A STUDY OF THE DOMESTIC FOWL UNDER CONDITIONS OF DRIVE INTERACTION AND GOAL INACCESSIBILITY

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I declare that this thesis has been composed by me
and that the work described is my own.

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SUMMARY

The domestic fowl was frustrated in various ways during nesting, feeding, incubation, brooding and sexual activity and a list was compiled of the responses which were elicited. Depending on the severity of the frustration and the stimulus situation, the most common responses were displacement preening, stereotyped pacing and increased aggression. When frustrated individually, birds showed displacement preening if the frustration was mild or short-term and stereotyped pacing behaviour if it was severe or long-term. When frustrated in pairs the dominant bird showed an increase in aggressive responses. The preening which occurred was classified as a displacement activity because it was unrelated to the thwarted tendency and also because it was qualitatively different from normal preening; individual preening movements being of shorter duration than usual. Frustration led to avoidance of the frustrating stimulus when this was permitted but there was no evidence that this avoidance tendency conflicted with the original approach tendency. Both approach and avoidance occurred in distinct bouts and the avoidance was accompanied by displacement preening. Since there was no evidence of a conflict the displacement preening could not be accounted for in terms of the disinhibition hypothesis. It was suggested that frustration was probably accompanied by the physiological defence response, which results in peripheral autonomic changes, although this was not reflected by a change in skin temperature. It was further suggested that the bird became excited and avoided the frustrating stimulus then switched its attention to the peripheral changes (possibly pteromotor activity) and preened. The preening was accompanied by the bird calming down and then approaching the frustrating situation once again. It is proposed that the displacement preening functions to allow homeostasis to occur and the bird to switch its attention back to the original stimulus. The stereotyped pacing movements at first appeared to be attempts to escape from the frustrating situation when complete avoidance was prevented. However, with repeated frustration the movements became very stereotyped. A tranquillizer which prevented the onset of the movements when given before the start of frustrating tests was only slightly effective in reducing their frequency once they had become established. It is therefore postulated that at this later stage they are motivated by something other than fear. The performance of the movements possibly helps the birds to adjust to the situation since there was no increase in plasma corticosterone level which is one of the indices of chronic stress. An increase in aggressive responses only occurred when a bird lower in the peck order was present. It is suggested that frustration again leads to a high degree of excitation and in this state the bird responds to the aggression-inducing stimulus of the submissive bird which before it had tended to ignore. Also since frustration is probably accompanied by the physiological defence response, the bird is physiologically prepared to make aggressive responses.

The relevance of these various behaviour patterns to poultry husbandry is discussed. Although none of the patterns needs necessarily be symptomatic of a pathological state in the bird, nevertheless, two of them, namely increased aggression and stereotyped pacing behaviour, may lower production efficiency mainly by wasting energy. Displacement preening, on the other hand, could act as a useful warning of the presence of frustration. The significance of frustration with respect to the welfare of the chicken kept under intensive conditions is difficult to assess. Frustrating situations do occur in practice and probably lead to some distress but the responses the bird makes may help it to adjust to the situation.

PART ONE

INTRODUCTION AND REVIEW OF THE LITERATURE

Introduction

Goal inaccessability is one particular type of frustration. The term "frustration" has a variety of meanings to different authors in the field of psychology. Some use it to refer to a frustrated organism, some to a frustrating situation and others to both. Yates (1962) suggested that "frustration" should be reserved to describe the state of an organism placed in an objectively defined frustrating situation. He also proposed that the term "frustrating situation" should be restricted to those situations in which an organism is prevented, by a physical barrier, from obtaining a physical goal by the performance of responses which previously led to the attainment of that goal. This usage of the terms "frustration" and "frustrating situation" will be adopted in this thesis.

Ethologists have tended to use the word "thwarted" rather than "frustrated" to describe animals in a position of goal inaccessability. They have thus tried to avoid the implication of a pathological state which has been suggested in the use of the word "frustration" by some psychologists and particularly psychoanalysts. However, there can be no doubt that in much of the literature the two terms "frustrated" and "thwarted" are used synonomously. No distinction will be made between them in this thesis.

There are three reasons why a study of the domestic fowl under frustrating conditions is of importance. Two of these are inter-related and are concerned with the effects of modern husbandry practices on the fowl. It is important to find out if these practices are likely to lead to frustration and then to discover what effect this has on production efficiency and the welfare of the chicken. For example in 1965 the report of Technical Committee set up by the British government to enquire into the welfare of animals kept under intensive livestock husbandry systems, under the chairmanship of Professor Rogers Brambell, was published (Her Majesty's Stationery Office 1965). In this report, in the section dealing with the domestic fowl, it was suggested that intensive husbandry systems often lead to frustration. For example the report stated, "Much of the ingrained behaviour is frustrated by caging. The normal reproductive pattern of mating, hatching and rearing young is prevented and the only reproductive urge permitted is laying. They cannot fly, scratch, perch or walk freely. Preening is difficult and dust-bathing impossible..... The caged bird which is permitted only to fulfil the instinctive urges to eat and drink, to sleep, to lay and to communicate vocally with its fellows, would appear to be exposed to considerable frustration". Since these statements are mainly surmises it is important to discover exactly how the fowl does behave when frustrated in a carefully controlled situation, and whether this behaviour is the same as, or resembles, that seen in intensive husbandry systems. The third reason is the intrinsic value of such a study. From a comparative point of view, little is known of the behaviour of this species in frustrating situations. Also, although both psychologists and ethologists have been working intensively on frustration for the past thirty years there remain many problems and paradoxes in this field.

CHAPTER 1

REVIEW OF THE LITERATURE

Introduction

The study of the effects of frustrating situations on the behaviour of organisms has, in the past, been carried out by isolated groups of workers, each engaged in one particular aspect of this experimental field. Until recently there has been very little attempted integration of theory between these groups with the result that frustration theory has suffered and is at present disjointed. As in other fields of behaviour, probably the widest gap lay between the theories of ethologists and those of American experimental psychologists and learning theorists. However, even the latter were divided into schools, each studying the effects of frustration in relation to only one of many dependant variables. The three most important of these variables, judged by the amount of research generated, have been aggression, fixation and regression. Fortunately the gaps are rapidly narrowing and some integration is beginning to appear. For example McFarland (1966a) discusses some of the psychological theories of frustration with respect to the ethological concept of displacement activities, Zeigler (1964) considers the implications that displacement activities have had in both ethological and psychological theories of motivation and Yates (1962) reviews all the important psychological theories of frustration and conflict. Notwithstanding this, the literature will be reviewed in five sections. The first section will deal mainly with displacement activities. The next three sections will cover in turn the effect of frustration on aggression, fixation and stereotypy, and regression. In the final section some of the theories of frustration will be reviewed.

Displacement Activities

In ethology one of the most important and certainly the most controversial phenomena associated with frustration and conflict has been displacement activities. These activities are important because they offer good opportunities for the study of the evolution of behaviour patterns (Tinbergen, 1951). Certain forms of behaviour, such as grooming, which occur as displacement activities early in the evolutionary history of the animal, acquire survival value as releasers in later evolutionary time through the pressure of natural selection. There are, however, other activities which occur in similar situations and which should be distinguished from displacement activities. Bastock, Morris and Moynihan (1953) have listed and described these. They are:

1. Ambivalent movements and postures. These are shown when two or more drives are weakly activated simultaneously and they usually consist of a combination of intention movements of the introductory appetitive behaviour, belonging to the drives concerned. For example when food is offered to a half-tame Moorhen it may peck towards the food while at the same time keeping its distance (Hinde, 1966 p. 275). Earlier work by Daanje (1950) had shown how many display, threat and begging movements could be understood as ritualised intention movements and Bastock, Morris and Moynihan suggest that ambivalent movements can undergo the same process.

2. Displacement activities. These will be discussed in detail later.

3. Neurosis. Bastock, Morris and Moynihan do not fully define this category. They suggest that the term "neurosis" has been used rather loosely by psychologists to describe several kinds of "abnormal" behaviour for which ethologists use different terms. They say that perhaps during certain intense conflicts and thwarting situations, displacement activities offer an insufficient outlet for surplus excitation and neurotic disorders result.

This is the weakest description of any of the categories covered by Bastock, Morris and Moynihan. They do not suggest what the definition of the term "neurotic" should be nor whether the behaviour is adaptive or maladaptive. They do not even say if the term "neurotic" should have the chronic implications given it by many psychologists (Wolpe, 1958; Eysenck and Rachman, 1964; Hamilton, 1969).

4. Overflow activities. These are regarded as simply reactions to suboptimal stimuli.

5. Redirection activities. They describe these as occurring when two or more incompatible drives are strongly activated by the same stimulus and the conflict of drives is resolved by the animal "venting" one of these drives upon some third animal or object. That is, the executive motor patterns of one of the activated, conflicting drives are transferred on to another external object.

To this list should be added another category described by Andrew (1956a).

6. Compromise behaviour. This class is similar to ambivalent behaviour but instead of a compound pattern with some components expressing one tendency and some the other, only one pattern is shown, which can express both tendencies.

For example, the feather settling movements shown by a male or female Emberiza calandra on meeting its mate after an absence, include more wing vibration than normal. Wing vibration itself indicates a sexual tendency, and so the feather settling with wing vibration may be considered as compromise behaviour. Andrew mentions that it is not always possible to distinguish strictly between ambivalent behaviour and compromise behaviour.

The second group of activities listed by Bastock, Morris and Moynihan (1953) were displacement activities and these will now be considered more fully. The term "displacement activity" was first used by Armstrong (1947) and by Tinbergen and van Iersel (1947) to describe irrelevant behaviour patterns which are seen frequently during agonistic or sexual encounters particularly between birds (Armstrong) and sticklebacks (Tinbergen and van Iersel). These activities had previously been grouped together independently by Tinbergen (1940) and by Kortland (1940) and some attempts made at a causal analysis. They were described as acts which were out of context with the behaviour immediately preceding or following them and which commonly occurred in a thwarting or conflict situation.

Tinbergen (1952) gave a list of displacement activities and the situations in which they occur, as he had observed them in a wide range of avian species with occasional reference also to sticklebacks. He stated that the main characteristics of displacement activities are:-

1. The movements shown do not belong to the executive motor patterns of the activated drive.*

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* The term drive is used meaning the complex of internal states and stimuli leading to a given behaviour (Thorpe, 1951).

2. Their irrelevance, or absence of the external stimulation normally associated with the action.

3. An incomplete or frantic performance.

Displacement activities were said to be allochthonous, that is, the behaviour was motivated by the drive built up by other activities. Behaviour motivated by its own drive was termed autochthonous. The term allochthonous implies a "surplus" hypothesis of motivation, with energy "sparking-over" from the activated drive to another drive as had been suggested earlier by Makkink (1936). Tinbergen (1952) suggested that the primary function of displacement activities is an outlet for excess internal action potential and so they form a defence against neurotic disorders. Some of them may act as social releasers and when acting in this way they differ substantially from their autochthonous example.

McFarland (1966a) criticizes this explanation of displacement phenomena. He supports Zeigler (1964) who says that the concept of General Drive is implicit in the sparking-over explanation of displacement. Their criticisms of General Drive theory will be discussed later.

Moynihan (1953) described two displacement activities of the Blackheaded Gull, namely, nest-building and preening. He found that both of these activities occurred when the incubation drive was partially or fully blocked. He noted that a bird showed nest-building during the incubation phase (1) after returning to the nest, if one or more eggs had been removed, (2) when sitting on awkward-shaped egg models, (3) before rising and shifting its eggs, (4) immediately after nest-relief by its mate and, (5) on approaching the nest to relieve its mate. He thought that this list of situations justified calling the nest-building a displacement activity. In the first three situations the external stimuli, transmitted via the brood patch, were in some way too insufficient or abnormal to release the complete consummatory response of sitting, although sitting did, in fact, occupy a large proportion of the time available. In the last two situations there was simply a surplus of incubating motivation, which was denied expression either because the mate acted as a powerful releaser to leave the nest or because the mate was actually sitting. Moynihan described the displacement nest-building as being almost identical to autochthonous nest-building apart from the absence of one element (scraping). However he did state that, "In certain cases, when a gull apparently has a very large surplus of brooding motivation, its displacement building may become remarkably hurried. This building appears somewhat disorganised or disorientated, as the bird begins a second movement before it has quite completed the first."

Moynihan carried out some experiments with the incubating birds, which are interesting in that he introduced quantitative measurements of displacement. He removed none, one, two or all three of the eggs of the clutch and counted the number of nest-building movements made by the bird during the first fifteen minutes after its return. It was found that displacement nest-building increased as more eggs were removed. Moynihan also examined displacement preening which occurred in the same situations as, but to a lesser extent than, displacement nest-building. Once again there was an increase in preening as more eggs were removed from the nest. From the evidence available Moynihan dismissed the likelihood of this being either autochthonous preening or displacement preening due to a drive other than incubation being thwarted.

These two activities differed from previously described displacement activities in that the consummatory act (incubation) was performed and also the preening and nest-building movements were identical to their autochthonous examples. Since the consummatory act took place, the displacement activities could not be explained by the simple "surplus" hypothesis, which depends on motivational factors being denied expression in their own system. Bastock, Morris and Moynihan (1953) attempted to explain Moynihan's results of displacement activities occurring after the consummatory act had been performed. They suggested a mechanism along the lines of the Re-afference Theory of von Holst and Mittelstaedt (1950). According to this an output copy of the normally expected stimuli would be charged up in another neural centre during the appetitive behaviour and this could only be discharged by a set of stimuli, fed back during the consummatory act, which fitted this copy. Thus an incorrect feedback would lead once more to surplus of energy and a spark-over to a displacement activity.

Bastock, Morris and Moynihan (1953) also discussed the nature of the spark-over but drew no conclusions. They do suggest that most of the displacement activities so far described are long distance spark-overs, that is from one behavioural "hierarchy" (as described by Tinbergen, 1950) to another, e.g. sex to preening; or moderately long sparking-overs, that is from one end of a hierarchy to the other, e.g. sex to parental care. This could mean that there are probably many displacement activities caused by short spark-overs, which have gone unrecognised because they seem fairly relevant to the situation.

Finally Bastock, Morris and Moynihan considered alternative displacement activities. They distinguished "true alternative displacement activities", which are not dependant on external circumstances, from "apparent alternative displacement activities", which are. They also suggested that the term "true alternative displacement activities" covered two different phenomena; (1) those cases in which the alternatives are shown at the same level of motivation; and (2) those instances in which the alternatives are shown at different levels of motivation. They also thought that single displacement activities may be the result of natural selection acting on alternative displacement activities which are regarded as being more primitive. Selection pressure will also favour making displacement activities as little noticeable as possible to predators in the case of prey animals. However, this will often be more than counterbalanced by selection for displacement activities that possess a secondary function: (a) displacement activities with a releaser signal function; (b) displacement activities with a non-signal secondary function, e.g. nest-building in Black-headed Gulls may raise the nest above the water (Moynihan, 1953); sexual fanning in the Stickleback may prevent the nest from silting up (Morris, 1952). Conceivably such displacement activities might achieve neuro-physiological emancipation. They would then cease to be displacement activities and would become incorporated as autochthonous motor patterns in a new motivational system.

It was pointed out by Moynihan (1953) that a frantic or incomplete performance is not necessarily characteristic of displacement activities. Moreover, Andrew (1956a) reported that much apparently irrelevant behaviour occurs in response to the same stimuli as it does in its relevant occurrences. For example, a male Bunting (Emberiza spp.) shows warming and cooling responses when fearful of the female. Andrew suggested that this irrelevant behaviour is caused in the same way as normal heat regulatory responses, since sympathetic neural activity leads to constriction of superficial blood vessels and a fall in skin temperature. Morris (1956) also speculated on the behavioural significance of autonomic changes which accompany intense thwarting. He was particularly interested in piloerection and the possibility of the resultant feather postures becoming social signals.

In a second paper Andrew (1956b) suggested that peripheral stimuli which induced grooming, such as foreign material on the skin or disarray of the feathers, are likely to be continuously present and probably elicit grooming when other motivations are weak. However, the presence of these stimuli is not sufficient to explain grooming when other tendencies are strong. Andrew (1956b) observed that certain toilet activities such as feather-settling tend to occur at the change from one activity to another. It is possible that during the transition, the tendencies to give the two activities cannot be overtly expressed and, since peripheral stimuli are present, feather settling occurs. Similarly, a toilet behaviour pattern may be given in conflict situations because a weak tendency to give it can be overtly expressed at moments when two strong tendencies to give incompatible responses are balanced.

The Surplus Hypothesis was rejected by van Iersel and Bol (1958) after a comprehensive study of preening in breeding terns. They showed that displacement preening only occurs when two primary conflicting tendencies are equal and opposite. For example when, during brooding, escape and incubation were "sufficiently and not too unequally activated", preening occurred as a displacement. The Surplus Hypothesis had been largely built on the evidence that displacement activities are caused by (a) strong activation of a drive and absence of the appropriate external stimuli (b) a too quickly reached performance of a consummatory act and (c) a sudden cessation of external stimulation. All of these situations were said to lead to a "surplus of motivation" due to lack of a necessary external stimulus. Van Iersel and Bol maintained that in many of the examples of displacement activities, there was no indisputable evidence that the displacement was due to thwarting and "sparking-over of surplus motivation", and that no conflict played a role. They cited the following examples: (1) when Cormorants preen after being frightened during incubation (Kortland, 1940) there may be a conflict between incubation and escape; (2) fanning which occurs when male Three-Spined Sticklebacks are strongly motivated sexually and the female is not receptive (Tinbergen and van Iersel, 1947), may accompany a conflict between sex and aggression towards the non-receptive female; (3) nest-building after incubation at nest-relief in Herring Gulls (Tinbergen, 1952) may involve a conflict between incubation and escape; and (4) when Black-headed Gulls show nest-building after their clutch has been disturbed (Moynihan, 1953), there may be a tendency to rise conflicting with a tendency to sit and incubate.

Van Iersel and Bol (1958) suggested a mechanism which accounts for displacement activities in terms of the probability of other activities (effective equality) and the displacement activities own "positive factors". This suggestion is now known as the "disinhibition hypothesis" and is really a development of Andrew's (1956b) observations that displacement activities may be shown in conflict situations when the tendencies to give two incompatible responses are balanced. According to van Iersel and Bol if two tendencies, either of which on its own inhibits a third tendency, come into conflict and inhibit each other, then the third tendency may be "disinhibited" and allowed to appear. For example strong activation of the brooding system (B) inhibits preening (P) and only when B is not activated or is reduced and the causal factors for P are strong, will P become active. Escape (E) also inhibits P. Now E and B are also mutually inhibitive, and the theory is that in certain situations when there is a conflict between E and B, they will inhibit each other or "cancel each other out" and so disinhibit P. Van Iersel and Bol showed that the occurrence of displacement depends on the two conflicting tendencies not diverging too much from a certain ratio which they called "effective equality". The frequency and intensity of displacement activities are generally positively correlated with the strength of both conflicting drives. Thus a bird shows more frequent and more intense displacement preening when the escape and brooding tendencies are both strong rather than when they are both weak. In the case of a very strong escape tendency conflicting with a fairly strong brooding tendency, the intensity of displacement preening is high because, if a conflict occurs, it is intense. On the other hand the frequency of preening is low because of the reduced probability of "effective equality". Displacement activities only occur during the period of "effective equality" if some "positive factors" for them are present. These "positive factors" (the resultant of internal and external excitatory factors) are basically the same for all occurrences of grooming. Van Iersel and Bol differ from Andrew (1956a and b) in that they consider peripheral stimulation plays only a minor part in displacement grooming. They attribute most of the observed variation in grooming to the degree of disinhibition given by the strength of the conflict. However the positive preening factors may be increased by such things as rain on the plumage and this does raise the frequency of displacement preening.

Sevenster (1961) supported the Disinhibition Hypothesis with evidence from the courtship behaviour of the Three-spined Stickleback. He showed that the males displacement fanning during courtship is influenced by the same causal factors that influence parental fanning (an activity which serves to aerate the eggs). For example, all fanning occurs almost exclusively at the nest, therefore "being at the nest" must be indispensible. Parental and displacement fanning are both increased by a rise in the concentration of carbon dioxide in the water, the age and number of the eggs and other internal factors. Sevenster noted the "unfacilitated" courtship fanning is constant over a wide range of sex drive strengths. By "unfacilitated" fanning he meant fanning in the absence of eggs and excess carbon dioxide. This evidence of unfacilitated displacement courtship fanning shows that there are internal factors which are always present during the reproductive phase. Sevenster's views on disinhibition are not strictly the same as those of van Iersel and Bol. According to Sevenster, if, say, the sexual and aggressive tendencies in a male Three-spined Stickleback vary inversely (the evidence from the zig-zag courtship dance supports this) and they both inhibit the parental centre, then when the sexual tendency is strong it will inhibit both the aggressive and parental tendencies. If the sexual tendency decreases, its inhibition on the parental centre will diminish. However, at the same time, the aggressive tendency will increase along with its inhibitory effect on the parental centre. Sevenster supposed that "somewhere along this scale the decrease in inhibition from the sexual drive on the parental centre outweighs the increase in inhibition from the aggressive drive to such an extent that total inhibition is at its lowest". Therefore total inhibition will be minimal when both tendencies are intermediate in strength. When either of the conflicting tendencies is strong its inhibition on the parental centre is large. Sevenster maintains that this mechanism will operate even if the two conflicting tendencies are not strictly inversely correlated or if their relative rather than absolute values are considered. These changes only affect the position and value of the minimal total inhibition and not the general principle. Van Iersel and Bol on the other hand, think that there is a greater chance of effective equality, and so disinhibition, the greater the strength of the conflicting tendencies.

Rowell (1961) carried out a series of experiments with Chaffinches to investigate further the effects of peripheral stimulation on grooming. His experiments confirmed that displacement grooming has the normal causal factors, and its unusual features are due solely to differences in opportunity to occur in conflict and other situations, differences which are themselves in no way absolute. The primary drives, say approach and avoidance, only regulate grooming by allowing the opportunity to respond to the stimulation. An equilibrium state occurs when there is an equal tendency to perform both the actions of the primary conflicts and it is the duration of this equilibrium state which controls the likelihood of grooming. Thus Rowell found that in conflict situations (approaching and flying away from the perch) when stimulation is constant, the probability of grooming is directly proportional to the average length of visit to the perch. Therefore the controlling factor is the probability of interruption. According to Rowell, therefore, disinhibition only acts as an off-on switch. However Rowell can be criticised on one point of his argument. In his introduction he emphasised that displacement activities, particularly grooming in birds, are frequently not incomplete or in any way different from the "normal" movements. He cites Armstrong (1950) and van Iersel and Bol (1958) on this matter, and quotes Thorpe (1961) as stating "incompleteness or imperfect orientation..... is not a feature of displacement activity as such, but is merely a characteristic of all behaviour, resulting from low intensity drives". However incompleteness can be caused by more than one means. An incomplete movement may be an intention movement (Daanje, 1950) resulting from a low intensity drive as suggested by Thorpe (1951). However incompleteness could also occur if a behaviour pattern was performed at such a high speed that certain elements were missed out. For example Moynihan (1953) described the displacement nest-building in the Black-headed Gull as "......remarkably hurried..... appearing somewhat disorganised or disorientated, as the bird begins a second movement before it has quite completed the first". Now although Tinbergen's (1952) third characteristic of displacement activities was "An incomplete _or_ frantic performance", (see page 7) many of the previous descriptions had used words like hurried, frantic, nervous or vigorous. It would therefore seem more likely that the incompleteness was of the latter type and due to the hurried performance, and not of the former type due to low intensity drive. In his summary Rowell (1961) writes "As interruption is the main controlling factor of displacement grooming, it is considered that this explains the incomplete and 'frantic' performance which is often characteristic". The term 'frantic' implies an increase in speed in the performance of a movement, and interruption alone could have no effect on the speed of a previous movement although it could make it incomplete. If a series of movements were interrupted in quick succession, this would give the appearance of increased speed over the whole bout, but Rowell was dealing almost entirely with isolating "grooming acts," with only one movement per act.

The question of speed of performance and completeness of displacement activities was also discussed by Morris (1954). He described some displacement activities shown by the Zebra Finch (_Poephila guttata_) during reproductive behaviour. Displacement beak-wiping, which was performed by both sexes during the pre-copulatory displays, occurred often enough to allow some comparisons to be made between it and the true, cleaning movement. The bird normally perched with its body at right angles to the axis of the twig or branch, and to beak-wipe, it turned its body to face along the branch, lowered its neck and wiped the beak on the branch with a rotating movement of the head. Morris noted that occasionally in displacement beak-wiping the bird did not turn, and so when the head and neck were lowered the beak was 'wiped' in mid air. More commonly the turning movement was completed but the bird did not lower its neck or head sufficiently and so the beak was again wiped in mid air. Morris also got the impression that the displacement action was the faster of the two, but he was uncertain whether this was due to the incompleteness of the movement or whether there was a real increase in speed of action. Also a bout of displacement beak-wiping was shorter than a bout of normal beak-wiping because there were less wipes per bout.

If the Disinhibition Theory is accepted and displacement activities are regarded as autochthonous behaviour patterns, there seems a strong case for dropping the terms"displacement". Kruijt (1964) thinks that much of the confusion that has surrounded this field of work has arisen because there has been little differentiation made between functional and causal irrelevance. The notion of functional irrelevance depends largely on descriptive and functional criteria which are relatively easy to handle. Proof of the causal implications of irrelevance is much more difficult to obtain. Only Sevenster (1961) and Rowell (1961) of the workers so far mentioned have succeeded in presenting convincing evidence.

As far as nomenclature is concerned Sevenster (1961) suggests the continued use of the word "displacement" in a descriptive sense denoting displacement of an activity from its normal occurrence. Kruijt (1964) on the other hand thinks that the term should be defined as either functional or causal as the case may be.

One facet of displacement activities which requires further explanation is whether or not a conflict of drives is necessary or not. The Disinhibition Hypothesis depends on a drive conflict. However, according to Tinbergen (1940 and 1952) and Armstrong (1950) displacement activities occur in two situations besides conflicts:

(a) when there is strong activation of a drive and absence of appropriate external stimuli;

(b) when there is a too quickly reached performance of the consummatory act, or a sudden cessation of external stimulation. In fact, Armstrong (1950) states that when a displacement activity occurs it is usually due to the thwarting of a drive. (The underlining is mine).

However, both van Iersel and Bol (1958) and McFarland (1965) suggest that in cases of apparent frustration there may be, in fact, a conflict present. According to McFarland frustration itself may be aversive and generate an avoidance tendency which conflicts with the approach tendency. No evidence is presented to support this suggestion and it must remain supposition. In any case even if this were to be demonstrated it is doubtful if it could be called "a conflict between two behavioural systems" (Sevenster, 1961) since only one primary motivational system is activated.

McFarland's (1965) experiment with Barbary doves is a useful study of the methods available for testing a displacement activity to find out to which system it belongs. His experiment consists basically of comparing the effects of different factors on the displacement activity and on its "normal" example. He elicited displacement pecking in doves by thwarting their drinking behaviour using methods involving physical obstruction, induced avoidance or removal of water from the bowl. He was then able to (1) facilitate pecking by presenting grain, (2) facilitate pecking (when grain was present) by depriving the bird of food prior to testing, (3) obtain a response other than ground pecking which had previously been conditioned to feeding and (4) elicit the same displacement pecking using a different conflict. McFarland concluded that his results supported the views that some type of disinhibition mechanism is involved in displacement phenomena. However the disinhibition hypothesis as it stood could not account for the occurrence of displacement pecking in situations which were not strictly speaking conflict situations.

McFarland (1966a) has produced evidence which suggested that rather than thwarting leading to conflict in fact in an approach - avoidance conflict situation, avoidance blocks approach and allows displacement to occur in the same way as when approach is physically blocked. Barbary doves show two types of stationary posture in the experimental situation: "a stationary attentive posture (SAP), in which the bird was relaxed and looking around, and a stationary ambivalent posture (SAV), in which the bird fixated its objective and which was thought to represent a compromise between approach and retreat." McFarland found that (1) SAV occurred more often in conflict than in thwarting situations, (2) SAV was negatively correlated with displacement pecking plus SAP and (3) a high rate of displacement pecking was associated with a high SAP: SAV ratio. He concluded that displacement pecking is associated causally with SAP in both the thwarting and conflict situation.

