that effect, or some unexpected input may occur, or the animal may be frustrated in its attempts to show the behaviour. Extra energy is needed if an effect cannot be achieved but the activation of the adrenal systems to provide this energy does not necessarily have adverse effects on the animal. Stress is defined as the process by which environmental factors over-tax control systems in an individual thus activating responses whose effects are prolonged and ultimately detrimental to that individual in that they reduce its fitness. Indicators of stress in poultry are listed and the stressful effects of environmental unpredictability and frustration are described in

detail. The welfare of an animal would be considered to be bad if that animal were under stress as defined above. Welfare would also be considered bad if an animal had to spend much time, either correcting some deviation from the tolerable range so that stress did not occur, or being caused some pain or discomfort. A moral judgement based on scientific evidence is needed to decide the unacceptable levels. Ways of recognising attempts at regulation and ways of investigating motivational priorities are discussed but it is clear that we have much to discover before this is thoroughly understood. Meanwhile we should use the indicators of bad welfare which are available when taking decisions about husbandry methods.

Zusammenfassung

Wohlbefinden als Ausdruck des Gleichgewichtes

Tiere regulieren ihren inneren Zustand mit Hilfe von funktionellen Systemen, in denen Verhalten und physiologische Komponenten dazu dienen, Abweichungen von einem tolerierbaren Zustand zu korrigieren. Das Auftreten von Verhaltensabläufen, sei es im Rahmen der Wärmeregulation, Feindvermeidung oder anderer Funktionen, hängt von der Entscheidung ab, was wann zu tun ist. Solche Entscheidungen basieren auf einer Vielzahl von Einflußfaktoren, und wenn sie einmal getroffen sind, können folgende Situationen auftreten: Ein Verhaltensablauf führt zum gewünschten Effekt, das Tier ist nicht fähig, den Effekt zu erreichen, ein unerwarteter Input tritt auf oder das Tier wird beim Versuch, das Verhalten auszuführen, frustriert. Kann ein bestimmter Effekt nicht erreicht werden, benötigt das Tier zusätzliche Energie. Die Aktivierung des Nebennierensystems zum Erreichen dieser Ziele muß keinen negativen Einfluß auf das Tier ausüben. Streß ist als Prozeß definiert, in dem Umweltfaktoren das Kontrollsystem eines Individuums überfordern und dadurch langanhaltende und schließlich schädliche Reaktionen hervorrufen, die seine Fitness reduzieren. Indikatoren für Streß beim Geflügel sowie die Bedeutung der Unvorhersagbarkeit von Umwelteffekten und Frustration in Bezug auf Streß werden im Detail beschrieben. Das Wohlbefinden eines Tieres wird als beeinträchtigt angesehen, wenn die Tiere sich in einer - wie oben definierten - Streßsituation befinden.
Das Wohlbefinden wird auch dann als beeinträchtigt angesehen, wenn das Tier viel Zeit aufwenden muß, um zur Vermeidung von Streß Abweichungen vom tolerierbaren Bereich zu korrigieren oder Schmerzen und Unbehagen erleidet.

Zur Entscheidung über das akzeptable Ausmaß an Beeinträchtigung ist ein auf wissenschaftlichen Erkenntnissen beruhendes moralisches Urteil notwendig. Die Möglichkeiten, die Versuche zur Regulation zu erkennen und Prioritäten in der Motivation der Tiere zu untersuchen, werden diskutiert. Es ist allerdings offensichtlich, daß noch viele Vorgänge abzuklären sind, bevor diese Probleme geklärt werden können. Vorerst sollten verfügbare Indikatoren für mangelndes Wohlbefinden zur Beurteilung von Haltungssystemen herangezogen werden.