From a descriptive point of view the disinhibition hypothesis was similar in many respects to Sherrington's (1906) notion of positive induction in which a third reflex may be excited as a result of reciprocal inhibition of two other reflexes. Kennedy (1954) had already pointed out the resemblance between displacement and positive induction before the disinhibition hypothesis was formulated and other have commented on the analogy (McFarland, 1966b: Hinde, 1966). However Hinde (1966) warned that differences in complexity between the two systems preclude a very close comparison. Both of the systems involve response competition. McFarland (1966b) suggested that stimulus competition may be a possible alternative or additional mechanism leading to disinhibition. He postulated that ".....when an ongoing activity is blocked, attention is switched to stimuli other than those eliciting the ongoing activity .....and displacement occurs by being disinhibited via a switch of attention." One of the attractive features of this hypothesis is that it allows for displacement in thwarting situations where it is difficult to imagine a primary conflict. The physiological evidence which McFarland cites to support his argument is very meagre. The evidence from behavioural work on animals is better. For example Mackintosh (1962) showed that animals learn to reverse a discrimination more easily the more training they have had on the discrimination. He also showed (Mackintosh, 1963) that non-overtrained animals pay more attention to incidental cues during reversal of a discrimination.

Since the first part of reversal training involves non-reward (while the animal makes the old, wrong response) McFarland wondered whether it was as a result of being non-rewarded that animals paid more attention to irrelevant cues. He was able to demonstrate experimentally that this was true. Barbary doves which were non-rewarded did learn more about irrelevant cues and showed a greater response to novel stimuli. In addition the birds which took longer to extinguish a non-rewarded response also showed more displacement activity. McFarland concluded that frustration which may result from conflict, thwarting or non-reward, diverts attention. In this way attention may be displaced from the stimuli relevant to the predominant motivation and allow responses to underlying motivations.

In an excellent review paper McFarland (1966a) extended this theory to include a mechanism by which any disruption of behaviour causes a feedback discrepancy between the expected and the actual consequences of behaviour and it is this which causes the switch of attention. This idea was not new, of course, having been founded on the Re-afference Theory of von Holst and Mittelstaedt (1950) and mentioned in connection with displacement activities by others (Bastock, Morris and Moynihan, 1953; Hayes, Russell, Hayes and Kohsen, 1954).

There have been few studies of displacement activities in mammalian species although some authors have noted their occurrence in a purely descriptive way (Armstrong, 1950; Clark, 1956; Bolles, 1960; Grant and Mackintosh, 1963; Estes, 1969). Fentress (1968a and b) has recently carried out a more comprehensive study with two species of voles, Microtus agrestis and Clethrionomys britannicus. He found that grooming behaviour occurred after an initial response to a disturbing stimulus of fleeing or freezing and before other activities were resumed. The irrelevant grooming therefore took place at the transition of one activity to another. Others have observed the same phenomenon (Andrew 1956a and b; Bolles, 1960; Rowell, 1961). Microtus groomed more after the disturbing stimulus than during control trials and Clethrionomys (a more timorous species) groomed less. Also Microtus tended to groom sooner after the disturbance than Clethrionomys. Fentress (1968a) stated that these results could not be fully explained by the disinhibition hypothesis and that some additional mechanism is necessary. He suggested that there is some "optimal arousal level" at which grooming is most likely to occur. Fentress (1968b) explored this possibility experimentally by exposing the two species of vole to the disturbing stimulus with and without home pen cover (home pen cover had previously been shown to increase grooming in Microtus and reduce it in Clethrionomys) and under the influence of amphetamine (a stimulant) and Nembutal (a depressant). Of the conditions tried, cover and 0.8mg/kg amphetamine produced the most grooming in Microtus and no cover and 15mg/kg Nembutal produced the most grooming in Clethrionomys as predicted by the "arousal" model. Fentress (1968b) concluded that both the "arousal" and "disinhibition" models may be necessary to explain the varying amounts of displacement grooming shown by the voles.

Bindra (1959a) built up a theory of motivation based on "arousal" as the motivating factor and he gave an explanation of displacement phenomena to fit this theory (Bindra 1959b). Bindra (1959b) maintained that in a thwarting or conflict situation when an organism is prevented from engaging in an activity there are only two possibilities. Either it will perform the same or a similar act or it will perform a completely different act. Displacement activities fall into the latter category but the situation is not made clearer by referring to the act as a "displacement" of the original response tendency, energy or drive. The method of analysis should be aimed at finding out why a particular response is given rather than any other response. According to Bindra (1959a) the occurrence of every response is completely determined by four sets of factors; level of arousal, sensory cues, habit strength and state of blood chemistry of the organism. By "level of arousal" he meant the degree to which an organism is excited rather than calm. Bindra (1959b) argued that the level of arousal is raised whenever the organism is exposed to environmental change or novel sensory stimulation. Furthermore a thwarting or conflict situation involves a change in sensory stimulation of the type that substantially raises the level of arousal. It is this heightened arousal level (which lasts for some time after the actual change in stimulation) that is partly responsible for the activities that occur. Habit strength also affects which activity is shown, since at high levels of arousal there is an increase in activities of high habit strength, that is those that have been most often practised. This agrees with the fact that most of the descriptions of displacement activities have emphasised that they are all common in the animals' repertoires (Tinbergen, 1952; Zeigler, 1964; McFarland, 1966a). Finally Bindra (1959b) stated that any activity will be evoked by those sensory cues normally associated with it. He included proprioceptive as well as exteroceptive sensory cues and drew attention to the fact that some activities, notably comfort movements, would be linked primarily to cues arising in the animal's own body. Bindra did not attempt to say what part the blood chemistry played in his scheme. When one considers the autonomic changes which may take place during frustration or conflict these effects may be considerable indeed. They could, of course, be thought of as cues arising within the animal's body.

Delius (1967) produced some neurophysiological evidence to link displacement activities with arousal. He stimulated areas in the telencephalon and diencephalon of Herring and Lesser black-backed gulls and found loci which elicited preening and loci which did not. In the "preening areas" he also obtained significantly more staring down, pecking, yawning, squatting, relaxing and sleeping. Delius observed that all these activities have a high temporal and sequential association in normal unstimulated gulls. Moreover they can be elicited by the hypnotic drugs pentobarbital sodium and tribromoethanol. He concluded that these behavioural patterns reflect the activation of a system which leads to de-arousal. After examining evidence from other species Delius suggested that "preening and certain other movements are largely controlled by neurophysiological mechanisms which are also responsible for de-arousal and sleep". Now preening, staring down and pecking commonly occur as displacement activities in gulls in conflict and thwarting situations which had been thought (Bindra 1959a) to increase arousal. Delius overcame this apparent difference by proposing that after a period of arousal a homeostatic process leading to de-arousal would take place. During this latter period preening and the other associated movements would occur. Delius could not explain why these activities should be connected with de-arousal but he suggested tentatively that they might function to aid de-arousal through stimulus reduction, switch of attention or generation of repetitive stimulation.

In summary, the explanations put forward to account for the occurrence of displacement activities have been:-

1. "Sparking-over" of surplus, action-specific energy from one motivational system to another. (Makkink, 1936; Tinbergen, 1952).
2. Response to autonomic changes following frustration or conflict. (Andrew, 1956a).
3. Disinhibition of a third tendency when two primary tendencies are in conflict and incompatible. (van Iersel and Bol, 1958; Sevenster, 1961; Rowell, 1961).
4. Change in level of arousal and sensory cues affecting which responses are shown (Bindra 1959b).

There have been variations and combinations of these basic ideas such as the attention switching mechanism suggested by McFarland (1966) as an elaboration of the disinhibition theory and the de-arousal theory of Delius (1967). Also Fentress (1968a and b) found it necessary to use both the disinhibition and arousal models to account for the displacement grooming of his voles. Both Zeigler (1964) and Hinde (1966) think that there is sufficient experimental evidence to support the second and third theories (i.e. autonomic activity and disinhibition) and that one or the other or both of these will explain most of the occurrences of displacement activities.

Frustration and Aggression

The frustration-aggression hypothesis was introduced in 1939 by a group of Yale psychologists, Dollard, Doob, Miller, Mowrer and Sears. The hypothesis (Dollard et al, 1939) was based on two statements.

1. Aggression is always a consequence of frustration.
2. The occurrence of aggression always presupposes the existence of frustration.

Aggression was defined as "an act whose goal-response is injury to an organism (or organism-surrogate)". The theory was concerned with four basic aspects of aggression following frustration. These were (1) the factors determining the strength of instigation to aggression; (2) the factors determining whether this instigation would be inhibited or not; (3) the factors determining the object of aggression; (4) the cathartic effects of aggressive behaviour.

The original frustration-aggression hypothesis was stated in very strong terms. It said that every aggression could be traced to a frustration. However, the group later admitted (Miller, Sears, Mowrer, Doob and Dollard, 1941) that there was a misleading phrase in the book (Dollard et al., 1939) viz. "that the occurrence of aggression always presupposes the existence of frustration, and, contrariwise, that the existence of frustration always leads to some form of aggression". They stated that the first part was defensible but the second part unfortunate in that it suggested (a) that frustration has no consequences other than aggression, and (b) it fails to distinguish between instigation to aggression and the actual occurrence of aggression. Miller et al. (1941) suggested the following rephrasing: Frustration produces instigations to a number of different types of response, one of which is an instigation to some form of aggression. Dollard et al., (1939) defined an instigator as "some antecedent condition of which the predicted response is the consequence". They said that the instigator may be either internal or external, and such signs as facial expression or verbal comments may be used to infer the existence of the former. Yates (1962) thinks it would be more logical to use the term instigator for a sub-class of stimuli rather than the very wide meaning (including stimuli) used by Dollard et al., (1939).

It would seem from the Yale group's revised hypothesis, that instigation to aggression may occupy any one of a number of positions in the hierarchy of instigations aroused by a specific situation which is frustrating. If the instigation to aggression is the strongest member of a hierarchy, then acts of aggression will be the first responses to occur. If the instigations to other responses incompatible with aggression are stronger, then these other responses will occur at first and prevent, at least temporarily, the occurrence of acts of aggression. Two things may then happen; either the other responses may lead to a reduction in the instigation to the originally frustrated response and acts of aggression may, therefore, not occur; or the first responses may not lead to a reduction in the original instigation, with the result that the instigations to these responses will tend to become weakened through extinction, so that the next most dominant response, which may or may not be aggression, will tend to occur.

There have been many criticisms of the frustration-aggression hypothesis. Levy (1941) gave examples of cases where frustration did not lead to instigation of aggression. Puppies were fed so quickly that their suckling needs were not satisfied and a perverted sucking was shown. However, it could be argued that this was not a frustration situation since these perverted sucking responses may have led to a reduction in the sucking tendency. Levy's second example concerned hens which were allowed to feed but prevented from pecking off the ground. The hens did then peck other hens' feathers more than control but this "was not due to increased aggression but to increased pecking needs". This argument is circular in nature and the author clearly had no real appreciation of poultry behaviour. Thirdly he gave the example of frustration arising out of one's own inability to solve a problem and the tension being relieved by pencil-tapping or floor-pacing. He stated that these motor-actions are not aggressive. This may be true, but they may well contain an aggresive element. From these examples Levy concluded that frustrations were divisible into a type of physiologic frustration and the Yale group's type of social frustration. He stated that the latter is more likely to provoke aggression.

Maslow (1941) suggested a slightly different division between a deprivation which is unimportant to the organism (easily substituted for, with few serious after effects) and, on the other hand, a deprivation which is at the same time a threat to the personality, i.e. to the life goals of the individual, to his defensive system, to his self esteem or to his feelings of security. Maslow contended that only a threatening deprivation has the multitude of effects (usually undesirable and including increased aggression) which are commonly attributed to frustration in general.

These criticisms of the frustration-aggression hypothesis mainly concern the definition of frustration. Other workers have shown that aggression may be elicited by factors other than frustration. Scott (1958), in a useful review on aggression, suggested that there are certain primary stimuli, varying from species to species, which lead to aggressive responses. Among the more important of the factors which generally stimulate aggression are pain, territorial trespass and encounters involving possession of food or females. Furthermore certain stimuli become secondary releasers of aggression through association, conditioning and generalization and, at the same time, other stimuli develop a negative association with aggression.

The evidence for pain, or at least aversive stimulation, causing aggression is good and this has been intensively studied by Azrin and his co-workers at Anna State Hospital in Illinois. Scott and Fredericson (1951) showed that young mice will respond aggressively if their tails are pinched. Later Ulrich and Azrin (1962) demonstrated fighting between pairs of hamsters and several strains of rats in response to electric shock. They termed this reflexive or unconditioned fighting, to distinguish it from the fighting which can be produced using operant conditioning techniques (Miller, 1948a; Reynolds, Catania and Skinner, 1963; Ulrich, Johnston, Richardson and Wolff, 1963). Such reflexive fighting in response to pain-shock was demonstrated between pairs of mice (Tedeschi, Tedeschi, Cook, Mattis and Fellows, 1959), squirrel monkeys (Azrin, Hutchinson and Hake, 1963) and cats (Ulrich, Wolff and Azrin, 1964). In the last mentioned study the frequency and magnitude of fighting behaviour increased with the intensity of shock from 1.6 to 3.0 amperes. The same authors claimed to have elicited interspecific fighting behaviour in both directions between cats and rats. However, it is not made clear whether this could have been predatory behaviour by the cats and defensive fighting by the rats.

More recently it was shown that shock applied to squirrel monkeys' tails produced a biting attack on an inanimate object such as a tennis ball (Azrin, Hutchinson and Sallery, 1964). The tennis ball was later replaced by a rubber tube which could be connected to recording apparatus measuring the frequency and pressure of biting (Hutchinson, Azrin and Hake, 1966). It was then shown that reflexive attack against an inanimate object was simila to that against a conspecific, being a direct function of shock intensity and duration and a decreasing function of time since shock delivery (Hutchinson, Azrin and Renfrew, 1968). This latest technique in the study of aggression using inanimate objects is useful because there is no social interaction to take into account. A similar technique has recently been used in the study of shock-induced biting in rats (Azrin, Rubin and Hutchinson, 1968).

Other types of aversive stimulation have also been shown to produce aggression. Ulrich and Azrin (1962) showed that intense heat would elicit attack by a rat against another rat. Azrin, Hake and Hutchinson (1965) demonstrated that a physical blow could also induce attack in squirrel monkeys Finally Azrin and his colleagues showed that a pigeon responded aggressively to another pigeon when shifted from a high frequency of reinforcement to extinction in an operant-conditioning situation (Azrin, Hutchinson and Hake, 1966). They also showed that aggression occurred when squirrel monkeys were subjected to extinction and to several fixed ratio schedules in a Skinner Box (Hutchinson, Azrin and Hunt, 1968). The monkeys were trained to press a bar to obtain food and they also had the opportunity to bite a rubber tube mounted nearby. Biting occurred after transitions to higher fixed ratio requirements and also in extinction. The incidence of biting was also higher immediately after a food reinforcement and in the early part of the next train of responses. In the interpretation of the results Hutchinson et al (1968) did not mention the word "frustration" at all and yet the aggressive responses occurred in what has previously been defined as frustrating situations, i.e. situations in which an organism is prevented, by a physical barrier, from obtaining a physical goal by the performance of responses which previously led to the attainment of that goal (see p.1). It may be that the ommission of the word "frustration" was purely an attempt by these workers to restrict themselves to expressions that they could define objectively in terms of the operant techniques used. Nevertheless, it seems unnecessarily pedantic not to mention the frustration-aggression literature in connection with these results. Hutchinson et al (1968) state that there is evidence (Azrin, 1961; Thompson, 1964; Thompson, 1965) that fixed ratio schedules can in themselves be aversive and generate escape in the same part of the response run as aggression occurred in their own experiment. They thus seem to regard intermittent reinforcement simply as another form of aversive stimulation. However, there was one difference between this experiment and the others involving aggression and aversive stimulation. Extinction after intermittent reinforcement produced bouts of biting attacks lasting hours and even weeks afterwards compared to bouts lasting a few minutes for experiments in which pain, shock or heat was the aversive stimulus.

The evidence for Scott's (1958) other primary factors, which lead to aggression, is not as good. Part of the trouble is that territorial trespass and encounters involving possession of food or females may also involve some degree of frustration. There are examples of aggression being released in the above situations by certain simple, sign stimuli, and it seems improbable that frustration plays a part here, at least in the first instance. For example, in the spring the male threespined stickleback establishes a territory and behaves aggressively to other male intruders or even quite crude models with red bellies, (Tinbergen, 1951). Similarly, a tuft of red feathers placed in the territory of a male robin is enough to evoke threats and attack (Lack, 1943).

Scott (1958) stated that frustration is not a primary stimulus but is likely to lead to aggression for three reasons;

(i) frustration results in a high degree of excitation and in this state the organism will respond to stimuli, including primary and secondary aggression-inducing stimuli, to which it would normally respond; (ii) the physiological and emotional symptoms of frustration do not conflict with those of anger; (iii) aggression responses may be useful in removing the source of frustration and so they may be reinforced.

Isolation has also been cited as causing aggressiveness in rats by Hatch, Balazs, Wiberg and Grice (1963) and in rats and mice by Sigg, Day and Colombo (1966). However there are many social drives which could be frustrated by isolation, and the increasing aggression may well have been the result of this. Seward (1945) was unable to increase aggression in paired rats by frustrating them and concluded that frustration was not the only cause of aggression and that another cause, independent in operation and possibly in origin, was stimulation by a strange animal of the same species.

Lorenz (1966) emphasised the spontaneity of aggression. He argued firstly for the spontaneity of behaviour in general. He quoted the work of Wallace Craig (1918) on sexual deprivation in the Blonde Ringdove, Streptopelia risoria in which with increasing sexual deprivation, the male will court models showing less and less resemblance to the live female. Craig concluded from this and similar experiments that every instinctive motor pattern generates its own autonomous appetite whenever adequate stimulation is withheld. Lorenz based his own "psycho-hydraulic" model of motivation on such observations (Lorenz,1950). The shortcomings of such "energy models" of motivation have been discussed by Hinde (1969). One criticism of the psycho-hydraulic model is that it fails to predict the outcome of certain experiments. For example, Janowitz and Grossman (1949) found that when dogs with gastric fistulae were deprived of food and then had food placed directly into the stomach, they did not eat food put in front of them. The psycho-hydraulic model predicted that, since feeding behaviour had not been released for some time, there would have been a build-up of action-specific feeding energy and this would have been released by the stimulus of food. However Lorenz (1966) maintained that intra-specific aggressive behaviour could be predicted by the psycho-hydraulic model. The examples he gave were certain tropical fish species kept in aquaria and small groups of humans kept in abnormal situations such as prisoners-of-war or explorers. For example, a male cichlid may kill its mate if a "scapegoat" is not kept in the tank or if two pairs are not kept in the same tank divided by a glass screen so that each fish can "discharge its healthy anger on the neighbour of the same sex." Similarly in a small group of Polar explorers who are dependent on one another and prevented from venting aggressions on anyone outside the group, all aggression undergoes an extreme lowering of its threshold values. This results in aggressive responses to small mannerisms which would normally be ignored. However, there could be explanations other than "damming up of aggression" to account for these phenomena. For example, little is known of the natural territory size of cichlids. Perhaps a female cichlid has both stimulus properties for attack and a display which normally inhibits attacks by the male. In the close confines of an aquarium the male may habituate to the female's display and attack her. On the other hand a male in an adjoining tank may prevent habituation. This is only one suggestion which could explain Lorenz's observations and he presents no experimental evidence to show that damming up of aggression does occur. In the case of isolated groups of men, the situations cited are all very stressing, and the aggression could well be a reaction to frustrations such as sexual frustration or frustration caused by slow progress towards a goal.

Freud (1949) held somewhat similar views to Lorenz on aggression. He conceived aggression as an inherent amount of destructive energy possessed by the individual. This energy must be expressed in some form or other either externally, or internally against the individual himself. He also stated that deprivation of social contact (Liebesverlust) was among the factors strongly predisposing to facilitate aggression.

There have been theories of aggression based on frustration as the sole cause (Dollard et al, 1939). Others have accepted either overtly (Scott, 1958) or implicitly (Azrin, Hutchinson and Hake, 1966) that frustration may be one of many causes of aggression. Lastly, some theories ignore or pay very little attention to frustration as the cause of aggression. (Lorenz, 1966).

The frustration-aggression theory generated much discussion when it first appeared. It was a remarkable theory in that very little experimental evidence was cited (practically none was available) to support the hypothesis. More recently it has been analysed in detail and modified accordingly. For example, Haner and Brown (1955) investigated the factors affecting the strength of instigation to aggression following frustration. They found that more aggression was elicited when children were frustrated near the completion of a task. This can only be explained if instigation to action is conceived of as a joint function of drive and habit strength.

Finch (1942) working with chimpanzees found that "frustration responses", including aggression, increased in frequency with food deprivation in a frustrating situation. This was in agreement with Dollard et al (1939) hypothesis but he did not control for food deprivation itself leading to aggression. Others have explained the factors inhibiting aggression. Davitz (1952) found that subjects trained aggressively behaved more aggressively after frustration than subjects trained constructively, and, conversely, subjects trained constructively behaved more constructively after frustration than subjects trained aggressively. The responses to frustration were therefore modified by previous experience in situations similar to that in which frustrations were encountered. This investigation was followed by another, by Lesser (1957), who studied the effects of the maternal attitudes and practices toward aggression, on overt and fantasy aggression of young boys. He found that under conditions of relative maternal encouragement of aggression there was a greater degree of correspondence between overt and fantasy aggression than under conditions of relative maternal discouragement. It is obvious then that previous experience and expectations of punishment or reward affect the inhibition of aggression. An even more subtle effect was measured by Wiggins (1965). He found that in co-operative situations where the expectation of frustration was slight, fewer individuals became aggressive.when frustrated, than in competition or independence situations. However the intensity of aggression produced by frustration was greater under co-operation than under competition.

Most of the observations on frustration and aggression have been on human subjects and, in particular, on the modifying effects of personality and cultural factors. The rats and mice of the psychology laboratory have, of course, received their usual quota of attention but there have been few comparative or ethologically orientated studies in this sphere. Scott (1948) tested the effect of dominance on aggression produced by frustration in a group of 14 goats of both sexes. He found that frustration, produced by delayed feeding, increased the amount of aggressive fighting in dominant animals while it caused subordinate animals to take more punishment and almost never cause aggression in them. This applied to animals which were dominant in one relationship and subordinate in another. He concluded that frustration causes aggression in situations in which animals are in the habit of being aggressive. King (1965) noted the effects of decreasing the accessibility of feed on the peck-order of three stable flocks of domestic cockerel. In each case, aggression, as measured by inter-member peck frequencies, increased as accessibility was restricted. In general the peck-order remained linear but with severe restrictions disruptions occurred. There is the possibility in these experiments of Scott (1948) and King (1965) that hunger may have had an effect on aggression. Andrew (1957) investigated the effect of hunger on aggression in <u>Emberiza</u> species and found that hunger had no direct effect on the threshold of aggressive responses. However, in small flocks of captive yellowhammers the number of aggressive responses shown was proportional to the number of encounters between individuals. During food deprivation activity increased with the result that there were more chance encounters and thus an apparent increase in aggression. Similarly after fasting the number of aggressive encounters at food dishes rose because the birds were crowded together all trying to feed at once. Both Scott's (1948) and King's (1965) results could be explained on this increased encounter theory of Andrew. Alternatively all three experiments may involve frustration.

Finally in this section it is of interest to note that Moynihan (1953), in his paper on displacement activities of the Black-headed Gull, mentioned that aggressive responses were far commoner in birds from whose nests all eggs had been removed. There were 24 fights among birds from this group of 26 nests (all eggs removed) compared to a total of 7 fights among birds from the 89 nests of the other groups (0, 1 and 2 eggs removed). He also thought there was an increase in low intensity aggressive responses but was unable to score them. Moynihan stated that this fighting was perhaps a displacement activity. He thought it more likely, however, that all incubating gulls were fairly aggressive but that this was seldom allowed expression because they were "tied" to their own nest-sites. When all the eggs were removed from the nests the gulls were no longer so closely "tied" to the nests and so they moved about more and came into contact with neighbouring gulls. The increased fighting could, of course, be explained by the frustration-aggression hypothesis.

Frustration and Fixation

At the same time as the Yale group were formulating the frustration-aggression hypothesis, Maier and his students at Michigan were investigating frustration and fixated behaviour. Maier (1949) showed that when rats were forced to respond in an insoluble problem situation, a stereotyped behaviour pattern appeared which did not develop under conditions of trial-and-error learning. This behaviour was resistant to change when the problem was changed to a soluble one (Maier and Feldman, 1948). On account of these facts the term "abnormal fixation" was given to the behaviour pattern. The apparatus used by Maier in his experiments was the Lashley jumping stand (Lashley, 1930). This consists of a small platform about 1 metre in height on which a hungry rat is placed facing a board with two windows. Each window is covered by a card which may fall when the rat hits it or which may be locked in position. The rat is required to choose one of the cards (each has a different design) and jump at it. If the correct card is chosen, it falls over and the rat lands on a shelf behind the card where it receives a reward of food; if the wrong card is chosen the rat bumps its nose and falls into a net below, which is its punishment. The laboratory rat can learn fairly easily to jump to a particular card or, alternatively, to jump to a particular side, if it is rewarded for the required response. However the problem can be made insoluble by locking and unlocking the cards in a random sequence so that the rat will not always be rewarded and escape punishment for making the same response. When this is done the animal soon refuses to jump. It then has to be forced to jump by blasting it with air or tapping its tail. Maier (1949) states that this is a frustrating situation. His definition is very strict, namely that the animal is:-

1. faced with an insoluble problem.
2. forced to respond to the problem.
3. Highly motivated to respond.

Many of the previously discussed frustrating situations would obviously be excluded by this definition. When the rat is repeatedly presented with this frustrating situation it either always jumps to the same side (position-stereotype) or always jumps to the same card (symbol-stereotype) or give abortive responses by trying to jump over the apparatus, to the side of it, or directly into the net. Maier kept these abortive responses to a minimum by special training techniques and when he did this 80 per cent of his rats developed position stereotypes and the remainder symbol-stereotypes. Once established, stereotyped responses are very resistant to change. Maier, Glaser and Klee (1940) found that stereotyped responses were continued for several hundred trials despite the fact that the rats were being punished for half of the responses. Even when punishment was given on every trial, there was no change in the nature of the stereotyped responses. Maier (1949) emphasised the stereotyped nature of these responses by saying "In general the type of response made, the manner of execution, and the type of abortive behaviour that may appear under conditions of frustration show lack of variation and a degree of stereotypy that perhaps exceeds in specificity the execution of responses developed or maintained under ordinary learning conditions where reward is given in connection with the response. This occurs despite the fact that there is nothing in the punishing situation that demands or encourage highly specific behaviour." Hamilton (1916) had previously shown that animal and human subjects often developed stereotyped responses when given an insoluble problem involving choosing one of four doors to escape from an alley. However, his subjects were not forced to respond and so his conditions did not meet Maier's criteria of a frustrating situation.

Maier also found that stereotyped responses persisted when the problem was changed from being insoluble to soluble. The combined results of three of his experiments (Maier, Glaser and Klee, 1940; Maier and Klee, 1943 and 1945) showed that of the rats that developed position stereotypes, 29.4 per cent were able to change to a symbol-reward response in less than 200 trials. The 70.6 per cent which did not change their response were said to have abnormal position fixations. On the other hand 74.3 per cent of the rats that acquired a position-reward response were able to change to a symbol-reward response when the problem was changed.

Maier (1949) maintained that the development of abnormal fixations could not be adequately accounted for by learning theories then extant. However, the fixated rat does learn which card is rewarded and which is punished.

Feldman (1953) showed that when rats with position fixation were given a soluble problem they always jumped to the same side. However they jumped more quickly to the reward card than to the punishment card, which suggested that they had learned the problem but were unable to give the required response because of the compulsive nature of the fixation. Ellen (1956) used a three window situation to show that rats with position fixations would choose the correct card so long as this did not conflict with their fixated response. For example, a rat with a left position fixation would learn to choose correctly if a positive and negative card were placed on the left with a third card on the right. This did not destroy the fixation when the rats were retested in a two window situation. Feldman (1953) also showed that rats could be taught to walk to the correct window if a plank was provided, but this response did not generalize to the jumping situation.

Methods used for extinguishing learnt responses were unsuccessful when applied to fixated animals (Maier and Klee, 1941). However Maier, Glaser and Klee (1940) were able to destroy fixations and allow normal learnt responses to occur by using a method they called "guidance". If a rat had, say, a left position fixation, then the negative card was put on the left and the right hand card was removed to reveal the shelf with the food reward. The experimenter then prevented the rat from jumping to the fixated side with his hand and guided the rat towards the open window. After a few trials the rats chose the open window. The positive card was then replaced and the rats chose this. After more trials it was chosen regardless of its position. The position fixation was thus broken and the rats taught a symbol-reward response.

Maier (1949) discussed briefly the other work on frustration at that time such as the studies on frustration-aggression (Dollard et al, 1939) and frustration-regression (Barker, Dembo and Lewin, 1941). He described these behaviour patterns as being similar to fixations in having no "goal" and being inexplicable in existent learning theory. He stated, "For the present it seems desirable to retain the four classes of behaviour: aggression, regression, fixation and resignation as the characteristics of behaviour induced by frustration. The extent to which the traits expressed are functions of the situation and functions of the individual must be answered by future research". An obvious criticism of this grouping of these four terms is that they are not of the same order. While "aggression", "regression" and "resignation" describe something of the nature of the response, "fixation" only describes its persistence.

There have been many criticisms of Maier's work. For example, he gave no explanation of the fact that about 25 per cent of his control rats i.e. those which learnt a reward response, also developed fixations without any exposure to frustration. Also the variation between experiments in the proportion of rats which developed fixations was high (50%-90%) even under identical conditions. This suggests that there was some uncontrolled variable. Moreover the control groups of rats did not receive an air-blast or tail-tap since they would jump without forcing. This means that fixated and control groups did not have identical conditions.

Learning theorists criticised the term "abnormal fixation" maintaining that this behaviour pattern could be explained in terms of conventional S-R learning theory. For example, Wilcoxon (1952) tried to explain the phenomenon by distinguishing the effects of non-differential reinforcement and partial reinforcement. He said that the rigidity of the responses were due to partial reinforcement and contrary to Maier's findings non-differential reinforcement *per se* increased variability.

Wilcoxon also examined the data of one of Maier's experiments (Maier, Glaser and Klee, 1940) in which fixated rats persisted in their position habits after a difference in latency had appeared between jumps made to the positive versus the negative card. He found that differences in latency to jumping also appeared with rats which learnt the discrimination but long before the animals actually made correct choices. Since a difference in latency to the positive and negative cues were shown in animals which eventually learned the test, the analagous behaviour shown by fixated rats cannot be taken as an indication of abnormality. In addition Wilcoxon showed that abortive jumping during training prevents learning of the subsequent test discrimination, probably by reducing punishment. Finally he was able to break fixations without the use of guidance, using techniques based on learning principles.

Reviewers of Maier's (1949) book (Hilgard, 1950; McClelland, 1950, Mowrer, 1950) pointed out that an alternative explanation of fixations could be made in terms of anxiety-reduction and that this did not receive enough attention from Maier. The work of May (1948), Miller (1948b) and Mowrer (1939, 1940a and 1948) had shown that fear can be learned and serve as a stimulus for further learning and this was confirmed in later papers (Miller, 1959; Mowrer, 1956). Thus the air blasts and other punishment (bumping of the nose and falling in the net) could produce the internal drive, fear. Cues present before, and at the time of, punishment such as being placed on the jumping platform, are associated with fear and soon become conditioned stimuli. Thereafter any response which removes the animal from these conditioned stimuli will reduce fear and be reinforcing. Practically the only response available to the animal, which would remove it from the situation, are jumps to one of the cards and abortive jumps and since the abortive jumps are discouraged in Maier's experiments this means that the former response will occur very frequently. When the animal has made this response once and been reinforced for it, it will be more likely to make the same response the next time it is put in the fear-producing situation. This could also explain why many more of Maier's rats formed position-fixations than symbol-fixations since a jump to the same side will involve the same musclature and be more like the previous, rewarded response than a jump in the other direction to the same symbol. The persistence of the fixated responses and lack of any extinction could be explained by the findings of Solomon and Wynn (1954) that avoidance responses may be continued for hundreds of trials if the initial fear-producing situation is very traumatic. Just how persistent fixations can be was shown by Liddell (1960) who reported sheep and goats retaining fixated behaviour patterns for the normal life-span i.e. 10-13 years. Farber (1948) produced some confirmatory evidence that fixated responses may be anxiety-reducing. He found that rats which were fed in a T-maze arm where they were also shocked learned a new response more rapidly than rats which were shocked but not fed. This is the principle involved in the treatment of neurosis in human patients by reciprocal inhibition (Wolpe, 1958). Autonomic responses associated with the parasympathetic nervous system, such as the responses produced when the digestive system is stimulated in a hungry patient, are conditioned to the stimuli which evoke the response of the sympathetic nervous system characteristic of neurotic and anxiety states. Since parasympathetic and sympathetic responses are antagonistic the sympathetic responses giving rise to the neurosis tend to be cancelled out.

An alternative explanation of Maier's findings were given by Wolpe (1953). He suggested that the air blast may have induced a primary drive which the rat was able to reduce by jumping. The first jump would be reinforced and so the second and subsequent jumps would be more likely to be to this side. This theory is very similar to the anxiety-reduction theory of Mowrer (1956) and Miller (1948b; 1959). The difference is that Wolpe proposed that stereotypies were learned responses reducing a primary drive while Mowrer and Miller postulated that they reduced a secondary drive.

There is some evidence supporting Wolpe (1953) to show that in situations involving strong approach motivation (de Valois, 1954) or strong avoidance motivation (Kleemaier, 1942; de Valois, 1954) the responses elicited are characterized by lack of variability. This occurs in the absence of frustration and when the problem is at all times soluble.

Maier and his group replied to most of these criticisms and developed their theory in later papers (Maier, and Ellen, 1951; Maier, 1956; Maier and Ellen, 1959). For example, when Maier and Ellen (1951) examined the data supporting the anxiety-reduction hypothesis (Farber, 1948; Mowrer, 1948;

Mowrer and Viek, 1948) they were able to account for all the major results, as well as additional details in the data, within the framework of their frustration theory. On the other hand, when they tested the anxiety-reduction theory by applying it to data from abnormal fixation experiments, it could not explain why animals which have developed position fixations can learn a soluble problem (expressed by the manner of jumping) but cannot practise the correct response. In addition the anxiety-reduction theory could not explain the bimodal distribution of scores in the insoluble problem situation, the compulsive nature of the fixated response (even when an open window was available to jump to) or the differential effects of 100% and 50% punishment. Maier (1956) also refuted Wilcoxon's (1952) claims that partial reinforcement was responsible for the fixations. He maintained that Wilcoxon's partial reinforcement groups also received the most punishment and this was what caused the fixations. In answer to Wilcoxon's other suggestion that abortive jumping may prevent learning of the test discrimination, Maier (1956) pointed out that the converse could equally be true that failure to learn may cause abortive jumps.

Finally Maier (1956) discounted Wolpe's (1953) theory that fixations may reduce a primary drive. He cited the evidence of Maier, Glaser and Klee (1940) and Maier and Ellen (1954) that the frequency of fixations increased as the problem of discriminating between the two stimulus cards was made more difficult. If the fixations were simply responses to the air blast this should not have been so. Later Feldman (1957) showed that there was no positive correlation between the number of airblasts and the number to break a fixation under guidance, which would have been expected if Wolpe's theory had been true. Maier (1956) also quoted some of his earlier work (Maier and Klee, 1943 and 1945; Maier and Ellen, 1952) which had shown that once rats have developed fixations they are less likely to develop them again if they are placed in the same or a similar insoluble problem situation. The most damaging criticism of Wolpe's theory, however, was the fact that Klee (1944) had been able to obtain fixations in rats without the airblasts using only the hunger drive.

In two of his more recent papers (Maier, 1956; Maier and Ellen 1959) Maier has modified his theory considerably. For example, he pays much more attention to the role of cognitive expectancies and the application of his theory to real-life situations. When he does this he is forced to relax some of his very strict definitions and, for example, a frustrating situation becomes any situation in which there is interference with a goal response. In spite of inconsistencies between his experimental findings and his descriptions of real-life reactions to frustrations, Maier's work is an important contribution to frustration theory.

A type of behaviour related to fixation is the movement or series of movements, which is repeated regularly and which serves no apparent function in isolated and confined animals. These movements are called repetitive stereotypies and are commonly observed in zoos and pet shops (Holzapfel, 1939; Hediger, 1950; Morris, 1964). Some examples are "pacing" in bears, "head swaying" in elephants, head bobbing in parrots and trotting over a particular route in wolves, jackals and hyaenas. The causation and function of stereotypies is still obscure but they have been described in the following ways.

(1) thwarted intention movements to escape. (Lorenz, 1952),

(2) activities resulting from the restriction of movements. (Levy, 1944; Hediger, 1950; Draper and Bernstein, 1963),

(3) substitutes for normal activities denied expression by an impoverished environment. (Levy, 1938; Keiper, 1969),

(4) substitutes in an infant for maternal stimulation often missing in laboratory conditions. (Mason and Green, 1962; Davenport and Menzel, 1963) and

(5) mechanisms to relieve boredom. (Berkson, Mason and Saxon, 1963; Berkson and Mason, 1964; Nissen, 1956) or control arousal level (Berkson and Mason, 1964; Hutt and Hutt, 1965).

The first four of these descriptions probably all involve a frustrating situation. However, none of the researchers in this field has looked directly at the relationship between frustration and stereotypies but most have implied that the situations involved are frustrating. For example, Morris (1964) states that the characteristic stereotyped pacing to-and-fro of the caged animal may indicate the need for a greater territorial space in which to patrol. However, he also says that stereotyped pacing indicates that the animal has come to terms with its restricted space and has developed a rhythmic, modified version of patrolling. To-and-fro pacing may also be a side-to-side ambivalent re-orientation of a forward movement and Morris (1964) cites examples of the animal pressing forward and injuring itself through constant rubbing against the side of the enclosure.

In one of the few experimental studies dealing with birds, Keiper (1969) was able to reduce stereotyped route-tracing in caged canaries (*Serinus canarius*) by putting them in a much larger flight cage or providing a swinging perch.

This had no effect on another stereotype, spot-picking, which was reduced by making the canaries work for their food. Keiper concluded that stereotypies may fall into two categories; those related to physical restriction and those resulting from some form of sensory or motor deprivation. It can be seen that frustrating situations often involve one or other of these conditions.

Frustration and Regression

Most of the interest in regression was aroused by the report of Barker, Dembo and Lewin (1941) on the effects of strong frustrations on young children. They stated that 25 out of 30 children showed a decrease in constructiveness of play behaviour after the frustration of being separated from highly valued toys. They also reported a deterioration of social interaction and intellectual regression. The behaviour shown was characteristic of an earlier developmental stage being a change of behaviour to that of a less mature state and they called this "regression". Sanders (1937) and Mowrer (1940b) among others, had previously shown that frustrating a particular learned behaviour caused the organism to revert to earlier learned behaviour. Maier (1949) disputed this finding, claiming that adequate controls were not present in their studies for distinguishing between the return to a former response and the abandoning of the prevailing response for a new one that just happened to correspond to an earlier response. However, later experiments seem to show that there can be a regression towards an earlier response in a frustration situation (Whiting and Mowrer, 1943; Aebli, 1952; Barthol and Ku, 1959). Aebli (1952) attempted to show that the regression could be toward "an unlearned preference" as opposed to "an earlier learned habit". In his experiments he used the right or left turning preference of rats at a T junction in a maze. However the "unlearned preference" was in fact "learned" by practise earlier in the experiment and so one cannot really distinguish between Aebli's factors. Barthol and Ku (1959) described a study designed to test the hypothesis that under stress or frustration the person regresses to the earliest learned behaviour that is appropriate to the situation, even when the source of stress is entirely unrelated to the behaviour. Two groups of 9 college students were taught two methods of tying a bowline knot but in different order. The stressful situation was provided by a difficult intelligence test given late at night after which the students were asked to "tie a knot". 16 of the 18 students used the first method learned. In a non-stressful situation 9 used the first method learned and 9 the second. Barthol and Ku's idea of "regression to the earliest learned behaviour that is appropriate to the situation" could explain the increase in thumb-sucking by Benjamin (1961) when be frustrated infant rhesus monkeys by delaying the attainment of a preferred food object. He said that increase in non-nutritive sucking during frustration was due to the primary reinforcement of responses which preceded the ultimate attainment of food. The fact that only sucking was elicited was possible because the primary reinforcement acted on secondary cues provided by thumb sucking, which derived their strength from the original mode of attaining nourishment, nursing. Therefore in the example, appropriateness of available stimuli and stimulus generalization as well as regression to an earlier response all affected the final response.

Theories of Frustration

There have been only a few attempts to explain the phenomena reported in the three previous sections. These theories generally fall into one of two categories (a) those based on Hullian learning theory and (b) those of Maier and his colleagues.

Brown and Farber (1951) were among the first conventional learning theorists to approach the problem. They defined frustration as a hypothetical state or condition of an organism which is the consequence of either (1) the simultaneous activation of two competing excitatory tendencies or (2) the presence of a single excitatory tendency and an opposing inhibitory tendency. Frustration was therefore given a wide definition and could have as antecedents various kinds of interference with a response; physical barriers, delay, the presence of an incompatible response tendency, work or the omission or reduction of a customary reward. Brown and Farber postulated that the magnitude of frustration (F) was some function of the strengths of the competitive tendencies, perhaps:-

$$F = \frac{E_w{}^{n}}{E_s{}^{n-1}}$$

where $E_w{}^{n}$ = weaker tendency raised to the nth. power, and $E_s{}^{n-1}$ = stronger tendency raised to the (n-1)th. power. This treatment, therefore, makes the situations ordinarily defining conflict an antecedent to frustration. Brown and Farber treated frustration as an intervening variable in Hull's general drive theory (Hull, 1943). Frustration could therefore contribute to generalized drive strength (D) as had been suggested by Rohrer (1949) and Sheffield (1950) and it could also function as a stimulus (S_D). Brown and Farber tentatively suggested that such stimuli could provide the organism with a means of discriminating between frustration and other states. This theory of Brown and Farber, which emphasised the motivational properties of frustration, was later supported by experimental evidence from Tulane University. Amsel and Roussel (1952) used two alleys and goal-boxes placed in series to show that rats which had previously been trained under hunger motivation to run to Goal 1 for food then to Goal 2 for more food, had higher Runway 2 speeds following non-reward in Goal 1 than following reward in Goal 1. The difference between the vigour of performance following reward as compared with non-reward was termed the frustration effect (F.E.). In later papers Amsel and his group investigated the F.E. and the factors which affected its occurrence and strength, (Amsel and Hancock, 1957; Amsel, Ernhart and Galbrecht, 1961; Amsel and Penick, 1962). Unfortunately, in all the experiments the response showing the F.E. was the same as the frustrated response i.e. running down a runway. It would be interesting to find out if the same increased vigour would be shown if the second response were different, say bar-pressing. In another series of experiments Amsel and Ward (1954) were able to show that reward and non-reward could serve as discriminanda for selective learning. In their experiments rats were required to make one response (e.g. left turning) following reinforcement and another response (e.g. right turning) following non-reinforcement of the first response. This discrimination was learned by rats, but once learned it was unstable and quickly lost. Amsel and Ward showed that factors which presumably reduce peripheral cues (e.g. mouth-full versus mouth-empty) such as using drops of water, do not retard the learning. Later reports confirmed this finding that frustration could act as a cue in discrimination situations (Amsel and Prouty, 1959; Tyler, Marx and Collier, 1959). These studies support the hypothesis (a) that frustration provides drive stimulation, which gives it directive properties, and (b) that frustration reduction is reinforcing. A factor complicating this hypothesis was reported by Seward, Perebroom, Butler and Jones (1957). They obtained an apparent frustration effect (F.E.) in a double runway situation but in addition they observed that rats ran significantly slower in both Runway 1 and 2 if they were prefed either 0.5 or 1.0gm. of food before entering the first start box. They agreed that a food reward in Goal Box 1 would serve to depress performance as had feeding. Seward et al. concluded that part if not all the apparent F.E. was due to a decrement in drive or rewarded trials rather than frustration on non-reward trials. However, Wagner (1959) carried out an experiment designed to evaluate the frustration hypothesis and the response depression hypothesis. Three groups of rats were trained to run down a double runway for food in the second goalbox. Group 1 was reinforced with a food reward in the first goal-box on half the trials. Group 2 was reinforced in the first goal-box on every trial until the 77th trial and from then until the last trial (number 108) it was reinforced on half the trials. Group 3 was never reinforced in the first goal-box. All three groups were always reinforced in the second goal-box. In other words Group 1 experienced frustration soon after the start of the experiment, Group 2 only in the second part and Group 3 never. Group 1 showed faster running speeds than the other two groups when it was being frustrated and they were not. When

Group 2 was frustrated its running speed rose to that of Group 1 while the performance of Group 3 remained below that of the first two groups. His results conclusively supported the frustration hypothesis.

The frustration theory of Brown and Farber (1951) was revised and developed by Amsel (1958) in a theoretical paper. His definition of frustration was more restricted than that of Brown and Farber, namely "a condition which is the result of an interaction of a simple prepotent response with events external to the organism". He termed conflict, the condition which is the result of the presence of two or more response tendencies of about equal strength which are incompatible. Thus, unlike Brown and Farber, Amsel distinguished between frustration and conflict. His paper developed the position that under certain conditions non-reward is an active factor which may be termed frustrative non-reward. Such frustrative events are antecedents to a primary aversive motivational condition, frustration. He further postulated that a secondary learned form of the primary aversive condition termed fractional anticipatory frustration develops through classical conditioning. The frustrative non-reward events determine activating effects, which can be measured as an increase in the vigour of the behaviour which immediately follows the frustrative events. The fractional anticipatory frustration is responsible for the decrease in strength of the instrumental behaviour which is terminated by the frustrative event. However, this last statement only holds true if the instrumental response terminated by the frustrative event is incompatible with the subsequent response. Adelman and Maatsch (1955) demonstrated this point in an experiment in which 30 rats were trained to run down a straight alley for a food reward. For extinction they were divided into three groups according to the type of response to be learned in the frustrating situation. During extinction one group learned a temporally compatible escape response of jumping out of the goal-box, while a second group learned a directly incompatible response of recoiling from the goal-box. A third group was extinguished according to the traditional procedure of confinement in the goal-box for a 20 second period after frustration. The results clearly demonstrated that resistance to extinction is a function of the type of response elicited by frustration and the manner in which it interacts with the original habit. The directly incompatible recoil response to frustration produced rapid extinction of the approach response while the compatible escape response to frustration produced little or no extinction of the original response. The "normal" response led to an intermediate rate of extinction.

It is thus important to distinguish clearly between the effect of frustration on responses which follow the frustrating events (generally increased vigour), and those which precede it (generally decreased strength of response). Also any interaction between the response preceding and the response following frustration must be considered.

Amsel (1958 and 1962) also developed the argument that in partial reinforcement situations and the early stages of discrimination learning (both are situations in which a response pattern which occurs relatively consistently is rewarded inconsistently) frustrative factors are involved. He regarded discrimination learning as being a type of approach-avoidance learning with the avoidance component to the negative stimulus arising from anticipatory frustration reactions. In partial reinforcement situations, on the other hand, anticipatory reward and anticipatory frustration reactions are both evoked by the same stimulus. This leads to temporary competition between approach and avoidance tendencies and accounts for the fact that partial reinforcement acquisition is more variable than continuous reinforcement acquisition early in training. The temporary conflict in partial reward training is resolved in favour of performing the response for intermittent reward. Anticipatory frustration reactions thus become associated with the instrumental approach response. When extinction is carried out, partially reinforced subjects have been trained to respond (approach in the presence of antedating, frustration-produced stimuli) whereas consistently reinforced subjects have not. They therefore take longer to extinguish the response.

Amsel was mainly concerned with the facilitatory effects of frustration on relevant activities. However, he describes many irrelevant activities occurring in his experimental frustrating situations but unfortunately these are not described in detail. It would be interesting to know, for example, if these irrelevant activities were performed with any increased vigour. It would also be interesting to know whether Amsel would have ascribed any increased vigour to the F.E. However, none of the Hullian psychologists have attempted any explanation of displacement activities.

McFarland (1966a) has discussed the Hullian psychologists' work on frustration and in particular how Amsel and his colleagues have demonstrated F.E. Using their terms he gave what he called "The general drive explanation of displacement activities" but it should be stressed that this was his explanation and the phenomenon of displacement activities has been ignored by Hullian psychologists. McFarland's explanation went as follows, "Frustration which occurs when ongoing behaviour is blocked in some way, has drive properties and therefore increases the general drive state. As all types of behaviour can be activated by general drive, frustration increases the probability of occurrence of all activities for which appropriate stimuli are present. Such activities will include behaviour relevant to the ongoing behaviour, and may also include irrelevant activities which compete with the ongoing response". He stresses that this explanation of displacement activities involves general drive, and continues "..... the validity of the psychologists' point of view clearly depends on the empirical status of the general drive theory." After reviewing current literature he concludes that there is a serious lack of evidence on general drive theory and so he dismisses it along with Amsel's concept of F.E. and his own explanation of displacement activities in general drive terms. He mentions that most of the experimental evidence supporting a general drive theory involves emotionality, and states, "This suggests that 'emotionality' may have a facilitatory effect on certain types of behaviour, but it certainly does not support the view that all types of motivation are unspecific in their energising properties". It should be remembered that Amsel and his colleagues have never attempted to give a physiological explanation of the F.E. and have certainly never denied that emotionality may be involved. The fact is they have shown that in certain frustrating situations the vigour of the succeeding behaviour is increased. Since many of the descriptions of displacement activities in frustrating situations also emphasise a vigorous or frantic performance there would seem to be the possibility that this is the same phenomenon appearing in both cases. What is needed is more experimental work trying to link these two observations. As stated before, research is required to find out if the response following frustration shows increased vigour when it differs from the frustrated response. It is a small step from here to find out whether the same is true if the subsequent response is "irrelevant" rather than "relevant". This of course does not explain why "irrelevant" responses should be given at all.

Another theory of frustration was proposed by Festinger (1961) although he did not use the term "frustration" at all. He attempted to explain three problems in learning theory, namely that resistance to extinction is greater (1) after intermittent rather than continuous reinforcement; (2) after delayed rather than immediate reinforcement; and (3) for a response of greater rather than less effort. It should be noted that all these variables have been called at some time "frustrating". The first problem is a well known phenomenon and has been extensively investigated. The second and third problems are less well-known but experiments by Crum, Brown and Bitterman, (1951), Scott and Wike (1956) and Wike and McNamara (1957) have shown that delayed reinforcement can increase resistance to extinction, and Aiken (1957) has demonstrated that a high response effort during acquisition results in a greater resistance to extinction than a low response effort. Festinger's explanation was given in cognitive terms and involved a "nonfitting" relationship or "dissonance" (Festinger, 1957) between two pieces of information received by the subject. For example, when a hungry animal runs down a runway into a goal-box and finds there is no food there, the cognition that he has obtained nothing is dissonant with the cognition that he has expended effort to reach the goal-box. The animal then attempts to reduce the dissonance in one of two ways. If in future trials the non-reward situation is continually repeated, the animal reduces the dissonance by refusing to enter the goal-box. However, if the animal is occasionally rewarded, on each rewarded trial he reduces dissonance by enhancing the value of the goal. Festinger (1961) states, "This suggests that organisms may come to like and value things for which they have worked very hard or for which they have suffered. Looking at it from another aspect, one might say that they come to value activities for which they have been inadequately rewarded". A criticism of this argument is that it is a very large step from talking of valued things, such as food, to valued activities, such as working for food.

In some respects this cognitive dissonance theory is similar to the Reafference Theory of von Holst and Mittelstaedt (1950) which was used by McFarland (1966a) as the basis of an attention switching mechanism leading to displacement activities.

Olds (1953) had previously put a cognitive-expectancy interpretation on some of his experimental results in a similar manner to Festinger (1961). He had shown that tokens, which would ultimately be exchanged by children for more primary reward, increased in value when their presentation was delayed. Olds suggested that such a procedure constitutes a "practice at wanting" and such a practice at wanting increases the value of that which is wanted.

Amsel (1962) discussed these cognitive-expectancy interpretations of frustration phenomena and highlighted the main difference between them and neo-Hullian interpretations. He pointed out, in the cognitive language of Olds and Festinger, that whereas the cognitive-expectancy position has non-reward <u>increasing</u> the attractiveness of the non-reward situation, the S-R position implies a <u>decrease</u> in attractiveness. According to Festinger the effects associated with partial reinforcement are due to increased attractiveness. On the other hand Amsel maintained that they are the result of training to persist in behaviour despite decreased attractiveness. After comparing both of these approaches to frustrative non-reward, Amsel contended that neo-Hullian approaches employing conditioning-expectancy concepts go beyond cognitive-expectancy approaches in both specificity and predictive power..

There have been no major changes in Amsel's theory of frustration in recent years, although there has been an attempt to clear up some of the anomalies which exist in it (Hill, 1968; Hug and Amsel, 1969). It remains one of the most attractive theories of frustration.

Whereas Hullian psychologists have given general drive explanations of frustration phenomena, ethologists have tended towards specific drive interpretations of their particular interest in this field, displacement activities. There were two main lines of thought on the motivating factors responsible for displacement activities and these were discussed earlier. Makkink (1936), Kortland (1940) and Tinbergen (1940) suggested that displacement activities were allochthonous, that is motivated by energy which had "sparked-over" from another drive. Others, including van Iersel and Bol (1958), Sevenster (1961) and Rowell (1961), thought that displacement activities were autochthonous or energised by their own normal motivating factors.

McFarland (1966a) criticized the "sparking-over" explanation of displacement. He supported Zeigler (1964) who said that "sparking-over" of motivation implied the presence of a general drive. In other words the action-specific energy of Lorenz (1950) and the drive-specific energy of Tinbergen (1951) are contradictions in terms. If the energy can "spark-over" from one action or drive to another then it is no longer specific and the model must be regarded as a general drive one. McFarland (1966a) therefore rejected this theory of displacement because it inferred the concept of general drive. However, he did admit that there was an important difference between the general drive and "sparking-over" theories of displacement. The former stated that one type of drive can at all times activate other types of behaviour, while according to the latter, this can only occur when the behaviour is blocked. Also general drive can only motivate behaviour in the presence of appropriate external stimuli, therefore such stimuli must be present for displacement activities to occur. On the other hand, Tinbergen's theory was taken to imply that displacement activity can occur in the absence of the external stimuli which are normally regarded as relevant to that activity.

The theory of Maier (1949) differs basically from the others in that it postulates two selective processes, one operating under conditions of motivation, the other under conditions of frustration. The former mechanism selects behaviour according to the ways in which it is perceived to achieve incentives that satisfy needs, the latter according to other, different principles. However Maier's insistence that fixation of response is <u>the</u> criterion of frustration was modified in a later paper (Maier and Ellen, 1959) as mentioned before. This later paper states that fixation, aggression and regression are all possible reactions to frustration which may occur when the frustration threshold is reached. Maier and Ellen also say that the process underlying frustration behaviour is qualitatively different from the underlying problem-solving or goal-orientated behaviour. Thus frustration-instigated behaviour is more closely linked to the situation in which the organism finds itself, than is a goal-orientated behaviour. However this could easily be explained in terms of the amount of attention paid to incidental cues in non-continuous reward situations.

Lawson (1965) pointed out that Maier's (1949) definition of "frustration" and "fixation" were not independent. He used each term to define the other which suggested that insufficient work had been done on the antecedents of fixated behaviour. Another criticism of Maier's theory was that there was insufficient knowledge of the effects of punishment (Church, 1963) or punishment pattern (Yates, 1962) on behaviour, to reach an understanding of results from the Maier paradigm.

Feldman and Green (1967) carried out a series of experiments to investigate the antecedents of fixations including the role of punishment. They thought it would be helpful to think of the rat on the jumping stand as being in several "go-no-go" conflicts. For example, considering the left hand window, hunger, to a lesser extent, and fear of the goal, to a greater extent, contribute to an approach tendency while fear of a nose bump and fear of a fall into the net contribute to an avoidance tendency. Similar tendencies exist for the right hand window. Thus a rat choosing between these two spatial stimuli, Left and Right, would be in a double "go-no-go" conflict. In addition most of Maier's experiments had other, non-spatial stimuli, for example, light and dark cards in front of the windows. To each of these brightness cues an additional "go-no-go" conflict is possible. Finally there may be a conflict as to which of the two dimensions the animal is to respond to. Looked at in this way the insoluble problem situation on the jumping stand is a very complex one. Feldman and Green suggested that the stereotyped response may in large part be due to a powerful avoidance factor which "pushes" the animal away from the non-preferred stimulus while still leaving it in conflict along the dimension to which it has a stereotyped response. In other words when the animal finds itself in a multiple conflict situation with no alternative any more attractive than any other, it selects a cue with which it has received somewhat less punishment and responds to it exclusively. The response to this cue is compulsively maintained for the remaining duration of the insoluble problem phase and to a great extent during the ensuing soluble problem phase. Feldman and Green predicted on the basis of this model that any means of reducing the "go-no-go" conflict or limiting the choices within or between dimensions with which the conflict is associated, would prevent fixations from developing.

One way in which the "go-no-go" conflict might be reduced is by the administration of drugs such as tranquillisers to weaken the avoidance component. Feldman and Liberson (1960) found that reserpine elevated latencies to jump during the insoluble problem, but did not prevent fixations or aid solutions. In position-stereotyped animals, the reserpine elevated jumping latencies to the incorrect window while not affecting latencies to the correct one. These results indicated that reserpine had reduced fear of the goad shock, a finding consistent with those of Sidman (1956) and Wenzel (1959). Two other tranquillisers, chlorpromazine and meprobamate, also yielded latency increases and did not reduce fixations (Liberson, Feldman and Ellen, 1959a; Liberson, Feldman and Ellen, 1959b). On the other hand Feldman and Green (1967) cited an experiment by Bremner (1960, unpublished) which showed that phenelzine, a mono-amine oxidase inhibitor and antidepressant produced results opposite to those of reserpine. The decreased latencies shown were probably due to increased fear of the goad. Slightly more of the rats which had had phenelzine during the insoluble problem phase solved the problem when it was made soluble than control rats. However, Feldman and Green (1967) were not able to confirm this latter effect by increasing the intensity of the goad shock, a procedure which should theoretically have had the same effect, since it increased the fear of the goad. Finally Feldman (1962) showed that chlordiazepoxide (C.D.P.) when given during the insoluble problem phase and discontinued during the soluble phase, greatly increased the number of rats which solved the problem (from the usual figure of about 30% to 73%). However, if the drug was continued through the soluble problem phase the number of rats solving the problem remained fairly low (42%). Also the C.D.P. effected a gradual day-to-day decrease in latencies to jump during the insoluble phase.

Feldman and Green (1967) interpreted the results of these drug experiments in terms of their "go-no-go" conflict model. They attributed the increase in latency to jump under reserpine, chlorpromazine and meprobamate to a reduction in fear of the goad shock, while fear of hitting the locked window remained high. Thus a conflict between actual shock and fear of the locked window persisted.

The action of phenelzine appeared to be exactly opposite to that of reserpine; increasing the grid escape or "go" component of the conflict. This would lead to escape from the conflict and might explain Bremner's results of slightly more rats solving the problem. Feldman and Green thought that the increased percentage of problem-solvers that were found after treating with C.D.P. could be understood in terms of decreased strength of the avoidance components and less reaction to them. Since the principal "go" incentive is also negative (fear of goad shock) there is a reduction of all avoidance components, leading to a reduction of the "go-no-go" conflict. In other words giving C.D.P. when the problem was insoluble yielded a benefit of less reactivity to negative incentives and there would therefore be less conflict, and frustration and hence less fixated behaviour. When given during the soluble problem phase, this lowered reactivity led to inferior acquisition of the solution.

Feldman and Green emphasised that neither of the effective drugs had any beneficial effects if administered once fixations were established. Therefore, if these substances have fear-reducing qualities, the finding that fixations cannot be reversed by them fails to support the hypothesis that fixated behaviour is maintained by self-generating fear reduction.

They also showed experimentally that stereotyped responses could be attenuated by manipulating the problem situation in two other ways. Firstly if alternatives between stimulus dimensions were reduced, for example by removing the Light/Dark cues from the doors, then less rats fixated. Secondly, if additional cues such as horizontal versus vertical stripes on the doors were introduced and if these were related to predictable reward and punishment during the soluble phase then more rats solved the problem.

The "go-no-go" conflict model of Feldman and Green does seem to be a helpful way of looking at the antecedent conditions of fixation. It has predictive value as proved by the three manipulations described above. However it does not give any explanation of fixations at all and Feldman and Green can only conclude that, "It would seem on the basis of the frequency of its occurrence that response stereotypy and fixation is a normal reaction to insolubility that minimises effort in a hopeless situation".

In Conclusion

It can be seen from the review above that the experimental and theoretical work carried out on frustration in the past has been very fragmentary with different groups of workers studying completely different aspects of the subject. The whole subject may be simplified by considering all the possible responses to a frustrating situation. For example, Sears (1941) stated that there were three possible action sequences which could occur following frustration:-

1. The organism may continue to repeat the same instrumental acts leading to the same goal response. These acts are persistent and non-adjustive and more characteristic of lower animals and children than higher animals and adults.

Certain of the stereotyped movements would fall into this category. However, Sear's generalization that these acts are more characteristic of "lower" then "higher" animals might be questioned in the light of a recent paper by Hodos and Campbell (1969) which discourages the assumption that all living animals can be arranged along a continuous "phylogenetic scale" with man at the top. Also it would seem that Sears was equating lower animals with children and higher animals with adults, yet on any intelligence scale children would outrank the higher animals.

2. A different set of instrumental acts may be instigated in order to put the organism in such a position to perform the same goal response.

Trial and error behaviour appears to be largely of this kind as do certain types of regression.

3. A different set of instrumental acts may be instigated in order to put the organism in such a position that it may perform a different goal response from that which was originally frustrated.

Displacement activities and some aggressive responses would be included in this group.

To these three could be added another group:-

4. The same instrumental acts may lead to a different goal response.

This category would include what ethologists call redirection activities and what psychologists would class under the heading of displacement. It is not such a clear cut group as the other three since the goal response need not be very different from the original goal response. For example, when thwarted from striking one's boss by fear of the consequences, a possible reaction is to go home and strike one's wife. The actual aggressive response would be similar in both cases.

Sears went on to say that which of the action sequences will occur following frustration will depend, among other things, on how advanced or primitive the organism is phylogenetically, the organism's previous experience in similar situations, the strength of the frustrated drive, the nature of the environment and the organism's perception of this at the moment of frustration.

Sears stated that this analysis of responses to frustration in terms of instigation, instrumental acts and goal responses is useful because it provides a basis for the understanding of such behaviour which can be investigated experimentally. However, there are two immediate problems. The first is the exploratory problem of discovering the total repertoire of the responses to frustration available to any individual. The second is the determination of the specific factors which cause one kind of reaction to frustration rather than another.

This approach was taken in the next two parts of this thesis. Part Two consists of a description of the behaviour of the domestic fowl when thwarted in various ways. It was thus hoped to compile a list of the fowl's behaviour in as many thwarting situations as possible. Part Three consists of an investigation into some of the factors governing the responses to thwarting.

PART TWO

A GENERAL DESCRIPTION OF THE RESPONSES ELICITED BY THE THWARTING OF DIFFERENT ACTIVITIES

CHAPTER 2

THWARTING OF NESTING BEHAVIOUR

Introduction

The domestic hen about to lay an egg performs a certain behaviour pattern which varies in form according to the environment. This behaviour pattern has been well described by Wood-Gush (1954a and 1963). In a pen with trapnests the hen at first shows some restlessness and emits a characteristic, prelaying call. She then starts to examine various nests by peering into them. At first only the head is poked into the nest but gradually more and more of the body is inserted. Bouts of nest examination are interspersed with bouts of other activities such as feeding, preening or sleep. Eventually the bird enters a nest, settles down and sits with only occasional changes of position until oviposition occurs. Wood-Gush (1954a) suggested that in this prelaying phase there is a build-up of internal stimuli with at first, examination of suitable sites and then intention movements to enter these sites. He also thought that the bouts of preening which often occur during this phase might be displacement reactions indicative of frustration or conflict, probably to nest or not to nest. Once hens have become used to trapnests they use them regularly and very seldom lay eggs on the floor. Also the same nest is often used by a female for months on end (Wood-Gush, 1954a).

It was decided to use this situation as a starting point for the observation of responses in frustrating circumstances. It was argued that if a hen, which had previously been using a nest-box regularly, was prevented from entering a nest-box or, if the stimulus of the nest-box were removed, this would be frustrating.

Experiment 1

Material and Methods

Eight Brown Leghorn females of the Poultry Research Centre "J" line were used. These birds will be identified in the text by code letters. They were about 11 months old and had been kept since point-of-lay (5 months old) in a deep litter pen measuring 2.5m^2. The pen had walls of wire mesh but this was covered in tin sheet to a height of 60cm. from the floor. Along the back wall of the pen was a row of 5 trapnests. It was possible for the birds to jump on top of the trapnests and when in this position they could see over the tin into a neighbouring pen. The pen was also supplied with a food trough and drinking fountain. The pre-laying behaviour of the 8 hens had been recorded for 2 months prior to the start of the experiment. In this period all the birds had shown normal nesting behaviour and none had laid a floor-egg.

Each bird was exposed to two frustrating situations. On a day on which the bird was due to lay it was watched until it entered a nest-box and was then removed from the nest-box. It was then either placed back in the pen with all the nest-boxes closed and the other hens removed or placed in a 60cm^3 wire mesh cage with a wire mesh floor. Food and water were avilable in the cage, which was situated in a completely empty pen.

The observer was hidden from the bird, which was observed until oviposition or until lights went out (2000h). As far as possible the 8 hens were frustrated at different times during the light period (0600-2000h) to lessen the risk of any diurnal rhythm of activity interfering with results. Each hen was also observed in the same two situations on a non-laying day for one hour at the same time of day as the first hour of the frustration period. Four hens experienced the pen first and four the cage.

All the activities of the birds during the observation periods were recorded in short-hand form in a note-book. Particular attention was paid to those activities which have been described in the literature as common displacement activities such as comfort movements and pecking. These were quantified as follows:-

Preening; the number of preens were counted; a preen was considered finished when the bird lifted its head so that the bill was no longer in contact with the feathers. A preening bout consisted of a number of preens uninterrupted by other behaviour patterns. The locality of the plumage preened was also recorded using areas similar to those described by van Iersel and Bol (1958).

Breast = breast and throat
Belly = belly
Back = back and rump excluding the uropygeal gland
Shoulder = scapulars and wing joint
Outside Wing = front edge of wing coverts and pinion
Inside Wing = underwing coverts and flanks
Tail = tail coverts and tail
Vent = vent and fluff
Uropygeal Gland = uropygeal gland

Other behaviour patterns such as bill-wiping, head-scratching, head-shaking, tail-wagging, feather-raising and feather-ruffling were also counted. The first four movements are self explanatory; feather-raising is the short term act of raising all the contour feathers to give what Morris (1956) called a "ruffled" posture and McFarland and Baher (1968) called a "raised" posture. This posture was never maintained for longer than a few seconds and was followed by preening, a feather-ruffle or the feathers subsiding to a "normal" (McFarland and Baher, 1968) or "fluffed" (Morris, 1956) posture; feather-ruffling is a vigorous shaking of the feathers and it usually follows feather-raising. These six movements together with preening make up the hen's repertoire of comfort movements.

Pecking; the number of litter-pecks in the pen and the number of pecks to any part of the cage were counted.

One other frequent behaviour pattern was observed. This consisted of the bird walking quickly back and forward along one side of the cage or one wall of the pen or along the front of the nest-boxes. When walking back and forward the bird often pressed against the wire mesh and made small circular or up and down movements with its head as if trying to escape. For this reason one double back and forward movement without interruption was termed an "escape" movement but the validity of this term will be discussed later. The number of escape movements were counted.

Results

The time taken from placing the bird in the pen or cage until oviposition or lights-out varied from 1h 4min. to 8h 10min. Therefore, the amounts of activities occurring in the first hour after each bird had been placed in the frustrating situation were compared to the amounts occurring in the hour in the corresponding control situation. These hours were further divided into first and second 30min. periods. In addition the amounts of activities occurring in the 30min. before oviposition were compared to the mean of the amounts occurring in the first and second 30min. control periods. In the case of one bird (P) in one situation (Pen) the second 30min. frustration period and the 30min. period before oviposition overlapped; all the other birds took longer than 1h 30min. to lay. Seven birds laid in the light period in both the pen and cage. The eighth bird (P/Y) laid 1.5min. after lights out in the pen. This bird was treated as though it had laid at lights out and the 30min. observations previous to lights-out were used in the analyses.

The most prominent feature of the frustrating situation was the increase in escape behaviour compared to the control situations. The numbers of escape movements in the first hour are shown in Table 1.1A. An Analysis of Variance was carried out on these results and this is shown in Table 1.2A. The summarized results are given in Tables 1.1 and 1.2. The numbers of escape movements in the 30min. before laying and the Analysis of Variance of these results are given in Tables 1.3A and 1.4A respectively. Summaries of these results are shown in Tables 1.3 and 1.4.

Table 1.1. Mean numbers of escape movements occurring during frustrated nesting (first hour) ($n = 8$).

	Pen		Cage	
	Control	Frustrated	Control	Frustrated
First 30min.	3.7	10.5	2.0	7.9
Second 30min.	1.9	21.7	6.1	24.9

Table 1.2. Statistical analysis of treatment effects on escape movements (first hour). P - values.

Treatment	Mean no. of escape movements	Differences between treatments. P.
Situation (S) (n = 32)	Pen 9.4 Cage 10.2	n.s.
Frustration (F) (n = 32)	Control 3.4 Frustrated 16.2	∠ 0.001
Time (T) (n = 32)	First 30min. 6.0 Second 30min. 13.6	∠ 0.01
Interaction (FXT) (n = 16)	1st 30min. 2nd 30min. Control 2.87 4.0 Frustrated 9.18 23.31	∠ 0.05

Table 1.3. Mean numbers of escape movements occurring during frustrated nesting (30min. before laying) (n = 8).

Pen		Cage	
Control	Frustrated	Control	Frustrated
2.8	21.0	4.1	28.4

Table 1.4. Statistical analysis of treatment effects on escape movements (30min. before laying). P - values.

Treatment	Mean no. of escape movements	Differences between treatments. P.
Situation (n = 16)	Pen 11.9 Cage 16.2	n.s.
Frustration (n = 16)	Control 3.4 Frustrated 24.7	<0.01

It can be seen from these results that the incidence of escape behaviour was much higher in the frustrating situation than in the control situation. Also more escape movements occurred in the second 30min. of frustration than in the first. The data from the 30min. period before oviposition cannot be compared statistically with that from the first hour because of the overlap of information. However, it can be seen that most of the birds continued to show escape behaviour at a fairly high level. Three birds (P/B, P/Y and O) sat in the pen and one bird (P/Y) also sat in the cage for most of the 30min. before oviposition and this was reflected in an escape movements score of zero. The pen or cage situation had very little effect on the number of escape movements shown, but it should be remembered that the definition of an escape movement was completely arbitrary viz. one back and forward movement. If this movement was performed along one wall of the pen the bird in question could walk 5m compared to only 1.3m, if it was performed along one side of the cage. For this reason the number of back and forward movements may not be a very good quantitative measurement of escape behaviour. Notwithstanding this, the overall impression was that there was little difference in the amount of escape behaviour in the pen and in the cage.

The escape movements occurred in short bouts lasting from about 10sec. to about 2min. The bouts were interspersed with bouts of feeding, drinking, preening and, in the pen, litter-pecking. During these activities the birds seemed more agitated in the frustrating situation than in the control situation. The subjective impression was of a faster speed of performance of the activities with more of a sudden change from one activity to another. This was particularly true of preening which was very flurried in the frustrating situation. Also the preening seemed to be of a slightly different pattern with more attention being paid to the ventral surface of the body than in the control situation.

The number of preens occurring in the first hour and an Analysis of Variance of these results are given in Tables 1.5A and 1.6A respectively. The summarized results are shown in Tables 1.5 and 1.6. The corresponding data for the 30min. before laying are given in Tables 1.7A, 1.8A, 1.7 and 1.8.

In the first hour it can be seen (Table 1.6) that although the preening appeared to be qualitatively different during thwarting this was not reflected in a difference in total number of preens. In the 30min. before oviposition, however, the bird preened significantly less than in the control situation. There was no difference in number of preens between the pen and cage.

The hypothesis that more attention was paid to the ventral parts of the body during thwarting was tested by expressing preens to the belly as a percentage of total preens in each situation, i.e. control/pen, control/cage, frustrated/pen and frustrated/cage for all the birds for the first hour of observation. These 32 percentages, ranging from 0% to 39.4%, were then ranked and subjected to a Mann-Whitney U test. The results confirmed that more belly preening did occur in the frustrating situations ($U = 61$, $P < 0.01$).

Other comfort movements such as feather-raising, feather-ruffling, head-shaking, head-scratching, tail-wagging and bill-wiping did not occur sufficiently often to allow statistical analysis.

There were very few pecks other than food pecks shown in the cage but

Table 1.5. Mean numbers of preens occurring during frustrated nesting (first hour) (n = 8).

	Pen		Cage	
	Control	Frustrated	Control	Frustrated
First 30min.	44.9	35.1	59.2	47.6
Second 30min.	51.9	38.7	57.2	42.1

Table 1.6. Statistical analysis of treatment effects on number of preens (first hour). P - values.

Treatment	Mean no. of preens		Differences between treatments. P.
Situation (S) (n = 32)	Pen Cage	42.6 51.6	n.s.
Frustration (F) (n = 32)	Control Frustrated	53.3 40.9	n.s.
Time (T) (n = 32)	First 30min. Second 30min.	46.7 47.5	n.s.

Table 1.7. Mean numbers of preens occurring during frustrated nesting (30min. before laying) (n = 8).

Pen		Cage	
Control	Frustrated	Control	Frustrated
48.4	24.1	58.2	12.9

Table 1.8. Statistical analysis of treatment effects on number of preens (30min. before laying). P. - values.

Treatment	Mean no. of preens	Differences between treatments. P.
Situation (n = 16)	Pen 32.6 Cage 35.6	n.s.
Frustration (n = 16)	Control 53.3 Frustrated 18.5	≤ 0.01

litter-pecking was fairly common in the pen. The number of litter-pecks occurring in the first hour and an Analysis of Variance of these results are given in Tables 1.9A and 1.10A and the summarized results are shown in Tables 1.9 and 1.10. The data for the 30min. before laying are given in Tables 1.11A and 1.12A and summarized in Table 1.11.

Litter-pecking showed the same overall pattern as preening in that there was little difference between the control and frustrating situations in the first hour but the number of litter-pecks were significantly depressed in the 30min. before oviposition.

One other behaviour pattern was observed which wasthought to be of importance. When the hens were tested in the pen they spent quite a lot of time standing on top of the nest-boxes. In this position only the wire mesh separated them from some younger hens in a neighbouring pen when they happened to be standing on their nest-boxes. Four out of the eight hens showed some threatening behaviour towards these pullets at some time during their thwarting test. No threatening was observed during the control tests. However, not too much weight can be placed on these observations, since the stimulus situation was variable; a pullet was not always on the neighbouring nest-box.

Finally, the times from start of thwarting to oviposition are shown in Table 1.12. Ten out of the sixteen times were longer than any nest-box entry to oviposition time recorded in the previous 2 months. Frustration therefore tended to delay oviposition. There also seemed to be a tendency for the cage situation to delay oviposition more than the pen situation. However, this difference in delay of 57.25 ± 10.60min. was not significant ($t = 1.62$; $0.1 < p < 0.2$).

Table 1.9. Mean numbers of litter-pecks occurring during frustrated nesting (first hour) (n = 8).

	Control	Frustrated
First 30min.	32.6	32.2
Second 30min.	35.0	23.5

Table 1.10. Statistical analysis of treatment effects on litter-pecks (first hour). P - values.

Treatment	Mean no. of litter-pecks		Differences between treatments. P.
Frustration	Control Frustrated	33.8 27.9	n.s.
Time	First 30min. Second 30min.	32.4 29.3	n.s.

Table 1.11.. Mean numbers and statistical analysis of treatment effects on litter-pecking (30min. before laying).

Treatment	Mean no. of litter-pecks	Differences between treatments. P.
Frustration (n = 8)	Control 32.4 Frustrated 15.6	∠0.05

Table 1.12. Time taken from start of frustration to oviposition.

	Pen		Cage	
Birds	h.	min.	h.	min.
P	1	4	2	20
Y	2	41	7	14*
B/W	3	14*	3	16*
P/B	8	10*	6	58*
P/Y	8	10*	9	12*
G	1	54	2	16
O	3	31*	4	19*
B/O	2	11	2	58*

* longer than any nest-box entry to oviposition time recorded in the previous 2 months

Discussion

The most prominent feature of Experiment 1 was the appearance of escape movements in the thwarting situation in both the pen and cage. These movements took up quite a lot of the available time and, when considered along with the fact that a certain amount of time in the frustrating situation was taken up in sitting for short spells, this probably accounts for the decrease in preening and litter-pecking in the half-hour before oviposition. The backwards and forwards pacing which has been called escape did not occur continuously, but in bouts lasting two or three minutes interspersed with bouts of feeding, preening and other maintenance activities. Pacing in the pre-laying phase does occur in birds kept permanently in both pens with nest-boxes and cages (Wood-Gush, 1954a; Wood-Gush and Gilbert, 1969), so it could be regarded as a "normal" response in this type of environment. Feral domestic fowl leave the flock and examine two or three potential nest sites before selecting one for oviposition (McBride, Parer and Foenander, 1969). A certain amount of locomotion in the appetitive phase of nesting behaviour would therefore appear to be normal. However, the feral fowl in semi-natural conditions and the domestic hen in a pen with nest-boxes or even sometimes in a battery cage show sitting behaviour before laying (McBride, Parer and Foenander, 1969; Wood-Gush, 1954a; Wood-Gush and Gilbert, 1969). The pacing was unusual, therefore, in that it continued right up until oviposition, with the exception of a few birds which sat for about a minute immediately prior to laying. It could be argued that the escape movements were simply a form of the normal appetitive nest-seeking behaviour exaggerated by the inadequacy of the environment. On the other hand it is possible that the hens found the frustrating situation aversive and were trying to escape from it. The fact that the escape movements increased from the first to the second 30 minute period would support both these hypotheses.

The flurried action of the preening movements and the abrupt start and finish of preening bouts in the frustrating situation suggested that this was "displacement preening". However, it did not always appear "irrelevant" to the situation and in many cases seemed very similar to the preening in the control situations. There was one difference in that the belly region was preened more in the frustrated situation. It would be interesting to find out if the hens were responding to uterine movements or neuro-humoral changes in the oviduct at this time.

One of the most interesting features of this experiment was that no difference was observed in the escape movements or in the preening behaviour of the frustrated birds in the pen and in the cage. One would have expected the pen situation to have interfered less with the nesting responses since it provided a much richer environment including litter to nest in, regions of light and shade, and secluded corners, all of which were absent from the cage.

Oviposition tended to be delayed in both the pen and cage and there was a suggestion that the delay was longer in the cage. However, the experiment would need to be repeated with larger numbers to confirm this. Some of the times from the start of the thwarting (which was nest-box entry time) to oviposition were exceptionally long, i.e. 8 or 9 hours. It has been shown that injections of adrenaline can delay oviposition (Sykes, 1955a; Draper and Lake, 1967) and it would be interesting to know if the delay in laying in the present study was due to a release of catecholamines following frustration.

Little can be said about the occurrence of aggressive responses when the birds were frustrated in the pen. The possibility that these were responses to frustration will be examined in a later experiment.

CHAPTER 3

THWARTING OF FEEDING BEHAVIOUR

Introduction

There are certain advantages to be gained from working with feeding behaviour compared to nesting behaviour. For example, the experimenter can manipulate the strength of the tendency to feed, an operation which would prove difficult if not impossible with the tendency to nest. Also the time of testing can be at the discretion of the experimenter. It was hoped that these advantages could be put to use in the experiments described in this Chapter and so allow a more detailed description of behaviour under thwarting conditions than was possible in Chapter 2.

Wood-Gush and Guiton (1967) frustrated hungry, adult hens by presenting them with food under a glass cover. They found that at first the birds showed avoidance and escape behaviour, but this decreased, along with the attempted feeding, with successive tests. At the same time there was an increase in "irrelevant" grooming and sleeping behaviour until by the fourth test the birds were behaving as they did in the control situation. It seemed that thwarting generated a large amount of avoidance even when the animal was being frustrated for the first time and this could have produced an approach-avoidance conflict. However, there was no increase in irrelevant activities associated with this conflict and in fact they tended to increase with the passing of the conflict. Moreover the level of irrelevant activities did not increase to a level higher than that found in the control situation. It is possible then that the grooming and sleep were not direct responses to thwarting but "normal" responses appearing as the conflict passed.

Experiment 2 was basically similar to that of Wood-Gush and Guiton with the exception of the breed of birds used. Wood-Gush and Guiton used birds of indeterminate breed but which they thought were mainly Rhode Island Red while in Experiment 2 Brown Leghorns were used.

Experiment 2

Material and Methods

Four birds were used similar to those in Experiment 1. They were kept in individual cages called hereafter the "home cages". The cages were kept in a battery house on a 14 hours per day light schedule. The experimental cage was situated in a separate small room in which the temperature varied between 15^0 and 18℃ and the noise level was fairly low. The experimental cage was of wire mesh and measured $60cm^3$. There was a hole in one side measuring $8cm^2$ through which the bird could feed from a removable food trough. The food used was a proprietary mash in pelleted form. Water was always available in both the home cages and the experimental cage from a trough attached to one of the sides. The experimental cage could be observed from a hide fitted with one-way glass. A plan of part of the experimental room is shown in Figure 2.1.

Training: Each bird was deprived of food for 24 hours in its home cage and then placed in the experimental cage with food available for 30min. This training procedure was repeated daily and a record was kept of the food intake of each bird. The criterion for ending training was taken as three consecutive

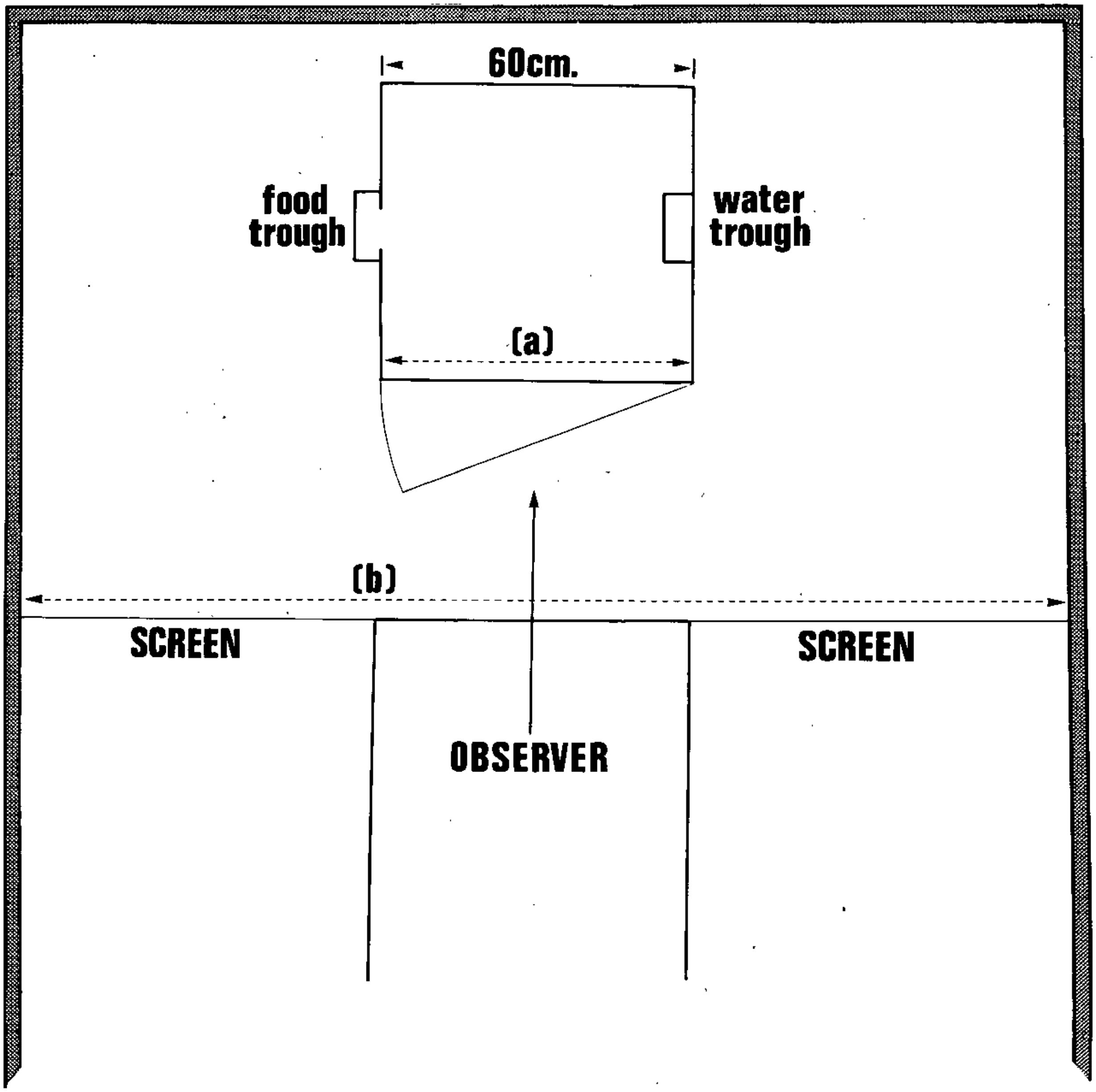

60cm.
food trough
water trough
(a)
(b)
SCREEN
SCREEN
OBSERVER

Figure 2.1. A plan of the experimental room used in Experiment 2.

days on which the food intake of each bird varied by less than 15%. This criterion was reached after 12 days when the birds were eating between 80 and 105g per day.

Testing: The hens remained on the 24 hours food deprivation schedule in the home cages and three testing situations were used:-

1. Hungry/food (H/F). The hen was placed in the experimental cage with food present and observed for 30min.

2. Not hungry/no food (NH/NF). The hen was allowed access to food in the home cage for the 24 hours prior to testing. It was then placed in the experimental cage with no food or trough present and observed for 30min.

3. Frustrated (F). The hen was placed in the experimental cage with food present under a perspex cover and observed for 30min. The hen was then removed to a holding cage in another room for a period of time varying between 5 and 30min. It was then returned to the experimental cage and allowed to feed for 30min. The purpose of this varying delay was to reduce the possibility of "superstitious" behaviour patterns being reinforced (Skinner, 1948).

Other control situations are possible,in this experiment, for example hungry/no food, but they run the risk of being thwarting. They are all examined more fully in the Discussion section of this experiment.

One trial consisted of exposing each hen to these three treatments in a randomized order every other day. On the days when testing did not take place the birds were treated as they were during training. The trials were repeated eight times.

If a hen laid less than 24 hours after an observation period the results were discarded (in case nesting behaviour had interfered with the observations) and the hen was tested the next day. This in fact only happened on one occasion.

Observations: Records similar to those in Experiment 1 were kept. In addition the following behaviour patterns were quantified as follows:-

Pecking: the number of pecks were counted and classified either as thwarted pecks, which were pecks to the perspex cover and which occurred during the Frustration test only, or redirected pecks, which were pecks to any other part of the cage.

Sleeping: the number of seconds the bird spent sleeping were counted. The criterion for sleep was both eyes completely closed or the head tucked into the plumage. Since sleep did not occur very often and since another position which always preceded sleep but was not always followed by sleep, was adopted more frequently, it was measured as well. The position consisted of the bird standing still with feathers slightly raised (the "fluffed" posture of Morris, 1956) and neck reflexed back so that the head appeared drawn into the body plumage. The eyelids often closed very slowly and opened again as soon as they had closed completely. This position was called "resting" and the number of minutes spent resting were counted. Resting was timed to the nearest minute rather than second because it was more difficult to assess exactly when it started and finished.

Vocalizations: the number of calls were counted and a tape-recording taken of each type of call. The calls were then classified after comparing the tape-recordings to a standard recording made by Collias (1960).

Results

At first the hens spent a lot of time pecking at the perspex cover in the frustrating situation. The number of thwarted pecks occurring in the frustrating situation in each of the trials is shown in Figure 2.2 and Table 2.1A and an Analysis of Variance of these numbers is given in Table 2.2A. The mean numbers of pecks per test were 447.5, 96.0, 49.7, 116.7, 190.0, 130.2, 155.5 and 43.2 for trials 1 to 8 respectively. Significantly more pecks were given in the first trial than in any of the others ($p \angle 0.01$).

The hens did peck at other parts of the cage in all the testing situations. Pecking occurred irregularly and appeared to be mainly exploratory pecking at small faecal particles adhering to the wire floor. The numbers of redirected pecks are shown in Table 2.3A and the Analysis of Variance on these results in Table 2.4A and the summarized results are given in Tables 2.1 and 2.2. There was no statistical difference between the number of pecks occurring in the 3 testing situations or in the 8 trials.

Once again there was a great deal of back and forward pacing shown in the frustrating situation. This was not a common behaviour pattern in the control situations. During the first few tests these movements were accompanied by circular head movements as though the bird was looking for an exit. They were also variable in speed and orientation but always occurred near the door. For these reasons, one such double movement without interruption was termed at

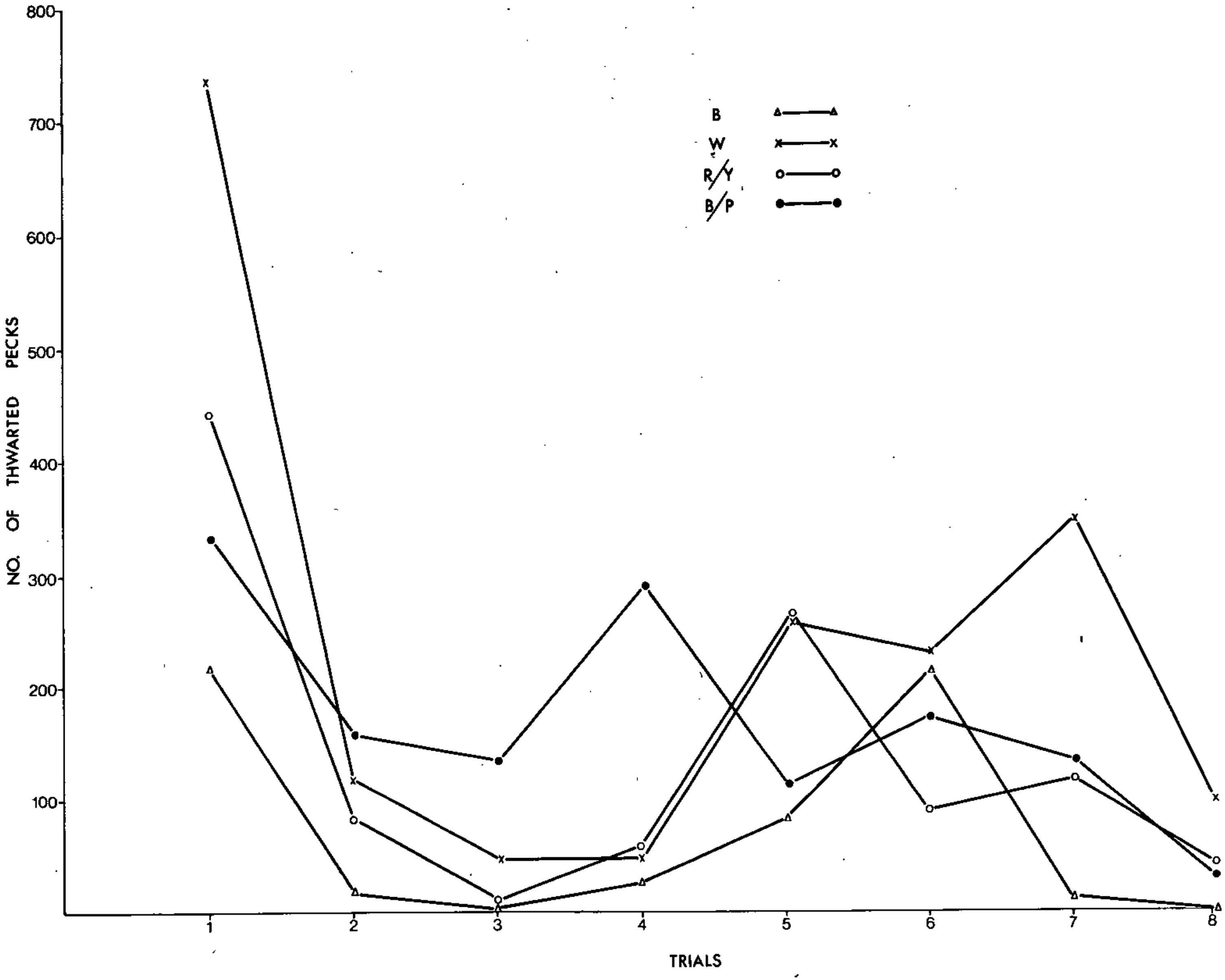

NO. OF THWARTED PECKS
800
700
600
500
400
300
200
100
TRIALS
1
2
3
4
5
6
7
8
B
W
R/Y
B/P

Figure 2.2. Numbers of thwarted pecks occurring during frustrated feeding.

Table 2.1. Mean numbers of redirected pecks occurring during frustrated feeding (n = 4).

Trials	H/F	NH/NF	F
1	3.50	21.25	5.75
2	14.50	7.00	7.25
3	3.25	19.50	19.25
4	10.00	12.75	2.25
5	13.50	12.00	2.25
6	4.00	7.00	28.25
7	9.75	26.00	10.00
8	7.75	31.25	15.75

Table 2.2. Statistical analysis of treatment effects on redirected pecks. P values.

Treatment	Mean no. of redirected pecks.		Differences between treatments. P.
Trials (n = 12)	1	10.17	n.s.
	2	9.58	
	3	12.33	
	4	8.33	
	5	9.25	
	6	13.08	
	7	15.25	
	8	18.25	
Frustration (n = 32)	H/F	8.28	n.s.
	NH/NF	17.09	
	F	10.72	

first an "escape movement" as in Experiment 1. However, the form of escape movements changed as the trials proceeded. In the first few trials they were variable in such features as number of steps taken, direction of turn, speed, position of head and orientation. By trial 8 they were much more uniform and showed a high degree of stereotypy. Although there were individual differences in the form of these movements, they were very constant within birds. Also by trial 5 all birds were performing the movements along the side of the cage with the door (path "a" in Figure 2.1). The name of the movements was therefore changed to "stereotyped movements"; this is purely a descriptive term and does not have any causal implications.

The number of stereotyped movements are shown in Table 2.5A and the Analysis of Variance on these numbers in Table 2.6A. The summarized results are given in Tables 2.3 and 2.4. Many more stereotyped movements occurred in the frustrating situation than in either of the control situations.

Stereotyped movements were once again the most prominent feature of the F situation apart from the first trial when thwarted pecking was very common. On the other hand, feeding was the commonest activity in the H/F situation and probably resting in the NH/NF situation, although this tended to be variable.

The stereotyped movements occurred in bouts lasting 2 or 3 min. interspersed with bouts of thwarted pecking, redirected pecking, preening and other comfort movements, and rest and sleep. Thwarted and redirected pecking have already beenddescribed and preening and comfort movements will now be dealt with.

The number of preens occurring during the experiment and the Analysis of Variance of these results are given in Tables 2.7A and 2.8A. The summarized

Table 2.3. Mean numbers of stereotyped movements occurring during frustrated feeding. (n = 4).

Trials	H/F	NH/NF	F
1	6.25	22.00	118.50
2	3.50	3.25	131.00
3	46.00	18.50	186.75
4.	0	21.50	173.25
5	12.50	26.00	173.00
6	22.75	1.00	127.75
7	7.50	45.50	205.50
8	11.25	11.50	172.50

Table 2.4. Statistical analysis of treatment effects on stereotyped movements. P values.

Treatment	Mean no. of stereotyped movements		Differences between treatments. P.
Trials (n = 12)	1	48.92	n.s.
	2	45.92	
	3	83.75	
	4	64.92	
	5	69.50	
	6	50.50	
	7	86.17	
	8	65.08	
Frustration (n = 32)	H/F	13.34	/_0.001
	NH/NF	188666	
	F	161.03	

results are shown in Tables 2.5 and 2.6. More preening occurred in the NH/NF situation than in the F situation and more in either of these than in the H/F situation. All these differences were statistically significant. The preening was very similar in all three situations. Occasionally it seemed more frantic in the F situation but a firm conclusion on this point could not be reached without an objective measurement.

Of the other comfort movements head-shaking, head-scratching, feather-ruffling and tail-wagging occurred only very infrequently and irregularly and will not be considered further. The incidence of feather-raising was also rather low (132 feather-raises in 48 hours of observations) and too much weight should not be given to these results. The numbers of feather-raises are shown in Table 2.9A and the Analysis of Variance for these results in Table 2.10A. The summarized results are given in Tables 2.7 and 2.8. The birds raised their feathers significantly more in the frustrating situation than in either of the control situations (p /_0.01). However even in the frustrating situation the birds only raised their feathers on average just more than twice in 30min.

Bill-wiping occurred slightly more frequently than feather-raising (315 bill-wipes in 48 hours of observations). Tables 2.11A and 2.12A give the numbers of bill-wipes and an Analysis of Variance of these numbers, and the results are summarized in Tables 2.9 and 2.10. The hens bill-wiped significantly less in the F situation than in the H/F or NH/NF situation (p /_0.01). The difference between the H/F (5.44) and the NH/NF (3.41) situations, although not reaching statistical significance ($p > 0.05$), is probably a real difference, more bill-wipes being associated with the actual act of eating.

Table 2.5. Mean number of preens occurring during frustrated feeding (n = 4).

Trials	H/F	NH/NF	F
1	12.00	58.25	31.25
2	3.75	48.25	13.25
3	2.50	23.50	18.50
4	3.00	37.75	30.00
5	1.50	44.75	51.75
6	1.25	85.00	21.00
7	16.25	64.50	23.50
8	5.50	30.25	11.25

Table 2.6. Statistical analysis of treatment effects on preens. P values.

Treatment	Mean no. of preens		Differences between treatments. P.
Trials (n = 12)	1 2 3 4 5 6 7 8	32.83 21.92 14.83 23.58 32.67 35.75 34.75 15.67	n.s.
Frustration (n = 32)	H/F NH/NF * F	5.34 49.03 25.12	/_0.001 /_0.01 */_0.05

Table 2.7. Mean numbers of feather-raises occurring during frustrated feeding (n = 4).

Trials	H/F	NH/NF	F
1	0.75	2.00	1.75
2	0.75	1.25	2.25
3	0.75	0.75	1.25
4	1.75	1.25	2.50
5	0.50	1.50	2.25
6	0.75	0.50	1.25
7	1.00	1.25	2.50
8	1.00	0.75	2.75

Table 2.8. Statistical analysis of treatment effects on feather-raises. P values.

Treatment	Mean no. of feather-raises		Differences between treatments. P.
Trials (n = 12)	1	1.50	n.s.
	2	1.42	
	3	0.92	
	4	1.83	
	5	1.42	
	6	0.83	
	7	1.58	
	8	1.50	
Frustration (n = 32)	H/F	0.91	/_0.01
	NH/NF	1.12	
	F	2.10	

Table 2.9. Mean numbers of bill-wipes occurring during frustrated feeding (n = 4).

Trials	H/F	NH/NF	F
1	4.25	4.75	3.75
2	5.25	1.00	0.50
3	1.75	5.25	0.75
4	7.75	7.75	1.25
5	12.50	3.00	0
6	4.75	0.75	0.50
7	5.25	4.25	0
8	2.00	0.50	1.25

Table 2.10. Statistical analysis of treatment effects on bill-wipes. P values.

Treatment	Mean no. of bill-wipes		Differences between treatments. P.
Trials (n = 12)	1	4.25	n.s.
	2	2.25	
	3	2.58	
	4	5.58	
	5	5.17	
	6	2.00	
	7	3.17	
	8	1.25	
Frustration (n = 32)	H/F	5.44	/_0.001
	F	1.00	/_0.05
	NH/NF	3.41	

The numbers of minutes the birds spent sleeping (to the nearest second) are shown in Table 2.13A. These results were not analysed statistically because of the infrequent occurrence of sleep but certain general conclusions can be drawn from the results. With one exception all the sleep occurred in the NH/NF situation. In the case where the sleep occurred in the H/F situation, the hen had finished feeding and so the situation was very similar to NH/NF.

The amount of time spent resting, including the time spent sleeping, is shown in Table 2.14A and an Analysis of Variance of these results is given in Table 2.15A. The summarized results are given in Tables 2.11 and 2.12. The birds spent significantly more time in the resting position in the NH/NF situation than in either the H/F or the F situation ($p < 0.001$). Also this behaviour pattern was rather variable from trial to trial, the three trials with the longest resting times being significantly different from the two trials with the shortest resting times ($p < 0.05$).

Calling during this experiment was infrequent. All the birds did call at some stage in the experiment and more calls seemed to be given in the F situation but this could not be proved statistically. The numbers of calls are given in Table 2.16A. It was thought that most of the calls were food calls but it is possible that they could have been low intensity alarm calls. These two calls can be difficult to distinguish without taking a sound spectrograph. On one occasion one of the birds gave a series of high intensity, ground-predator alarm calls but this was probably given in response to the alarm-calling, which occurred immediately previously, of hens and cockerels outside the room.

As an addition to Experiment 1 testing was continued for another 8 trials

Table 2.11. mean numbers of minutes spent resting during frustrated feeding (n = 4).

Trials	H/F	NH/NF	F
1	3.00	5.75	2.00
2	0	13.25	0
3	2.50	16.50	2.75
4	6.00	19.25	2.00
5	2.50	9.50	0.75
6	4.25	19.00	4.25
7	3.75	7.25	0.25
8	7.75	14.00	2.50

Table 2.12. Statistical analysis of treatment effects on minutes spent resting. P values.

Treatment	Mean no. of minutes spent resting		Differences between treatments. P.
Trials (n = 12)	1	3.58	$\angle 0.05$
	7	3.75	
	5	4.25	
	2	4.42	
	3	7.25	
	8	8.08	
	4	8.25	
	6	9.17	
Frustration (n = 32)	NH/NF	12.75	$\angle 0.001$
	H/F	3.72	
	F	1.14	

without observations being made. The hens were observed on Trial 16 and the number of stereotyped movements counted. These are shown in Table 2.13. As can be seen the hens now performed these movements at a fairly high level in the H/F situation as well as the F situation. In the H/F situation they spent a large part of the available time pacing and only fed in short bouts between bouts of pacing.

Two of the hens (B and W) were tested once again in the F situation only, and on this occasion the door was left open about 20cm. Hen W started to pace along route "a" (see Fig. 2.1) but after 1.5min. came out of the cage and wandered round to the food trough giving a few exploratory pecks on the way. She pecked at the perspex cover from outside the cage for half a minute then moved away and started stereotyped pacing along route "b" (see Fig. 2.1). The pacing continued for 15min. when observations ceased. Hen B followed the same pattern with a longer time course. She took 3.5min. to come out of the cage, wandered about more and spent 2.5min. pecking the perspex cover over the food before starting to pace along route "b". Her pacing occurred in bouts interspersed with bouts of thwarted pecking from outside the cage, and this continued until observations ceased 15min. later.

All four hens were then placed in their home cages with ad libitum food for 4 months. They were then tested again and the number of stereotyped movements counted. The results were shown in Table 2.14. The hens were still performing stereotyped movements at a similar rate to that shown in Trial 16.

Discussion

The most prominent feature of Experiment 2 was once again the appearance

Numbers of stereotyped movements occurring in Trial 16.

	Birds			
	B	W	R/Y	B/P
H/F	112	187	161	73
NH/NF	61	12	57	15
F	213	309	220	186

Table 2.14. Numbers of stereotyped movements occurring after an interval of 4 months.

	Birds			
	B	W	R/Y	B/P
H/F	103	91	150	110
NH/NF	0	53	14	39
F	165	214	189	221

of escape or stereotyped pacing movements in the thwarting situation. These movements at first appeared to be attempts to escape from the cage. This agrees with the findings of Wood-Gush and Guiton (1967) that physical thwarting generates a large amount of avoidance. However, in contrast to their results the high rate of escaping showed no signs of decreasing by the eighth or even the sixteenth trial. Also, when two of the birds were allowed to escape from the thwarting situation after Trial 16, they did not do so immediately but continued to pace up and down in front of the open door for a few minutes. The nature of the movements also changed and they became very stereotyped as described previously. In addition, by Trial 16 they were appearing in the H/F situation at a level not much below that of the F situation. A tentative explanation for their occurrence could be that the frustrating situation was in some way noxious and these movements at first were attempts to avoid or escape from the frustrating situation. Supporting this theory is the fact that at first the pacing movements were accompanied by circular head movements and pressing against the mesh as if the hens were looking for an exit. Also all the movements were orientated towards the door of the cage where the hens would expect to find an exit, having been taken in and out through there during training. Since, by the 16th Trial they were not longer primarily attempts to escape (they were performed when immediate escape was possible) they must have changed in the intervening period. It is possible that the elements of escape dropped out because they were not rewarded by actual escape and the pacing remained because it was in some way rewarding. The appearance of stereotyped pacing in the H/F situation at a high level in Trial 16 could mean that the birds were generalizing from the thwarting situation to this control situation.

Another difference from the results of Wood-Gush and Guiton was that after the drop in thwarted pecking in the first trial, the birds continued to try to feed at a fairly high level. They were therefore not habituating to the thwarting situation as they did in Wood-Gush and Guiton's experiment. The difference may have been due to a difference in procedure; Wood-Gush and Guiton tested every day whereas in this experiment testing days alternated with training days. Also in the earlier experiment the birds were not removed from the cage after a frustration test but before feeding. Therefore the chance of a hungry bird obtaining food when placed in the experimental cage was 50% in Wood-Gush and Guiton's experiment and 83% in Experiment 2. The expectancy of food would thus be much greater in the present experiment. This difference in expectancies probably accounts for thwarted pecking persisting in Experiment 2 and extinguishing in the other experiment. Since the attempted feeding responses did extinguish in Wood-Gush and Guiton's experiment it is possible that the birds were then no longer thwarted and this would lead to the observed extinction of escape behaviour.

A further feature of this experiment was that preening, bill-wiping, redirected pecking and sleeping, all of which have been observed to occur as displacement activities in frustrating and conflict situations in other avian species (Tinbergen, 1952; Andrew, 1956a and b; van Iersel and Bol, 1958; Rowell, 1961; McFarland, 1965), occurred less frequently (the redirected pecking not significantly so) in the F situation than in the NH/NF situation. On the other hand feather-raising occurred more often in the F situation than in the NH/NF situation. This was unusual, because as mentioned before feather-raising is often followed by preening (see also McFarland and Baher, 1968) and preening was depressed in the F situation. Morris (1956) stated that, "if a bird is intensely aroused and is then thwarted in some way, the autonomic changes which will accompany the somatic reactions to this situation will involve marked pilomotor activity, which sometimes takes the form of pilo-erection". Andrew (1956a and c) considered that feather-raising is a heat regulatory mechanism which may operate in response to circulatory changes at the body surface soon after fear has been aroused. However, he thought that warming responses (fluffing) soon after fear should be followed by cooling responses (sleeking) after a short lag. The feather-raising in the present experiment produced the ruffled posture which both Morris and Andrew thought was a cooling response. More recently McFarland and Baher (1968) have shown that all degrees of feather-raising tend to reduce heat loss. However, they have also shown that food-deprived birds raise their feathers, probably to reduce heat loss and compensate for the reduced heat gain resulting from reduced food intake. It has also been shown that feather-raising occurs in aggressive and defensive birds (Vowles and Harwood, 1966; McFarland and Baher, 1968). The causation of feather-raising is therefore complex and may involve more than one motivational system. Nevertheless it is possible that in the present experiment the changes in feather posture seen in the F situation, although only transitory, could be a reflection of autonomic changes taking place during thwarting.

Thwarting the hunger drive affected most of the behaviour patterns measured. However, certain of these patterns also differed between the two control situations, H/F and NH/NF. For example, there was more bill-wiping and less sleeping and resting in the H/F situation compared to the NH/NF situation. This is mainly due to the fact that some activities are associated with the actual act of eating and others are inhibited by it. It is therefore necessary to decide what a suitable control situation is. There are 5 possibilities:-

1. Hungry/food present; the act of eating may mask other behaviour patterns.

2. Hungry/no food present; there is bound to be some thwarting through the bird generalizing to secondary cues.

3. Not hungry/food present; the sight of the food would probably stimulate feeding. Otherwise this is similar to H/F after the bird has fed.

4. Not hungry/food present but covered with perspex; the sight of food would probably stimulate attempted feeding and the bird would then be thwarted.

5. Not hungry/no food present; this situation appears to offer the least risk of the bird being thwarted, since both the internal motivational and stimulus factors for feeding are reduced to a minimum.

In further experiments involving thwarting of feeding behaviour this last control situation was the only one used.

The stereotyped movements in Experiment 2 in some ways resembled the fixated responses of the rats described by Maier (1949) which were exposed to an insoluble problem. The F situation fitted Maier's definition of a frustrating situation in that (a) the animal was faced with an insoluble problem

(b) the animal was not permitted to escape or leave the field in any other way and (c) the animal was highly motivated to respond. The stereotyped movements were apparently non-adaptive, very uniform, permanent and occurred when the problem was made "soluble" i.e. they occurred in the H/F situation in Trial 16. In all these features they resembled fixations.

If in fact the stereotyped movements are a similar phenomenon to fixations they should not occur if the animals are not highly motivated to respond. This hypothesis was tested in Experiment 3.

Experiment 3

Material and Methods

Sixteen experimentally naive hens aged between 6 and 7 months and of similar breed and strain to those in Experiment 2 were used. The experimental method was the same as Experiment 2 with the following exceptions:-

Training: The hens were randomly divided into two groups of 8. One group was placed on a 24 hours food deprivation schedule and the other on a 6 hours food deprivation schedule. The training and testing periods were reduced from 30 to 20min. in order that all the birds could be tested in a day. It was felt that little information was lost by doing this. The criterion for ending training, which was the same as in Experiment 2, was reached after 16 days. The hens on the 6 hours deprivation schedule had food available in the home cage when not deprived.

Testing: Two testing situations were used. The control situation was not hungry/no food (NH/NF) in which the hen was allowed access to food in the home cage for the 24 hours prior to testing. It was then placed in the experimental cage and observed for 20min. with no food or trough present. In the frustrated (F) situation, the deprived hen was placed in the experimental cage with food present under a perspex cover and observed for 20min. It was then fed after a variable delay as in Experiment 2. One trial consisted of exposing each hen to the two treatments in a randomized order every other day. Three trials were conducted.

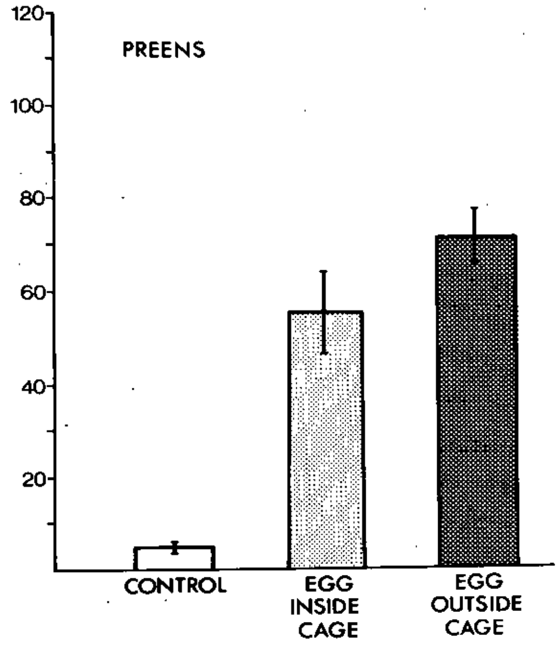
Observations: The numbers of preens and stereotyped movements were counted.

Results

The numbers of preens are shown in Table 3.1A and Figure 3.1. Analyses of Variance for these results are given in Table 3.2A. The numbers and Analyses of Variance for stereotyped movements are given in Tables 3.3A and 3.4A respectively. The mean numbers of these movements occurring in each situation are also entered in Figure 3.1.

In the 6 hours deprivation group the hens preened much more in the F situation than in the NH/NF situation ($p < 0.001$). Once again this preening gave the impression of being slightly more hurried than normal preening. There were also few stereotyped movements shown in either of the situations, and those that did occur tended to be variable in nature. Nevertheless significantly more stereotyped movements did occur in the F situation ($p < 0.001$).

On the other hand in the 24 hours deprived group. although there was a significant decline in preening from the first to the third trial ($p < 0.01$), there was no overall difference in the number of preens occurring in the F and


PREENS
120
100
80
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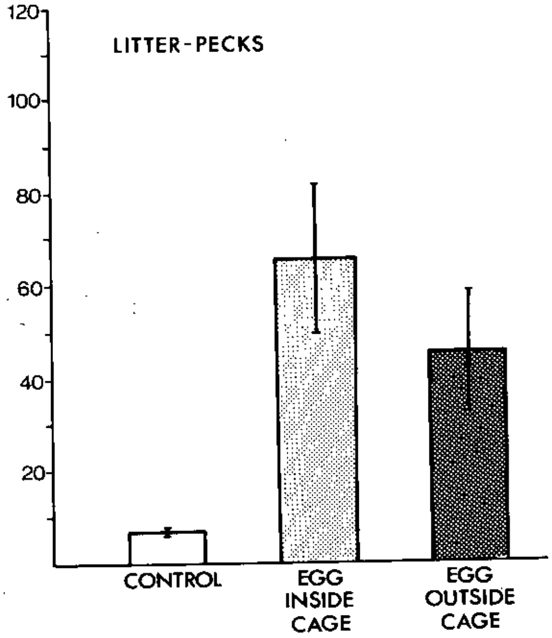
CONTROL
EGG INSIDE CAGE
EGG OUTSIDE CAGE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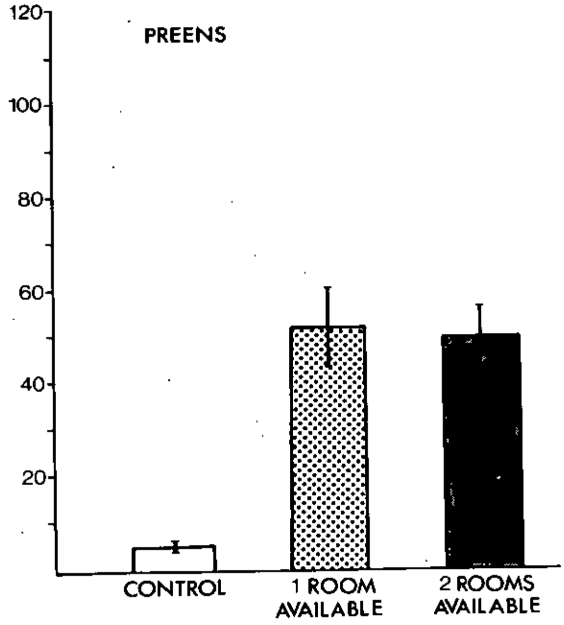
CONTROL
EGG INSIDE CAGE
EGG OUTSIDE CAGE


PREENS
120
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CONTROL
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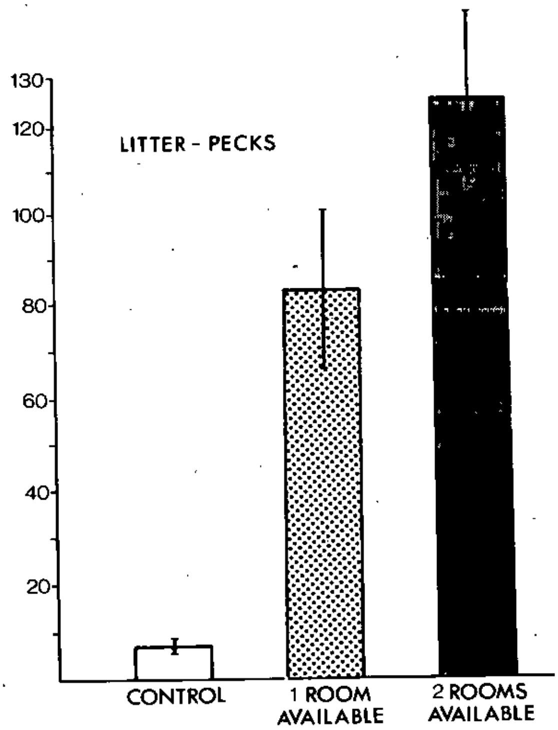
2 ROOMS AVAILABLE


LITTER - PECKS
130
120
100
80
60
40
20
CONTROL
1 ROOM AVAILABLE
2 ROOMS AVAILABLE

not near the nest. Occasionally elements of pacing behaviour appeared round the perimeter of the pen but there was not enough to quantify. During the wandering about the hen would suddenly appear to see the nest again and move quickly towards it. The whole cycle would then be repeated. This continued until the end of the observation period. When the cage was raised the hen would immediately stop whatever she was doing, approach the nest and go through the procedure of nest-entry and sitting as described for the control situations.

In the FO situation the bird would look at the eggs in a standing position and turn facing each side in succession. This turning often took place with the hen in a crouched position. Typically bouts of litter-pecking and scratching would alternate with bouts of frantic preening. Often the bird would also sit with some settling movements and while in the sitting position, egg rolling movements of the bill, head and neck were very common. However, sitting never lasted more than about a minute and the hen would stand again and continue turning. While in the sitting position 4 of the 7 hens showed dust-bathing behaviour on at least one occasion. During this the feathers were fully ruffled and the birds rolled half on to one side spreading the opposite wing and scraping litter over themselves. When the eggs were replaced the birds went through the sitting and settling procedure as described before.

The number of preens occurring during thwarted incubation are shown in Figure 6 and Table 6.1A and an Analysis of Variance of these results is given in Table 6.2A. It can be seen that far more preens occurred in both the frustrating situations than the control situation ($p \angle 0.001$). The number of

Particular attention was paid to preening and litter-pecking and also to any escape or pacing behaviour that occurred.

Results

In the control situations the hens approached the nest, carefully stepped into it and sat down adjusting the position of the eggs with their bills as they did so. They then made settling movements and adjusted the position of any of the eggs which were still in front of them and not covered by breast feathers by rolling them in with the bill and tucking them underneath themselves. This was often followed by a few rudimentary nest-building movements in which pieces of litter were picked up from in front of them and dropped on either side or on the back. This whole operation took about 3 or 4 min. and thereafter the bird sat very still with the feathers in the fluffed posture and the head pulled well into the plumage. There was occasional preening or litter-pecking but in general the control situations were characterized by inactivity apart from the initial act of sitting and settling.

On the other hand the birds tended to be much more active and very restless in the two frustrating situations. In a typical FI situation the bird would return to the nest and then walk quickly round and round the cage looking at the eggs and occasionally pushing at the mesh with the breast as if trying to get in. After 2 or 3 min. of this behaviour the hen would break away and approach one of the ends of the pen scratching and pecking in the litter on the way. Bouts of litter-pecking would be interspersed with bouts of frantic preening and this would continue for a few minutes with the hen wandering about but generally and passed through a ring in the ceiling to the observation window of that pen. The cages were left in position for 48 hours then, in turn, the 60 watt light in each room was switched on and the cage raised. Within 10min. of the cage being raised each hen had come off its nest. This procedure was repeated on 3 successive days and by the third day all the hens were leaving their nests within 4min. of the cages being raised.

Testing: Each hen was allowed off its nest once in the later part of each day and then subjected to one of three testing situations:-

1. Control (C). The hen was allowed to feed and re-enter the nest. The cage was then lowered and the bird observed for 20min.

2. Frustrated/eggs inside cage (FI). While the hen was off the nest feeding the cage was lowered. The hen was then observed for 20min. starting from the moment she made her first attempt to re-enter the nest. The cage was then raised, the hen allowed to re-enter the nest and the cage lowered again.

3. Frustrated/eggs outside cage (FO). The hen was allowed to feed and re-enter the nest and the cage was lowered. Immediately, the eggs were removed from under the hen and placed round the outside of the cage, two on each side. The hen was then observed for 20min. and the eggs replaced.

After the tests the 60 watt lights were switched off and the hens left undisturbed until the next test the following day.

One trial consisted of exposing each hen to these three treatments in a randomized order on successive days. Three trials were conducted.

Observations: Similar records to those in Experiment 2 were kept.

windows of one-way glass at one end facing into a corridor. Each room was divided into two equal pens by a partition 1.25m. high running at right angles to the corridor and one hen was put in each pen. In the middle of each pen was placed a 30x30cm. tray with a 4cm. lip and containing some litter and 8 eggs. A water trough was placed within reach of this "nest" and a food trough was put at one end of each pen. Each room was lit with a dim 15 watt pilot light from 0600h to 2000h and the temperature varied between 15° and 18°C. There was also a 60 watt light in each room which could be switched on from the corridor during testing periods.

Within 15min. of their introduction to the pens all the hens were sitting on the eggs. They were observed casually over the next 3 days to see when they came off the nests to feed. Three of the hens came off twice per day, once early and again late in the day, while the other 4 came off once only in the later part of the day. The usual pattern was that they came off, wandered away from the nest, defecated, approached the food and fed for about 6 - 8min. and then returned to the nest and settled down on the eggs. They were never off the eggs for longer than 10min. The idea of this experiment was to thwart the birds by blocking their re-entry to the nest after they had been off to feed. However, it was obviously going to save a lot of time if the birds left the nest when the observer wanted them to rather than watching one bird all day until it rose spontaneously. This was accomplished by covering each nest and sitting bird with a 30cm^3 wire mesh cage. This kept the birds on the nest without restricting changes of position on the eggs. The birds could reach the water through an 8cm^2 hole cut in one side. Each cage could be raised and lowered from the corridor by a wire attached to the top of the cage

CHAPTER 4

THWARTING OF INCUBATION BEHAVIOUR

Introduction

Selection of poultry for egg production characters has almost eliminated broodiness from laying stock at the present time. The Brown Leghorn J-line birds used in the previous experiments were typical in this respect and showed no tendency towards broodiness at all. For this reason a different breed of birds was used in the experiments described in the next two chapters. The results obtained from these experiments are therefore not strictly comparable to the other results in this thesis. However, birds from the broody strain were tested in a food thwarting situation in order that they could be more closely compared to Brown Leghorns and the results from that experiment are given at the end of Chapter 5.

Experiment 6

Material and Methods

Seven hens aged about 14 months and derived from New Hampshire x Columbian parents were used in this experiment. They came from a breeding farm of a company which specialized in producing broiler stock and they had been broody for about a week when they arrived. By "broody" is meant that they were not laying, sat almost continuously in nest-boxes on eggs if allowed, emitted a characteristic "clucking" call if disturbed on the nest and had well developed brood patches.

They were placed in rooms measuring 3x3m. with litter floors and observation

servation and not by the speed of execution of the movements.

The present finding that individual preens are of shorter duration than normal is difficult to explain in terms of disinhibition. One would have to postulate a mechanism which inhibited and disinhibited preening in very quick succession thus having a truncating effect on each preen and this seems very unlikely.

It should be noted that all the preens (105 normal, 190 displacement) analysed in this experiment were complete, in that once the head started to move towards the plumage the bill came into contact with the feathers for a measurable period of time. There were no intention movements to preen. This agrees with van Iersel and Bol who stated that incompleteness was not a characteristic of displacement preening by terns. However the shorter displacement preens may have been functionally incomplete. Not enough detail could be seen on the film to judge whether an equivalent amount of work was performed on the plumage in both cases.

but the film analysis proved that this was not the case.

The difference in the proportion of parts of the plumage preened is very similar to the difference between displacement and normal preening in terns (*Sterna spp*) described by van Iersel and Bol (1958). They argued that the order in which parts of the plumage were preened "after bathing" (which they considered as normal preening) represented differences in threshold value of the preening movements. They thought that higher threshold-values went together with greater complexity of motor pattern and in fact their order of threshold-values is very similar to the order of plumage areas in Table 5.3. They also found that when terns preened after bathing there was a positive correlation between number of preens per minute and the threshold value of the part preened. They also found that some cases of preening were specifically connected with ambivalent aggression or escape and stated, "This preening has to be considered as displacement because of the (sometimes) frantic appearance and mainly because of the context. Moreover its composition differs from that of preening 'after bathing' in that low threshold movements are especially frequent". However nowhere did van Iersel and Bol measure the speed of displacement preening nor does the disinhibition hypothesis explain why it should be frantic. They did say that the strength of the escape drive is directly correlated with the intensity of displacement, as indicated by the proportion of higher threshold movements and by an increase in the number of movements *per case* (the underlining is mine). Therefore, although they were talking about an increase in intensity, which could occur in certain circumstances, this was only measured by the parts preened and the number of preens per ob-

Table 5.3. Percentage time spent preening various parts of plumage.

	Birds					
	W		B/W		B/P	
	C	F	C	F	C	F
Breast	15	12	16	34	8	22
Belly	8	9	0	4	2	8
Shoulder	2	7	8	13	6	13
Outside Wing	6	20	8	4	15	30
Inside Wing	16	30	22	21	26	3
Back	7	8	1	4	21	3
Tail	18	3	34	10	11	5
Vent	18	8	10	10	8	10
Uropgeal gland	10	3	1	0	3	6

Table 5.4. Percentage time spent preening "near" and "far" parts of plumage.

	Birds					
	W		B/W		B/P	
	C	F	C	F	C	F
Breast Belly Shoulder Outside Wing	31	48	32	55	31	73
Inside Wing Back Tail Vent Uropgeal gland	69	52	68	45	69	27

C = Control situation

F = Frustrating situation

(B/W) to 1.1 sec. (B/P) in the frustrating situation and from 1.3 sec. (W) to 2.2 sec. (B/P) in the control situation.

The fact that less head movements are shown in Table 5.1 than preens in Table 5.2 is because it was not always possible to tell exactly when a head movement started, and the doubtful ones have been omitted.

The percentage time spent preening various parts of the plumage was calculated and is shown in Table 5.3. These results seem very variable. However, the areas of plumage in Table 5.3 were put down approximately in order of motor complexity and when they were divided into two groups a definite pattern emerged. The areas were divided into (a) those parts which can be easily reached by the bill with little head or neck movement and with no other body movementsand (b) those parts which require more effort to preen. In this experiment group (a) were called the "near" parts of the plumage and included the Breast, Belly, Shoulder and Outside Wing, while group (b) were called the "far" parts and included the remainder of the plumage. The grouped results are shown in Table 5.4. In the control situation all the hens spent about a third of their preening time dealing with "near" parts of the plumage whereas in the frustrating situation they spent from half to three-quarters of their preening time on "near" parts.

Discussion

The shorter duration of preens in the frustrating situation is the reason for the frantic or hurried appearance of displacement preening described in previous experiments. It had been thought that the bird darted its head from one part of its plumage to another more quickly in the frustrating situation

Table 5.2. Mean duration of preens in frames (± S.E.) with "t" values.

Bird	Situation	Duration	t	P
W	Control (n = 39)	42.76 ± 8.05	1.98	<0.05
	Frustrated (n = 92)	28.90 ± 3.09		
B/W	Control (n = 33)	51.15 ± 7.80	2.79	<0.01
	Frustrated (n = 19)	19.26 ± 3.87		
B/P	Control (n = 33)	71.42 ± 8.13	4.88	<0.001
	Frustrated (n = 69)	34.33 ± 3.46		

Table 5.1. Mean duration of head movements towards feathers in frames (± S.E.) with "t" values.

Bird	Situation	Duration	t	P
W	Control (n = 31)	7.35 ± 0.94	0.45	n.s.
	Frustrated (n = 71)	8.01 ± 0.86		
B/W	Control (n = 27)	6.70 ± 1.29	0.20	n.s.
	Frustrated (n = 11)	6.18 ± 2.23		
B/P	Control (n = 30)	5.47 ± 1.13	0.28	n.s.
	Frustrated (n = 67)	5.13 ± 0.61		

about 3min. of film had been collected for each bird. Wood-Gush (1959) found a diurnal rhythm of preening in the fowl with more occurring in the morning and evening than at other times of the day. He thought that tactile stimuli may gain in relative strength at these times and lead to preening. For this reason it was thought that this could probably be regarded as "normal" preening.

The film was processed and examined on a film analyser. Two measurements were taken in frames; the length of time it took from the start of a movement of the bird's head towards the feathers to the moment the bill touched the feathers and the duration of each preen. The lengths of time spent preening different areas of plumage (as described in Chapter 2) were also measured in frames.

Results

The mean duration of head movements towards feathers are shown in Table 5.1. A 't'-test was carried out between the figures obtained in the control situation and the frustrating situation and the 't'-values are also given in Table 5.1. As can be seen the head movements were very fast (about 0.2sec.) but there was very little difference between the duration of the movement in the two situations.

Similar results for duration of preens are shown in Table 5.2. In each case preens were significantly shorter in the frustrating situation. In two of the birds they were less than half the length of those in the control situation. It is interesting to note that the duration of a preen (given here for convenience in seconds) varied considerably between birds, from an average of 0.6 sec.

Experiment 5

Materials and Methods

The same experimental room and cage were used as in Experiment 4. A Bolex H16 reflex cine-camera was set up in the hide (see Figure 2.1). The one-way glass was removed from the hide and replaced by a curtain through which the lens of the camera could poke. The position of the cage was adjusted so that the camera lens was 60cm from the centre of the cage. Additional illumination was provided by two 200 watt lamps placed slightly above and behind the camera, one on each side. A 10mm lens set at f4 was used, the exposure time was 1/110 sec. and the film was Kodak Tri-X Reversal (ASA 160). Preening was filmed at 32 frames per sec. (normal film speed is 24 frames per sec.) in an attempt to get as much detail as possible on to the film.

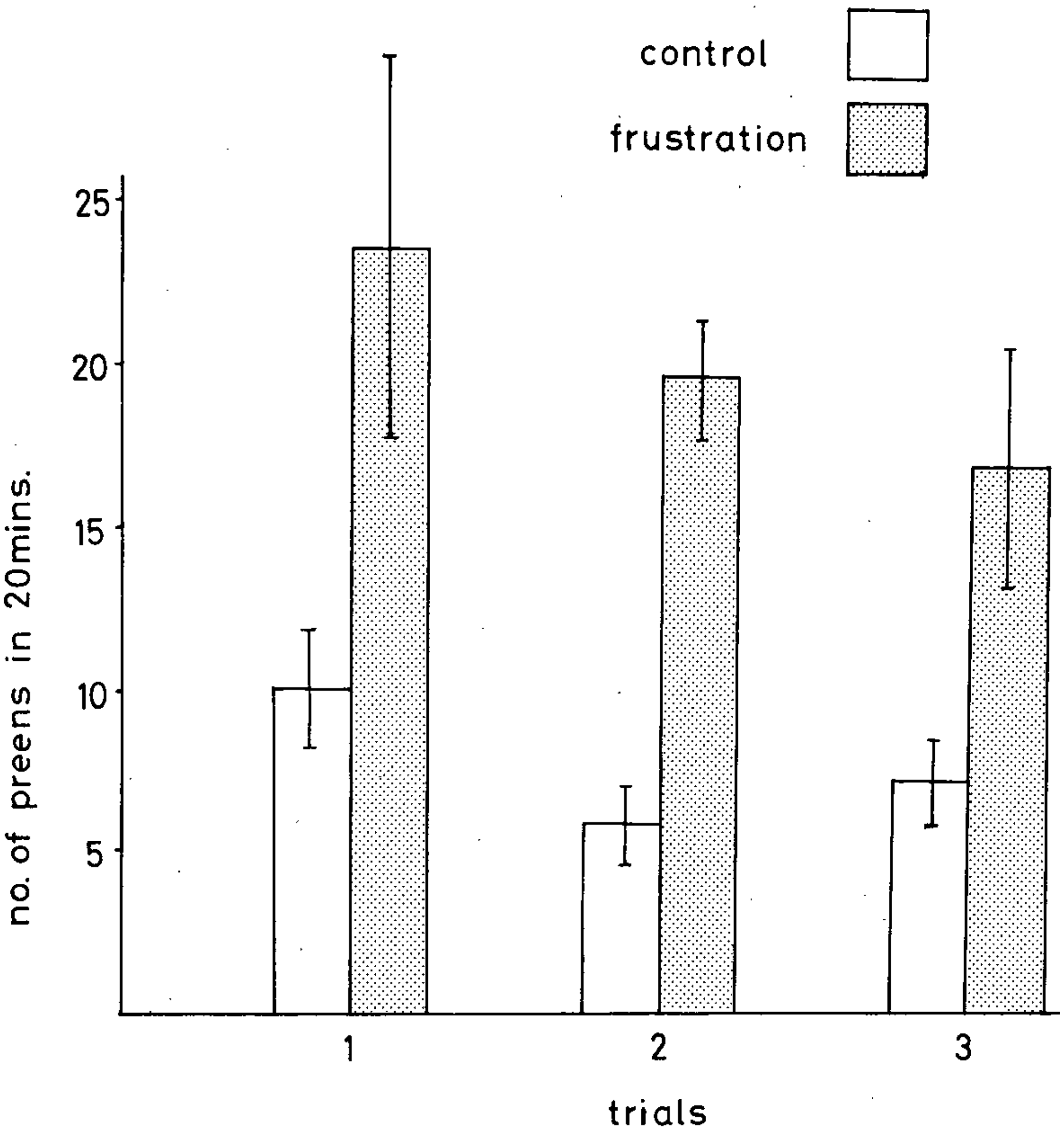
Four hens (W, B/W, B/P and B) which had shown a lot of displacement preening in Experiment 4 were used in this experiment. They were kept on a 6 hours food deprivation schedule and fed in the experimental cage for 20min. on 3 days with the motor of the camera running intermittently to let them become accustomed to the noise. They were then placed in the F situation and the training situation for 20min. on alternate days. Preening which occurred in the F situation was filmed, the aim being to get about 3min. film of preening for each bird. However, one bird (B) became ill and was killed mid-way through the experiment. After 6 days enough film had been taken and the birds were given food <u>ad libitum</u> in the home cages. On the next three successive evenings each bird, in turn, was put in the experimental cage with food present, for the last hour of the light period (1900 - 2000h). Any preening which occurred was filmed until

Discussion

The results obtained in this experiment are very similar to those from the 6 hours deprived group in Experiment 3. In both cases thwarting resulted in displacement preening. It seems therefore that social thwarting has a very similar effect to physical thwarting after 6 hours food deprivation.

The preening that occurred in thwarting situations in Experiments 1, 3 and 4 was called "displacement preening" only on a descriptive basis. It showed two of the features which Tinbergen (1952) stated are characteristic of displacement activities. These are that the movements shown do not belong to the executive motor patterns of the activated drive and they show an incomplete or frantic performance. Tinbergen also said that the absence of the external stimulation normally associated with the action is characteristic of displacement activities, but little can be said about this point here. The external stimuli which elicit preening are probably continuously present on the surface of the skin as suggested by the fact that all the hens showed some preening in the NH/NF situation. The fact that the hens showed more preening in the thwarting situation without any obvious additional external stimulation is not the same as preening occurring in the absence of external stimuli.

The displacement preening that occurred in Experiments 1, 3 and 4 was described as being more hurried and frantic than normal preening. However, this was only a subjective impression and it was decided to investigate the matter objectively in the next experiment by means of frame by frame film analysis.



control
frustration
25
20
15
10
5
no. of preens in 20mins.
1
2
3
trials

the experiment. Food was available from 3 troughs placed on 3 sides of each home cage. Casual observations were taken of the pairs in the home cages to find out which hen of each partnership was dominant.

Training: The birds were put on a 6 hours food deprivation schedule and fed individually in the experimental cage for 20min. each day. The criterion for ending training was reached after 11 days.

Testing: The same two testing situations were used as in Experiment 3 i.e. NH/NF and F. In the NH/NF situation both hens of a partnership were allowed access to food in the home cage for the 24 hours prior to testing. Both birds were then placed in the experimental cage with no food or trough present and the submissive bird observed for 20min. In the F situation, both deprived hens were placed in the experimental cage with food present and the submissive bird observed for 20min. It was then fed on its own after a variable delay as in Experiment 3. One trial consisted of exposing each pair to the two treatments in a randomized order every other day. Three trials were conducted.

Observations: The numbers of preens were counted.

Results

The dominant birds occupied the food hole for most of the 20min. observation time in the thwarting test. The number of preens are given in Table 4.1A and Figure 4.1. An Analysis of Variance of these results is given in Table 4.2A.

The submissive birds preened far more in the F situation than in the NH/NF situation. Once again most of this preening gave the subjective impression of being slightly more hurried than normal preening.

critical level between 6 and 24 hours food deprivation, the hen performs stereotyped movements instead of displacement activities.

It is also not clear why the 24 hours deprivation group in this experiment should have differed from the birds in Experiment 2 in showing increased preening in the first thwarting test. There were certain differences in procedure. For example, the training and testing times were shorter in the present experiment but the birds were trained for a longer period. This problem of the effects of length of training period will be investigated in a later chapter.

Experiments 2 and 3 used a perspex cover over the food to thwart the hens. In the next experiment a hungry, dominant, cage-mate feeding at the one available food source was used to frustrate each hen. The thwarting was then partly physical, since the hole in the cage through which the birds fed measured only 8cm x 8cm, and partly psychological, since fear of the dominant bird would inhibit the hen from approaching the food.

Experiment 4

Material and Methods

Twelve experimentally naive hens 8 months of age and of similar breed and strain to those in Experiment 3 were used. The experimental method was the same as for the 6 hours food deprivation group in Experiment 3, with the following exceptions:-

The birds were randomly grouped into 6 pairs 2 months before the start of the experiment. These pairs lived in slightly larger home cages before and during case. However, the results from the first trial on the 24 hours deprivation schedule resembled more the results from the 6 hours deprivation schedule with more preening in the F situation and an intermediate number of stereotyped movements being shown.

The stereotyped movements may inhibit displacement preening only if they reach a certain frequency or, more likely, if they undergo some qualitative change. For example, the movements after 6 hours deprivation may be simple escape movements while those after 24 hours deprivation may be stereotyped or fixated movements. Support for this possibility comes from the fact that the movements increased with number of trials in the 24 hours deprivation group but did not in the 6 hours group. This agrees with Maier's (1949) description of how fixations increase in constancy with repeated frustration. The movements in the 6 hours group were also more variable in nature than those of the 24 hours group. It could therefore be postulated that in the first frustrating test on the 24 hours deprivation schedule, simple escape movements occurred and later developed into stereotyped or fixated movements in the second and third trials. In the first trial before becoming fixated, these movements did not inhibit displacement preening as they did in the subsequent trials.

On the other hand most of the results could be explained by saying that the movements were all of the same type and only inhibited displacement preening when some threshold value in their frequency was reached.

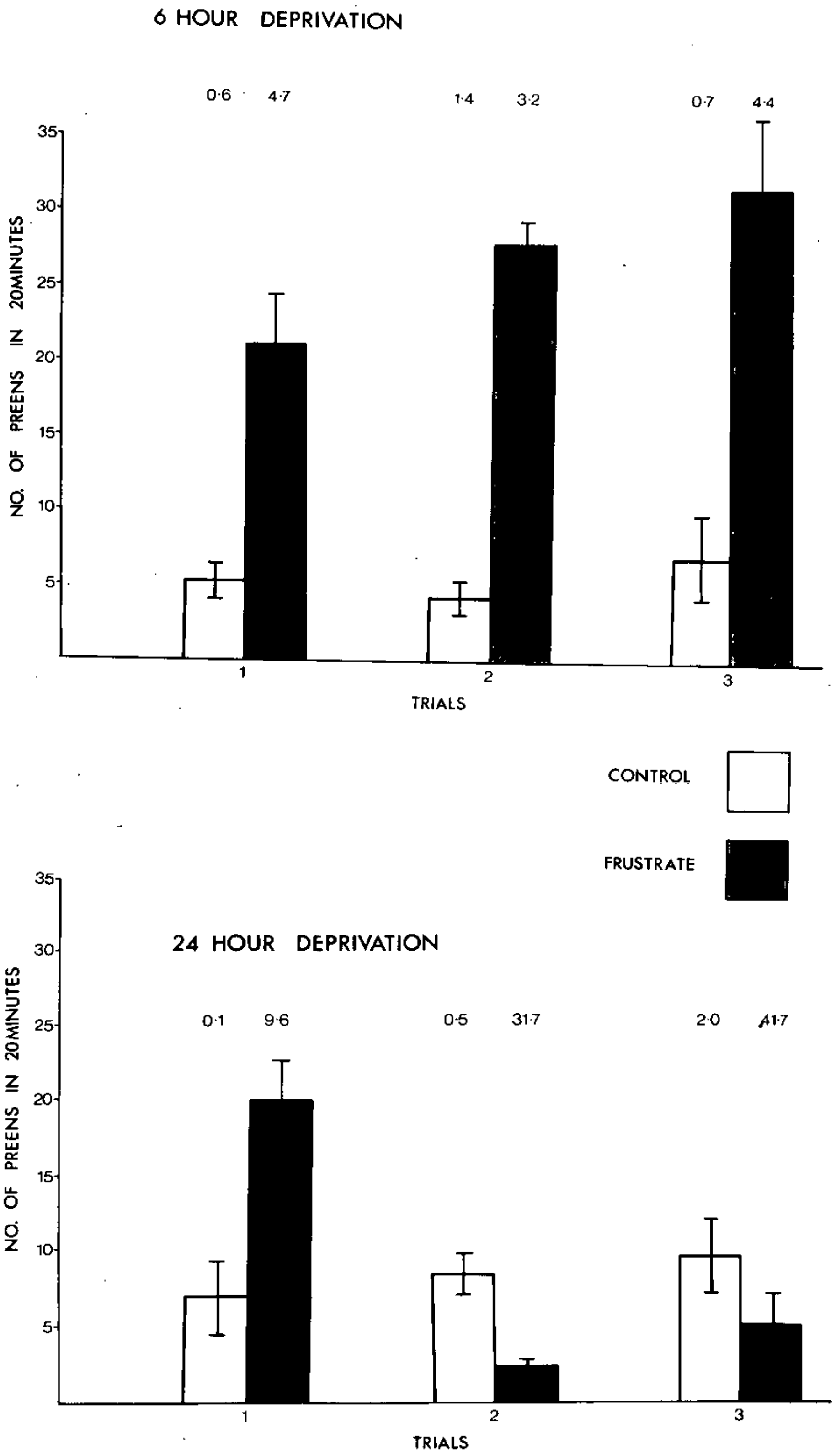
Why there should be this difference in quality or frequency of escape movements after 6 and 24 hours food deprivation has not been explained. Presumably the strength of the frustrated tendency is important and when this reaches some the NH/NF situations. However the Trial x Frustration interaction was highly significant ($p < 0.001$) and when paired 't'-tests were carried out on the figures for each trial separately, the following results were obtained. In the first trial there were more preens in the F situation than in the NH/NF situation ($t = 7.43$: $p < 0.001$). In the second trial there were less preens in the F situation than in the NH/NF situation ($t = 4.43$: $p < 0.01$) and this was also true in the third trial but the difference did not reach statistical significance ($t = 2.18$: $0.05 < p < 0.1$). There were many more stereotyped movements in the F than in the NH/NF situation ($p < 0.001$) and there were also more in the second than first trial ($p < 0.05$) and third than second trial ($p < 0.05$).

It could be argued that preening and stereotyped movements were two of a very limited number of responses available to the bird. If this were the case, in the time available, the bird might be able to execute one of these behaviour patterns only at the expense of the other. To test this theory the correlation coefficient was calculated for the number of preens and number of stereotyped movements ($n = 96$). If these activities were simply varying inversely they should show a high negative correlation. In fact the correlation coefficient was negative but small ($r = -0.18$: $0.05 < p < 0.1$) thus answering the argument.

Discussion

The results of this experiment suggest that displacement preening occurred when the hens were thwarted after 6 hours food deprivation and stereotyped movements occurred after 24 hours food deprivation. It is possible that the occurrence of stereotyped movements inhibited displacement preening in the latter

Figure 3.1. The mean numbers of preens (± S.E.) occurring during frustrated feeding after two levels of deprivation. The mean numbers of stereotyped movements are entered above the corresponding columns for preening.



6 HOUR DEPRIVATION
0·6
4·7
1·4
3·2
0·7
4·4
NO. OF PREENS IN 20MINUTES
35
30
25
20
15
10
5
1
2
3
TRIALS
CONTROL
FRUSTRATE
24 HOUR DEPRIVATION
0·1
9·6
0·5
31·7
2·0
41·7
NO. OF PREENS IN 20MINUTES
35
30
25
20
15
10
5
1
2
3
TRIALS

Figure 6. The mean number of preens and litter-pecks (± S.E.) occurring during frustrated incubation.

Figure 7.1. The mean number of preens and litter-pecks (± S.E.) occurring during frustrated incubation.

litter-pecks are shown in Figure 6 and Table 6.3A and an Analysis of Variance of these results is given in Table 6.4A. Litter-pecking showed the same pattern as preening with far more occurring in the two frustrating situations than the control situation. However, it was more variable than preening and this probably accounts for the lower level of statistical significance ($p \angle 0.05$).

An interesting feature of this experiment was that in the FI situation, 90% of the preening occurred close to one or other of the ends of the pen. This meant that bouts of attempted entry into the nest alternated with bouts of preening at the far ends of the pen. Litter-pecking usually occurred while the birds were moving away from the nest and between bouts of preening. The subjective impression was that during the bouts of attempted entry the hens became very aroused or excited and during the bouts of preening the hens calmed down again.

One of the short-comings of this experiment was the lack of a satisfactory control period. Just as, in the H/F situation in Experiment22, the act of feeding masked other behaviour patterns so, in the control situation in this experiment, the act of incubation had the same effect. For this reason 6 of the birds were tested again (M/Y died) 3 months later when they were in a non-broody condition. In the intervening period they had been used in Experiment 8 and then kept together in a deep-litter pen where they had all lost their broodiness and started to lay again. Each hen was placed under the same cage in the same pen as it had been tested in before. Each nest contained 8 eggs which had been hard-boiled to prevent them breaking. The hens were left under the cages for 24 hours with the food trough out of reach at one end of the pen but with water available. They were tested by raising each cage and allowing the bird to feed and then taking observations for 20min. after feeding finished. This procedure was repeated twice and the numbers of preens and litter-pecks which occurred in the observation periods are shown in Tables 6.1 and 6.2 respectively. It should be stressed that this is not a proper control for Experiment 6 but it does give some idea of what the birds do in this situation when incubation is not masking other behaviour patterns. It can be seen that preening occurred very infrequently and that which did occur appeared to be normal preening (i.e. it was not frantic or hurried). Also the 3 birds which preened, did so while standing in the middle part of the pen. This is further evidence that the preening which occurred in the two frustrating situations was displacement preening and a response to the thwarting. It also suggests that there may be some significance in the fact that the birds preened at the ends of the pen in the FI situation.

On the other hand the non-broody birds litter-pecked on average 197± 15.3 times in the 20min. observation periods, which is considerably more than they did when broody. Also there was no noticeable difference in execution of the litter-pecking in the two situations.

Discussion

Displacement preening was once again a prevalent response to thwarting. It was accompanied by a lot of litter-pecking which could also have been a displacement activity, although this seems unlikely for two reasons; (1) the

Table 6.1. The number of preens occurring in 20min. when the birds from Experiment 6 were tested in a non-broody condition.

	Birds					
	P/Y	G	B/G	M/R	Y	G/Y
Test 1	0	0	20	0	0	5
Test 2	0	8	0	0	0	0

Table 6.2. The number of litter-pecks occurring in 20min. when the birds from Experiment 6 were tested in a non-broody condition.

	Birds					
	P/Y	G	B/G	M/R	Y	G/Y
Test 1	276	197	82	187	241	129
Test 2	262	188	188	213	240	164

birds litter-pecked more in a control situation when non-broody and (2) the litter-pecking was no different from its "normal" example.

The subjective impression that during attempted nest-entry the hens became very excited and during bouts of preening they calmed down again is interesting in the light of a suggestion by Chance (1962) that certain displacement activities may serve to "cut-off" disturbing stimuli and also in view of two recent papers by Wilz (1970 a and b) who investigated this subject experimentally. In a theoretical paper Chance examined some existing data on social encounters between rats (Grant, 1963), the courtship of the Blackheaded Gull (Tinbergen and Moynihan, 1952; Moynihan, 1953) and preening in nesting terns (van Iersel and Bol, 1958). He pointed out that many of the displacement activities in these situations involved postures in which the eyes were closed or the head averted thus serving to remove or "cut-off" the aggressive partner from the field of vision. He postulated that these displacement activities "bring about a sensory 'cut-off' and thus allow a predominant mood to wane so as to permit a change in the behaviour if this is appropriate". The advantage of this mechanism would be to lower flight or aggressive tendencies and enable a threatened animal to remain close to its partner or nest. However, when dealing with displacement preening in terns during a conflict between escape and incubation (van Iersel and Bol, 1958) Chance probably tried too hard to make the data fit his theory. He stated that "those forms of preening which provide clear 'cut-off' (breast and shoulder preening) do appear after conflict in which an escape tendency is present as would be expected if their function was to reduce the tendency for the bird to leave the nest unduly". In fact it would seem more probable that vent or inner-wing preening would provide a better 'cut-off' than breast or shoulder preening. Chance's argument that these low threshold elements are common in displacement preening because they provide a better 'cut-off' would therefore appear to be false. Nevertheless his ideas on the function of certain displacement activities probably deserve more attention than they have received in the past. More recently Wilz (1970 a and b) investigated dorsal pricking behaviour and displacement nest activities in the courtship of the male three-spined stickleback (Gasterosteus aculeatus L.) in terms of self-regulation of motivation. Normally when a ripe female stickleback enters a male's territory he leads her to the nest but occasionally, when in a relatively aggressive state, he reacts with dorsal pricking. This induces the female to stop following and the male then performs displacement nest activities, after which he generally leads the female to the nest. Wilz postulated that the performance of displacement nest activities functions to facilitate a switch from a highly aggressive state to a predominantly sexual one. He supported his theory with the evidence that if the performance of displacement nest activities was prevented the male did not switch from aggressive to sexual behaviour (as measured by the tendency to lead).

The examples given by Chance and Wilz all occurred in social situations and it is a big step from there to the non-social, artificial situation in the present experiment. Nevertheless it is possible that the displacement preening in this experiment did 'cut-off' the disturbing stimulus of the "unobtainable" eggs and allow the birds to calm down and attempt to approach them again. There was evidence from Wood-Gush and Guiton (1967) and from Experiment 2 that frustrating situations can be aversive and this was supported by the fact that in the FI situation in this experiment the birds moved away to the ends of the pen after attempted nest-entry and it was here that preening occurred.

An interesting feature of the results from the FO situation was the occurrence of dust-bathing. It is possible that this was an alternative displacement activity to preening. Bastock, Morris and Moynihan (1953) commented on the phenomenon of alternative displacement activities and the subject was discussed in the Review of the Literature (p. 10). Since dust-bathing did not occur in any of the other situations it was not possible to say whether the pattern was frantic or not. However, it was completely out of context with incubation behaviour. Movements of the feet in the nest during incubation were slow and deliberate while standing or crouching and settling movements while sitting were also very careful. On the other hand the dust-bathing movements were very vigorous indeed. In the FO situation it appeared that the birds were in a conflict between trying to approach the eggs and at the same time sit on the nest. This resulted in an ambivalent crouching posture, and it was this that seemed to develop into dust-bathing. Tinbergen (1952) mentioned the possibility of "postural facilitation" of displacement activities and it is possible that in the FO situation the crouching posture facilitated dust-bathing instead of preening. It is known that a high intensity illumination can stimulate dust-bathing (McFarland and Baher, 1968) but positive factors at the skin surface are probably important as well and no doubt preening and dust-bathing share some of these positive factors. It has already been argued that these positive factors were present (either continuously or through autonomic activity) in both the frustrating situations, since preening did occur.

Therefore it is possible that in the FO situation the ambivalent crouching position facilitated dust-bathing.

It is possible that a closer examination of the times spent by the birds in various parts of the pen in an FI situation may be instructive. With this in mind another experiment was conducted with incubating birds and more attention was paid to this feature.

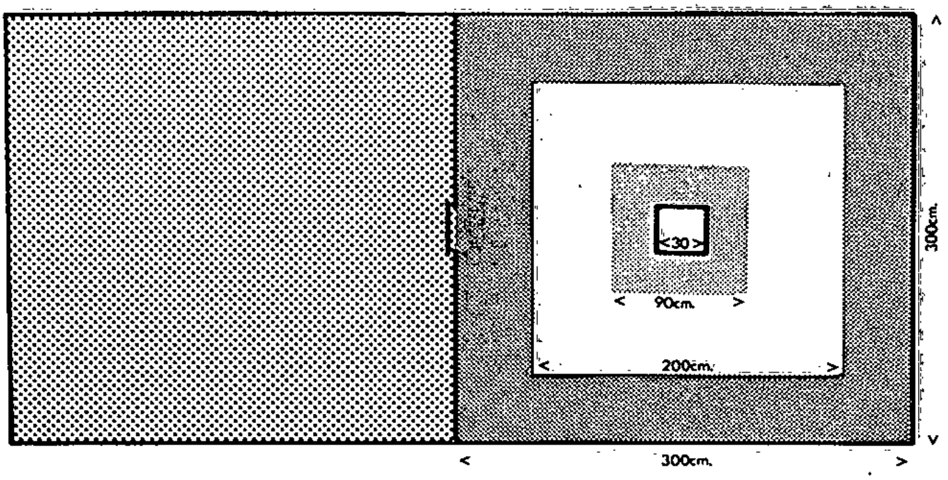
Experiment 7

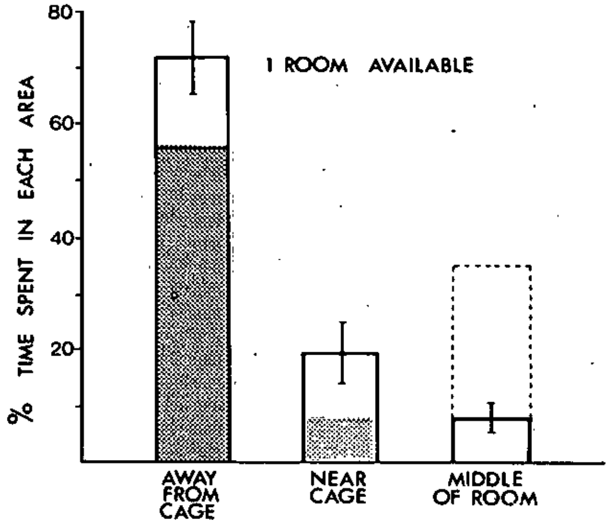
Material and Methods

Six broody hens of the same age and strain and from the same source as those in Experiment 6 were used in this experiment.

The same rooms were used as in Experiment 6 with the partitions removed and each hen was placed on 8 eggs in a nest under a cage in a separate room. Each hen therefore had twice the area compared to Experiment 6. In addition the area could be increased even more by opening a small door in one of the side walls and allowing the bird access to an adjoining room (Room II) equal in area to the room with the nest and the eggs (Room I). Room II, which could also be observed from the corridor through a one-way glass window, had a deep-litter floor but was otherwise empty. Room I was imagined to be divided into 3 areas; an area near the nest (Near), an area near the perimeter walls, away from the nest (Away) and the remaining area (Middle). The dimensions of the areas are shown in the plan of the two rooms in Figure 7.2. Judging the boundaries of the areas was aided by chalk marks on the walls and wires projecting from the top of the cage.

PLAN OF EXPERIMENTAL ROOMS





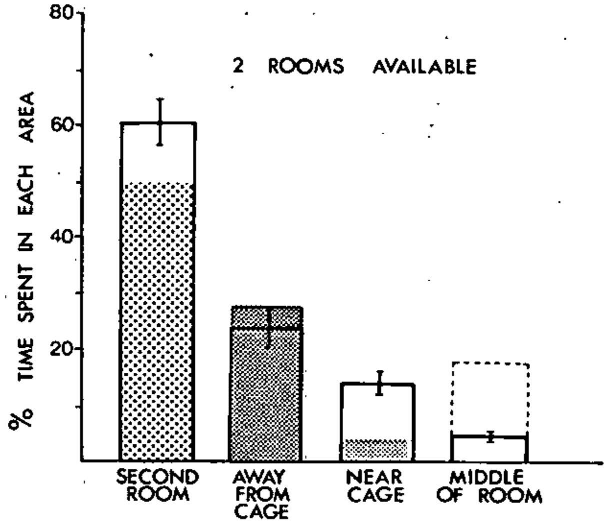


Figure 7.2. The mean percentage time spent in the various parts of the room(s) (± S.E.). The percentage area of each part is shown by the height of the shading in each column and, in the case of the "Middle" area, by the height of the dotted outline.

Training: The hens were trained for 3 days to come off their nests once a day for food as in Experiment 6. During this time the doors to Rooms II were open but none of the hens approached them.

Testing: Each hen was allowed off its nest once in the later part of each day and then subjected to one of the three testing situations:-

1. Control (C). The hen was allowed to feed and re-enter the nest. The cage was then lowered and the bird observed for 20min. The door to Room II was open during this time.

2. Frustrated/eggs inside cage/access to Room I only (F/I). While the hen was off the nest feeding the cage was lowered. The hen was then observed for 20min. starting from the moment she made her first attempt to re-enter the nest. The cage was then raised, the hen allowed to re-enter the nest and the cage lowered again. The door to Room II was closed during this time.

3. Frustrate/eggs inside cage/access to Rooms I and II (F/II). This was exactly the same as F/I but with the door to Room II open.

One trial consisted of exposing each hen to these three treatments in a randomized order on successive days. Two trials were conducted.

Observations: Similar records to those in Experiment 6 were kept. In addition the amount of time spent by each hen in the various areas was scored in the following way. The 20min. tests were divided into 15 second periods and at the end of each period, the area that the hen had spent most of that period in, was noted.

Results

In the control situations the hens showed the same nest-entry behaviour as they did in Experiment 6. They never entered Room II or for that matter even approached the door.

The behaviour shown in the two frustrating situations in many ways resembled that in the F/I situation in Experiment 6. Bouts of attempted nest-entry alternated with bouts of litter-pecking and displacement preening. The number of preens occurring during thwarted incubation are shown in Figure 7.1 (p. 132) and Table 7.1A and an Analysis of Variance of these results is given in Table 7.2A. It can be seen that far more preens occurred in both the frustrating situations than the control situation ($p < 0.001$).

The number of litter-pecks are shown in Figure 7.1 and Table 7.3A and an Analysis of Variance of these results are given in Table 7.4A. Once again litter-pecking was far more common in the frustrating situations than the control situation and was not so variable in this experiment with the result that the difference was highly significant ($p < 0.001$). The difference in the number of litter-pecks occurring in the F/I and F/II situations approached significance and was probably a real difference ($0.05 < p < 0.1$).

The amount of time spent in the various areas available is shown in Figure 7.2. If the hens had wandered about at random, the time spent in each of the available parts should have been proportional to the area of that part. A Null Hypothesis was adopted that there was no difference between the results obtained and what would be expected by the hens walking around at random. The Hypothesis was tested by carrying out a 't'-test to investigate the difference between the mean proportion of time spent in the various parts of the rooms and the proportion of area for the corresponding part. The results are shown in Table 7.1. The Null Hypothesis was rejected since the hens were obviously spending more time in the "Away" and less time in the "Middle" parts of the room in the F/I situation and more time in the "Near" and Room II and less time in the "Middle" parts in the F/II situation than they would if walking at random. These results are further evidence that the hens were actively avoiding the frustrating situation for part of the time and actively approaching it for part of the time.

It is perhaps surprising that the birds spent so much time in Room II in the F/II situation when they had no previous experience of this room at all. In fact all the birds entered Room II within the first 8min. of their first F/II test. This could have been a reflection of an active avoidance of the frustrating situation but on the other hand it could simply have been an indication of an active exploratory tendency. The differences between the two frustrating situations are interesting in that the total time spent away from the nest tended to be longer and the time spent near the nest tended to be shorter when the birds had access to Room II, although these differences did not reach statistical significance.

Once again most of the preening occurred away from the nest. In the F/I situation 91.3% of the preening occurred in the "Away" parts of the Room and in the F/II situation 78.1% occurred in Room II and 14.5% in the "Away" parts in Room I.

Discussion

The results of this experiment are very similar to those of Experiment 6. They provided further evidence that displacement preening is a common response

Table 7.1. The mean percentage of time spent in the various parts of the rooms compared to the percentage area of the corresponding part (n = 12).

Situation	Part of room	Mean % time ± S.E.	% area	t	p
F/I	Near	19.43 ± 5.54	8.10	1.94	n.s.
	Middle	7.73 ± 2.13	35.80	12.54	<0.001
	Away	72.84 ± 6.33	56.10	2.51	<0.05
F/II	Near	13.52 ± 2.06	4.02	4.38	<0.01
	Middle	2.73 ± 0.64	17.81	22.48	<0.001
	Away	23.20 ± 3.29	27.92	1.36	n.s.
	Room II	60.09 ± 3.84	50.25	2.44	<0.05

to this type of thwarting. Since the preening occurred after the birds had moved away from the nest and eggs and before they returned to them again it is possible that it was in some way allowing the birds to calm down or at least change from avoidance behaviour. It had been thought that displacement preening might have been functioning to 'cut-off' the disturbing stimulus of the "unobtainable" nest and eggs but this now seems unlikely since the birds performed an equal amount of displacement preening when, for a large part of the time, the nest and eggs were out of sight.

The fact that the birds tended to spend less time in the "Near" position and more in Room II and the "Away" position in the F/II compared to the F/I situation could be explained by saying that the visual stimulus of the nest and eggs was the main factor eliciting return to the "Near" position. There would therefore be a greater chance of the birds approaching the "Near" position in the F/I situation, where the likelihood of the nest and eggs being in the visual field was greater. In fact, this actually happened. There were an average 6.5 approaches to the nest and eggs in the F/I situation compared to 5.0 in the F/II situation.

The tendency for more litter-pecking to occur in the F/II than the F/I situation is probably a reflection of the increased time spent in positions away from the nest.

CHAPTER 5

THWARTING OF BROODING BEHAVIOUR

Introduction

The experimental work described in this chapter is a natural progression from that described in the last chapter. Hens brooding chicks were thwarted by separating them from the chicks and then preventing their access to them. The distress call of the chick is thought to be a very powerful stimulus eliciting approach in the broody hen and it was decided to make use of this fact to get a strong approach tendency. At the same time it was decided to investigate the classic experiment of Bruckner (1933) described and illustrated in "A Study of Instinct" by Tinbergen (1951). In this experiment a broody hen ignored a chick in obvious distress which she could see but not hear and ran to a chick which was distress-calling out of her sight.

Experiment 8

Material and Methods

The same 6 birds were used in this experiment as had been used in Experiment 6 (one bird, M/Y, had died in the interval). They were kept in the same pens, which occupied half of each room, as in Experiment 6. The birds had by this time been broody for about 4 weeks and had been sitting on eggs continuously (apart from the testing sessions of Experiment 6) for 3 weeks. The 8 eggs were removed from each hen and replaced by 6, day-old Brown Leghorn chicks. The cages were raised and the birds left to settle down for 48 hours, by which time all the birds had switched from incubating to brooding behaviour.

In each of the tests the stimulus eliciting approach was three chicks with small weights attached to their legs so that they could not move freely. When this was done they tended to struggle and give distress calls almost continuously. The birds were then subjected to each of the following testing situations in a random order on consecutive days:-

1. Visual and auditory contact (VAC). The three distressed chicks were placed under the cage in the centre of the room. The other chicks were then removed and the hen observed for 20min.

2. Auditory contact (AC). The three distressed chicks were placed in a cardboard box under the cage. The box had lots of air-holes punched in it and the distress calls sounded quite loud and normal to the human ear. The rest of the brood were removed and the hen observed for 20min.

3. Visual contact (VC). The three chicks were placed under a small bell-jar, under a larger bell-jar under the cage. This was not completely soundproof and the observer could hear some of the distress calls very faintly when he was close to the cage. Once again the other chicks were removed and the hen observed for 20min.

4. No contact (NC). This situation was exactly the same as the last one (VC) with a black cloth completely covering the outer bell-jar.

5. Together (T). The three distressed chicks were placed in the "Middle" part of the room outside the cage, the other chicks removed and the hen observed for 20min.

This last situation was meant to be a control situation but, as will be apparent later, it suffered from the same inadequacies as the control situations in Experiments 6 and 7. Since it was thus thought that "Control situation" would be a misnomer, it was given a different name.

Observations: The pen was imagined to be divided into 3 areas, "Near", "Middle" and "Away" as in Experiment 7. The dimensions of the various parts are shown on the plan of the pen in Figure 8.1 and the observer was helped to judge the boundaries of the parts by chalk marks on the walls and wires projecting from the cage. The amount of time spent in each of the parts was scored as in Experiment 7 but 12sec. intervals were used instead of 15sec. intervals. The number of preens were also counted.

Results

The general pattern of behaviour was similar to that in Experiments 6 and 7. When separated from the chicks the hens appeared much more agitated than normal. Bouts of attempted approach alternated with bouts of avoidance and displacement preening.

However, there were some very interesting differences between the treatments. In the T situation the broody hen quickly ran to the struggling chicks and brooded them. Occasionally she pecked at the weight but this never lasted and the chicks were soon out of sight under the feathers. The hen usually brooded the chicks at the place where they had been laid down and this behaviour often continued, broken only by small bouts of preening until the end of the observation period. This situation was therefore not a very good control situation since the act of brooding masked other behaviour patterns.

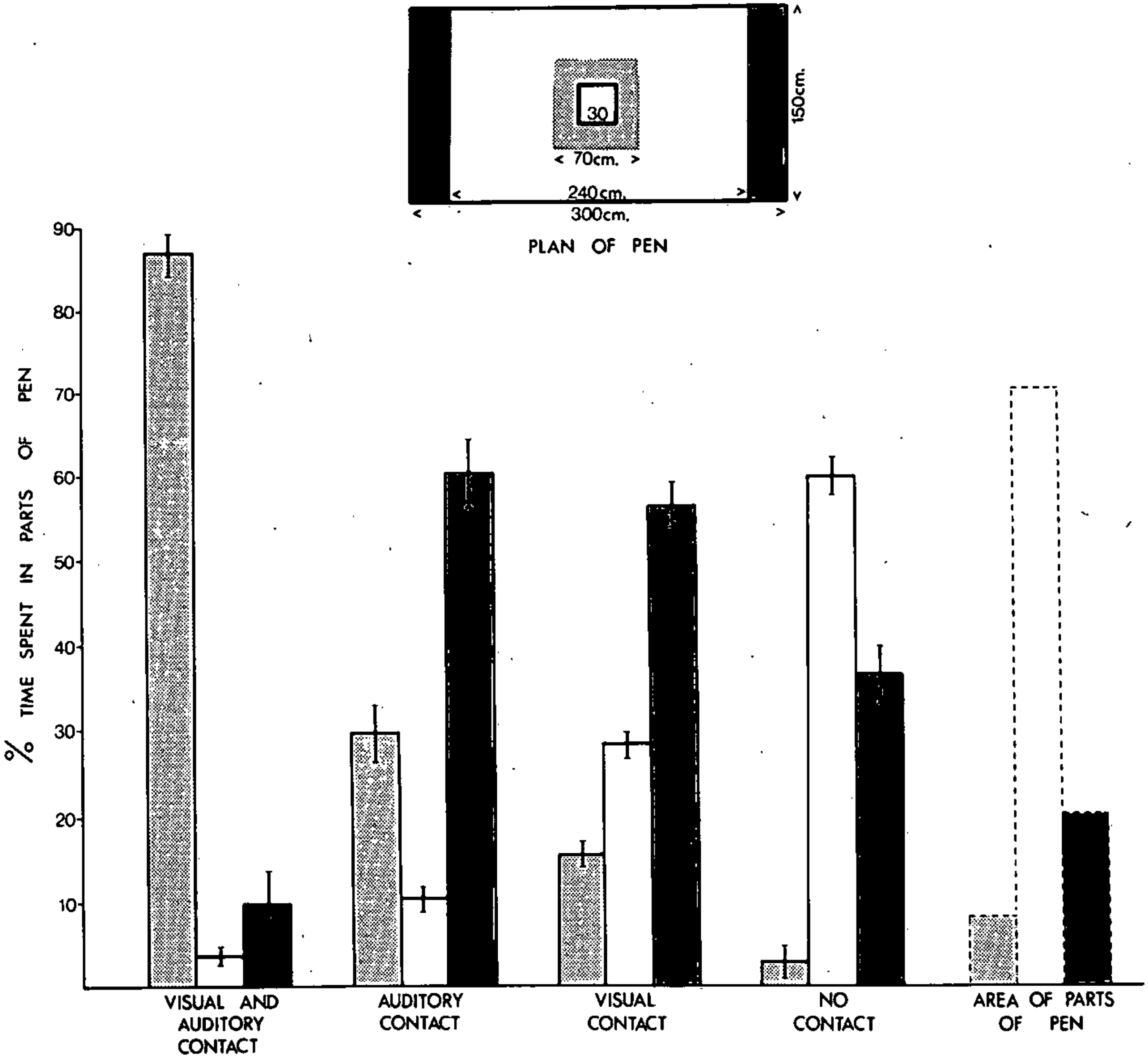

30
< 70cm. >
< 240cm. >
< 300cm. >
150cm.
PLAN OF PEN
% TIME SPENT IN PARTS OF PEN
90
80
70
60
50
40
30
20
10
VISUAL AND AUDITORY CONTACT
AUDITORY CONTACT
VISUAL CONTACT
NO CONTACT
AREA OF PARTS OF PEN

Figure 8.1. The mean percentage time spent in the various parts of the pen (± S.E.). The percentage area of each part is shown in the left-hand histogram with the dotted outline.

The time spent in the three parts of the pen in the other four situations are shown in Table 8.1A and also in Figure 8.1 along with the proportions of the areas of the parts of the pen. The most striking feature of this diagram is the large differences between most of the actual results and what would be expected by chance if the birds were walking round at random and also the differences between the situations themselves. A series of 't'-tests were carried out to test the statistical significance of these differences, and the results are shown in Tables 8.2A, 8.3A and 8.4A. These results may be summarized as follows. In comparison to what was expected by random walking about, the birds spent:-

(a) more time in the "Near" area except in the NC situation when they spent less time than expected;

(b) more time in the "Away" areas except in the VAC situation when they spent less time than expected;

(c) less time in the "Middle" area.

These results support the conclusions from Chapter 4 that a frustrating situation of this type is aversive and generates avoidance which tends to alternate with the original approach tendency. Let us suppose that the strength of the approach tendency is reflected by the amount of time spent in the "Near" area, and similarly, the strength of the avoidance tendency is reflected by the amount of time spent in the "Away" areas. Then if the situations are ranked in order of increasing approach tendency, to some extent, this is also the order of increasing avoidance tendency as shown in Table 8.1. It thus seems that an in-

Table 8.1. The four frustrating situations ranked in order of increasing approach tendency.

Situation	% time in "Near" area	% time in "Away" areas
No contact	4.0	36.5
Visual contact	15.3	56.2
Auditory contact	29.6	60.0
Visual and auditory contact	86.9	9.7

creased approach tendency leads to a more severe frustrating situation and increased avoidance. The exception to this pattern was the VAC situation and here it appeared that the sight and sound of the distressed chicks was such a powerful stimulus eliciting approach that the avoidance tendency was not fully expressed.

It should be noted here that the stimulus situation was not constant and the chicks reacted to the hens as well as the hens to the chicks. This was particularly so in the VAC situation where the chicks struggled and distress-called less if the hen remained close to the cage. As soon as she moved away the chicks increased their struggling and calling dramatically, and this attracted the hens back to the cage again.

The number of preens occurring in the 5 situations are given in Table 8.5A and Figure 8.2. A series of 't'-tests were carried out to test the statistical significance of differences between the situations and the results are shown in Table 8.6A. These results may be summarized by saying that more preening occurred in the NC situation than in the AC and (probably) the VC situations and more in either of those than in the VAC and T situations. It is interesting that when the situations are ranked in order of decreasing numbers of preens this is the same order, shown in Table 8.1, for increasing approach tendency. The relationship between amount of preening and strength of approach tendency was investigated further by calculating the correlation coefficient between number of preens and % time spent in the "Near" area for each bird in the 4 situations NC, VC, AC and VAC. The correlation coefficient (r) was equal to -0.78 ($p \angle 0.001$; n = 24). When the correlation coefficient was

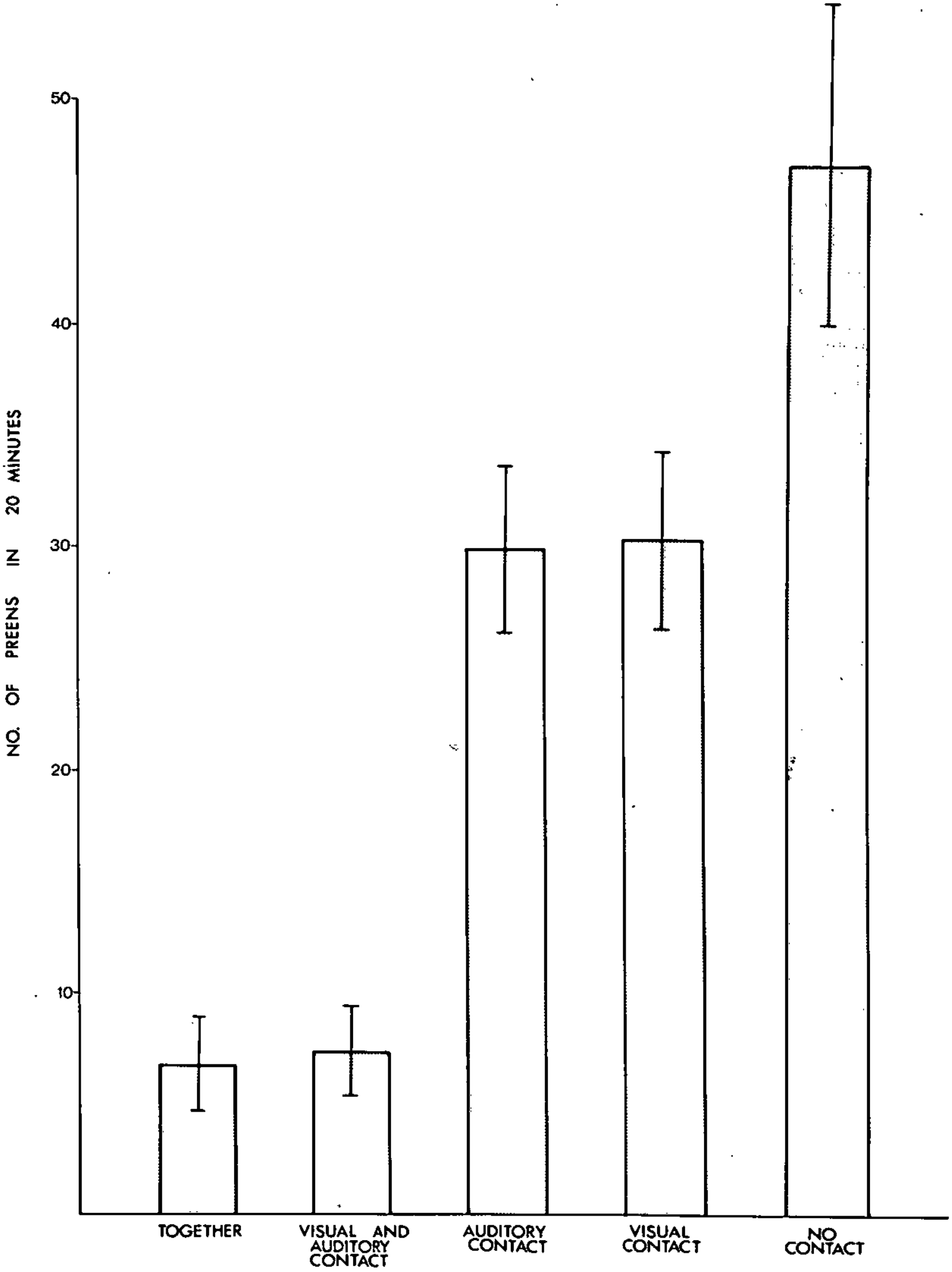

NO. OF PREENS IN 20 MINUTES
50
40
30
20
10
TOGETHER
VISUAL AND AUDITORY CONTACT
AUDITORY CONTACT
VISUAL CONTACT
NO CONTACT

Figure 8.2. The mean number of preens (± S.E.) occurring in the different situations during frustrated brooding.

calculated omitting the results from the VAC situation (which was perhaps atypical), it was still negative and fairly large ($r = -0.59$; $p < 0.01$; $n = 18$).

Most of the preening was once again frantic in appearance and also fairly noisy. The bill could often be heard clicking as it preened feathers with stiff shafts such as the primary and secondary wing feathers. As mentioned earlier the displacement preening generally occurred in bouts when the hens were at some distance from the cage. However, there were some interesting differences between the situations in this respect. In the VC, AC and VAC situations, 91.1%. 97.2% and 90.7% of the preening occurred in the "Away" areas, whereas in the NC situation the figure was only 49.1%.

Discussion

The results from this experiment are similar in many respects to those of Experiments 6 and 7. When the distressed chicks could be seen or heard in the cage there was a general pattern of approach accompanied by agitation or excitement followed by avoidance accompanied by displacement preening and calming down.

The results of Bruckner's (1933) experiment were not supported by the results from this experiment. The evidence was that the hen responded to both the sight and sound of distressed chicks. The sound however did seem to be the more powerful stimulus and the hen spent significantly longer near the cage when she could only hear the chicks compared to when she could only see them. Also the visual and auditory stimuli seemed to be additive in their effect on the hen. A possible explanation for Bruckners results could be that what he observed was the hen actively avoiding the chicks under the bell-jar. However a more probable explanation for the differences between the experiments is that the bell-jars were not completely sound-proof in Experiment 8 and a faint auditory cue was enough to draw the bird's attention to the visúal stimulus.

However, ignoring the implications that the results have on the perception of the broody hen, the experimental technique was useful because it introduced a variable into the experiment. It provided further evidence that a thwarting situation can elicit an avoidance tendency which may alternate with the original approach tendency. Moreover it suggested that the stronger the original approach tendency, as measured by the time spent near the cage, the stronger the avoidance tendency as measured by the time spent far away from the cage. If this was taken to its logical conclusion, then when the approach tendency was at its strongest, the avoidance tendency would also be at its strongest and the hen would spend x% of its time close to the cage, and (100-x)% of its time far away from it, and one would not be able to increase without the other decreasing. In fact this stable position was not reached and in the VAC situation the hens spent 87% of their time near the cage and reduced their time far away from it to only 10%. However, as mentioned earlier staying close to the cage in this situation was probably reinforced by a reduction in the chick's distress calling.

The fact that in the NC situation the hens divided their time among the areas as much as one would have expected if they had been wandering at random, strengthens the hypothesis that in the other situations they were reacting to the stimulus of the chicks with positive approach and avoidance. However, even in the NC situation they spent more time in the "Away" areas than would be expected by chance. This could be accounted for by postulating that in the complete absence of chicks they would search for the chicks in the pen and then try to widen their search by concentrating on the perimeter of the pen.

The relationship between the amount of displacement preening and the proportion of time spent close to the cage is interesting. It does not necessarily mean that there is a cause and effect connection between the two variables. However it could be argued that a strong approach tendency gives rise to a more aversive situation at the cage and this leads to a strong avoidance tendency and under these conditions displacement preening is less likely to appear. This would agree with the results from Experiment 3 where displacement preening was infrequent when the thwarting was severe, i.e. when the feeding tendency was strong, and common when the thwarting was mild, i.e. when the feeding tendency was weak. An alternative explanation of the negative correlation between amount of preening and time spent near the cage could be simply that since displacement preening practically never occurred when the birds were in the "Near" area, then the longer they stayed in this area, the less chance there was of preening occurring. However, it was unlikely that the explanation could be simple as this for the following reason. A similar argument could be developed that since most of the displacement preening occurred in the "Away" areas then the longer the birds spent in those areas the greater the likelihood of preening occurring. But when the correlation coefficient between number of preens and % time spent in the "Away" areas was calculated, it was found to be only +0.47 ($p \angle 0.02$; $n = 24$). Thus preening was more highly negatively correlated with % time spent in the "Near" part ($r = -0.78$), than it was positively correlated with time spent in the "Away" parts (r = +0.47). The amount of displacement preening shown, therefore, was not purely dependent on the amount of time spent in the "Away" parts so why was it inversely related to the time spent in the "Near" part, to such a high degree? It seems more probable that the former explanation, in terms of the strength of the thwarted tendency, is correct.

Finally to be discussed is the fact that in the 3 situations in which there was positive approach to and avoidance of the frustrating object, over 90% of the preening took place in the "Away" areas while in the situation in which this behaviour was absent, only 49% of the preening occurred in the "Away" areas. This suggests that in the former situations the displacement preening was closely connected to the avoidance tendency and was not simply occurring because the hen was in a specific area. In the latter situation where there was no focal point to approach and avoid, the preening occurred throughout the pen.

As mentioned before in the introduction to Chapter 4 the results from Chapters 4 and 5 are not strictly comparable to those from the rest of this thesis because a different breed of birds was used in these Chapters. In order to give the results more meaning some of the birds which had been broody were tested in a hunger thwarting situation similar to that used in Experiment 2. It should be stressed that this experiment was not designed as a comprehensive comparison of the behaviour of different breeds in a hunger thwarting situation.

Experiment 9

Materials and Methods

This experiment was carried out 5 months after the Brooding and Incubation experiments had finished. Only 4 of the hens had survived this time, R and Br from Experiment 7 and Y and G from Experiments 6 and 8, and they were used in this experiment. In the intervening period they had been kept for three months together in a deep-litter pen and for two months in individual battery cages.

The same testing cage was used and the birds were trained on a 24 hour deprivation schedule, as in Experiment 2. The criterion for ending testing (3 consecutive days on which the food intake of each bird varied by less than 15%) was reached after 10 days.

Two testing situations were used, Not hungry/no food (NH/NF) and Frustrated (F). These situations were the same as they had been in Experiment 2 and one trial consisted of exposing the birds to the two situations in a random order every other day. Five trials were conducted.

The birds behaviour was recorded as before with particular attention being paid to preening and stereotyped movements.

Results

There was an overall impression that these hens did not find the F situation as aversive as the Brown Leghorns had done in Experiment 2 for the hens in this experiment were only slightly more agitated or excited in the F situation compared to the NH/NF situation.

The numbers of stereotyped movements and preens occurring in the 30min. observation periods are given in Tables 9.1 and 9.2 respectively. These results were not subjected to statistical analysis because they obviously do not fall

Table 9.1. The number of stereotyped movements shown by broiler-type birds during frustrated feeding.

Trial	Situation	Birds			
		R	Br	Y	G
1.	NH/NF	0	4	0	0
	F	7	21	5	39
2.	NH/NF	0	1	1	3
	F	2	12	3	116
3.	NH/NF	15	7	0	48
	F	0	1	0	105
4.	NH/NF	0	1	0	10
	F	13	4	2	19
5.	NH/NF	0	2	1	5
	F	0	2	0	11

NH/NF = Not hungry/no food
F = Frustrated

Table 9.2. The number of preens showed by broiler-type birds during frustrated feeding.

Trial	Situation	Birds			
		R	Br	Y	G
1.	NH/NF	38	28	8	21
	F	52	10	15	0
2.	NH/NF	70	39	31	12
	F	82	85	49	0
3.	NH/NF	26	86	22	4
	F	101	90	130	13
4.	NH/NF	33	22	13	9
	F	61	61	40	78
5.	NH/NF	14	45	26	19
	F	82	77	53	49

NH/NF = Not hungry/no food
F = Frustrated

into a normal distribution. It can be seen that one bird (G) showed a lot of stereotyped behaviour in the first three F tests and in the third NH/NF test but after this the stereotyped movements decreased in frequency. The movements were very similar in form to those performed by the Brown Leghorns. They were pacing movements back and forward along the cage-door and were accompanied by circular head movements and the bird pressing its breast against the mesh as if trying to escape. These elements decreased as the frequency of the pacing movements themselves decreased in Trials 4 and 5. It is therefore probably a mistake to call the movements "stereotyped" since they did not at any time have the uniformity that they did in Experiment 2. The other three birds showed very little stereotyped behaviour. They preened a great deal in both situations but more so in the F situation. Bird G on the other hand showed very little preening in the first three trials. However, it increased its preening in the F situation in Trials 4 and 5 to a frequency similar to that of the other three birds. Although on certain occasions the preening in the F situation was frantic and typical of displacement preening, at other times it seemed little different from that which occurred in the NH/NF situation.

Discussion

In many ways the results from this experiment resembled the results obtained when Brown Leghorns were thwarted when trying to feed. Stereotyped pacing movements and preening, which was probably displacement preening, both occurred. However, only one bird (G) showed the stereotyped behaviour which was so characteristic of the Brown Leghorns in this situation and even this was not true stereotyped behaviour since it began to disappear by Trials 4 and 5. In this respect bird G was very similar to the birds used by Wood-Gush and Guiton (1967) in their thwarting experiment. The other birds showed an increase in preening in the F situation as the Brown Leghorns did in Experiment 3 when thwarted after 6 hours of food deprivation. In fact the bird which showed the stereotyped behaviour behaved very like the Brown Leghorns on a 6 hour deprivation schedule; it showed stereotyped pacing in the first few tests followed by increased preening in the later tests. In Experiment 3 the hens showed stereotyped pacing in the first test followed by increased preening.

It therefore appears that these broiler-type birds when thwarted after a 24 hour food deprivation, behaved as Brown Leghorns would have done after a 6 hour food deprivation. This may have been because they were larger birds and so a 24 hour period of food deprivation had less effect on them than on the smaller Brown Leghorns. Alternatively, it could be that they have a different temperament and require to be more severely frustrated than the Brown Leghorns to show the same responses. In any case the behaviour of the heavier birds during thwarting of the feeding tendency was similar enough to that of the Brown Leghorns to justify using the results from Experiments 6, 7 and 8 to help in the interpretation of other results.

CHAPTER 6

THWARTING OF SEXUAL BEHAVIOUR

Introduction

Coitus in the domestic fowl is preceded by various courtship displays which synchronize the sexual activities of the males and females. The cock typically takes the initiative in courtship and generally plays a much more active role than the hen (Guhl and Fischer, 1969). For this reason it was decided to thwart cocks rather than hens in the experiment to be described.

Experiment 10

Material and Methods

Six J-line Brown Leghorn cockerels aged between 9 and 11 months were used in this experiment. They had been reared in brooders and cold-cages in large, hetero-sexual groups until 8 weeks of age and then each was transferred to a large battery cage with 3 females of the same age. Three days before the start of training they were placed in individual battery cages out of sight of the group of three females, which were left in the original cages.

The experimental room, which had deep-litter on the floor, measured 3m^2 and had a one-way glass observation window. In the centre of the room was a circular cage, 1m in diameter and 60cm high constructed of 3cm mesh wire and having no floor. A food and water trough were put both inside the cage and outside near one wall. of the room.

Training: Each cock was released into the Experimental room for 20min. every day where he found the 3 females with which he had been reared. J-line Brown

Leghorn males tend to be nervous and take a long time to settle down in new surroundings. Training therefore continued for 9 days by which time all the cocks were courting and copulating with the hens almost immediately they were released into the room.

Testing: Three testing situations were used:-

1. Control (C). The cock was released in the room with no hens present and observed for 20min.

2. Sexual contact allowed (S). The cock was released in the room, which contained his 3 females, and observed for 20min.

3. Frustrated (F). This situation was the same as the S but the females were placed under the cage.

One trial consisted of exposing each cock to the three testing situations in a random order on consecutive days. Four trials were conducted.

Observations: The recording method was the same as in previous experiments. Particular attention was paid to any preening or stereotyped behaviour which occurred. The various courtship displays were also recorded; they included Waltzing, Tidbitting, Cornering, Wing-flapping, Feather-ruffling and Head-shaking and have all been described in detail by Wodd-Gush (1954b,1956). Mounts and copulations were also counted in the S situation.

Results

The cocks spent most of the time in the C situation standing in an alert posture looking round. They also occasionally fed, drank and pecked the litter- but these activities looked perfectly normal. In the S and F situations most of the time was occupied by courtship displays and feeding and drinking. In the S situation the cock also spent a little time actually copulating. The number of copulations varied between 3 and 8 per test and there was no sign of a decrease in sexual vigour during the course of the experiment.

Wing-flapping was the only courtship activity which showed an increased frequency in the F situation compared to the S situation, a wing-flap being defined as the series of movements between the raising of the wings and their final folding. The numbers of wing-flaps are shown in Table 10.1A and an Analysis of Variance of these results is given in Table 10.2A. The summarized results are shown in Table 10.1 and 10.2. It can be seen that almost twice as many wing-flaps occurred in the F situation as in the S situation.

Of the other courtship displays there was less waltzing, and the same amount of tidbitting, cornering, feather-ruffling and head-shaking in the frustration situation compared to when the hens were available. Very few of these displays occurred when the hens were absent.

The cocks spent most of their time in the F situation displaying round the perimeter of the cage. However, certain of the courtship activities took them away from the cage. For example, cornering involved the cocks running away from the hens to a corner of the room where they stamped their feet and lowered themselves to the ground. Also tidbitting was often performed at the food trough which was next to one of the walls of the room and some distance from the cage. However, as these movements away from the hens also occurred during courtship in the S situation and ended in copulation, they cannot be used as evidence of the cocks avoiding an aversive situation. The cocks did not

Table 10.1. Mean numbers of wing-flaps occurring during frustrated sexual behaviour (n = 6).

Trial	Control	Sexual contact	Frustrated
1	1.8	9.7	15.7
2	3.3	8.6	14.8
3	2.7	6.8	19.5
4	3.3	12.5	17.2

Table 10.2. Statistical analysis of treatment effects on number of wing-flaps. P - values.

Treatment	Mean no. of wing-flaps	Differences between treatments. P.
Frustration (n = 24)	Control 2.8 Sexual contact 9.4 Frustrated 16.8	< 0.01 < 0.001
Trials (n = 18)	1 9.0 2 8.9 3 9.7 4 11.0	n.s.

distribute their time spent in the available area in any other obvious pattern.

Casual observations of the hens during the tests suggested that they responded very little to the cocks during the F test. No hen ever crouched while under the cage. They did, however, approach the side of the cage nearest the cocks in response to tidbitting.

Discussion

The fact that no preening or stereotyped movements were shown by the cocks when thwarted in this experiment suggests that they probably behave quite differently from hens in this respect. Also since courtship consists of a much longer stimulus response chain than, say, a simple activity such as feeding, there is a much greater chance under natural conditions of a link in the chain breaking. When this happens it would be quite natural for the cock to initiate the chain of responses again? The situation that arises when the chain is broken artificially (as in this experiment) is therefore probably not very different from what might be expected in normal circumstances. For this reason the F situation was probably not so frustrating as might be expected. The fact that most of the courtship displays occurred at a similar frequency whether or not they were followed by copulation supports this argument. The lower frequency of waltzing in the F situation could mean that close contact with the hen is important in stimulating this response.

Wood-Gush (1956) reported very similar results to this experiment when he obstructed sexual behaviour in Brown Leghorn cocks. He found that most of the normal courtship displays were performed during thwarting including waltzing, wing-flapping, tidbitting, cornering, head-shaking and feather-ruffling but he did not compare their frequencies under normal courtship and thwarting conditions.

The most interesting feature of this experiment was the increased frequency of wing-flapping in the F situation. Wood-Gush (1956) suggested that wing-flapping was compromise behaviour between approach and avoidance. The increase during thwarting may be further evidence that frustration is aversive and generates avoidance which then conflicts with the approach tendency.

PART THREE

AN INVESTIGATION INTO SOME OF THE FACTORS GOVERNING THE RESPONSES TO THWARTING

Introduction

In accordance with Sears' (1941) suggestion, Part Three of this thesis examines some of the factors influencing the responses to thwarting. It is divided into two sections, A and B, dealing with internal and external factors respectively. Section A is concerned mainly with fear as a possible motivating factor for stereotyped movements. However, it also includes a chapter on two physiological parameters which may or may not affect the behavioural responses which occur during thwarting. Section B deals firstly with the effects of additional peripheral stimulation on displacement preening and secondly with the consequences of social stimulation during thwarting.

A Internal Factors

CHAPTER 7

AN INVESTIGATION OF THE CAUSATION OF STEREOTYPED MOVEMENTS

Introduction

It was mentioned in the discussion of Experiment 3 that there were certain discrepancies between the results of that experiment and the previous one which might be explained by differences which occurred in the training of the birds. It was thought that the length of training period, in particular, might be important in governing which responses occur following thwarting, and the next experiment to be described was designed to investigate this point.

Experiment 11

Material and Methods

Fifty-four J-line Brown Leghorn females aged between 10 and 12 months were used in this experiment. They were randomly divided into 9 groups of 6 birds and kept in individual home cages as in Experiment 2. The experimental method was the same as in Experiment 2 with the following exceptions:-

Each group was randomly assigned to one of the following treatments:

(i) 0 days training, 6 hours food deprivation.
(ii) 0 days training, 10 hours food deprivation.
(iii) 0 days training, 24 hours food deprivation.
(iv) 3 days training, 6 hours food deprivation.
(v) 3 days training, 10 hours food deprivation.
(vi) 3 days training, 24 hours food deprivation.
(vii) 10 days training, 6 hours food deprivation.
(viii) 10 days training, 10 hours food deprivation.
(ix) 10 days training, 24 hours food deprivation.

Training: The groups were trained according to the training schedule shown in Table 11.1. The 3 groups on 10 days training were trained and tested first, then the groups on the 3 days training and finally the groups on the 0 days training. The groups on 10 days training received all their training in the experimental cage and never had food in their home cages. The groups on 3 days training were put on their various food deprivation schedules for 7 days in their home cages and then had 3 days training in the experimental cage. The

Table 11.1. Training schedule used in Experiment 11.

Group	Time of deprivation	Time of start of 20min. training
24 hours deprivation	First bird at 0900h on day before training, others at 20min. intervals.	First bird at 0900h on first day of training, others at 20min. intervals.
10 hours deprivation	First bird at 0800h on first day of training, others at 20min. intervals.	First bird at 1800h on first day of training, others at 20min. intervals.
6 hours deprivation	First bird at 0800h on first day of training, others at 20min. intervals.	First bird at 1400h on first day of training, others at 20min. intervals.

groups on 0 days training were put on their various food deprivation schedules for 10 days in their home cages before testing in the experimental cage.

Testing: Two testing situations were used. The control situation was not hungry/no food (NH/NF) in which the hen was allowed access to food in the home cage for the 24 hours prior to testing. It was then placed in the experimental cage and observed for 20min. with no food or trough present. In the frustrated (F) situation, the deprived hen was placed in the experimental cage with food present under a perspex cover and observed for 20min. It was then fed after a variable delay as in Experiment 2. Each bird received two F tests then one NH/NF test on consecutive days.

Observations: The behaviour of the birds was recorded as before with particular attention being paid to preening and stereotyped movements.

Results

Displacement preening and stereotyped pacing movements were once again very common responses in the F situations. The displacement preening was very frantic and noisy and the pacing movements generally took place along the side of the cage with the door. The numbers of preens and stereotyped movements given by all the birds are shown in Tables 11.1A, 11.2A and 11.3A. For each of the activities and for each bird the two numbers from the first and second F test were averaged and then the figure from the NH/NF test was subtracted from this average. The group means (± S.E.) for the differences are shown in Figure 11.1. All the differences shown in this diagram are significantly different from zero apart from the figure for stereotyped movements in the 10 days trained/6 hours deprived group, which is not. 't'-tests were also carried out between certain of the groups to find out if the differences between them were statistically significant. Regarding stereotyped movements, the figure for the 10 days trained/10 hours deprived group is significantly greater than that for the 3 days trained/24 hours deprived group ($t = 7.19$: $p < 0.01$), but not significantly less than that for the 10 days trained/24 hours deprived group ($t = 1.25$: $p > 0.05$). With regard to preening the groups seemed to fall into 3 classes:

(i) Those groups which showed a large increase in preening in the F compared to the NH/NF tests. Included in this class are all the 0 days trained groups and all the 6 hours deprived groups.

(ii) The 3 days trained/10 hours deprived and 3 days trained/24 hours deprived groups which showed a moderate increase in preening in the F tests.

(iii) The 10 days trained/10 hours deprived and 10 days trained/24 hours deprived groups which showed a decrease in preening in the F compared to the NH/NF test.

The lowest figure in class (i) is significantly greater than the highest in class (ii) ($t = 2.91$: $p < 0.02$), and the lowest in class (ii) is significantly greater than the highest in class (iii) ($t = 10.96$: $p < 0.001$).

It can be seen looking at Figure 11.1 that 0 days training and 6 hours food deprivation both led to an increase in displacement preening. However, as each of these variables increased, the displacement preening became less and then stereotyped movements appeared and preening was actually depressed. It should

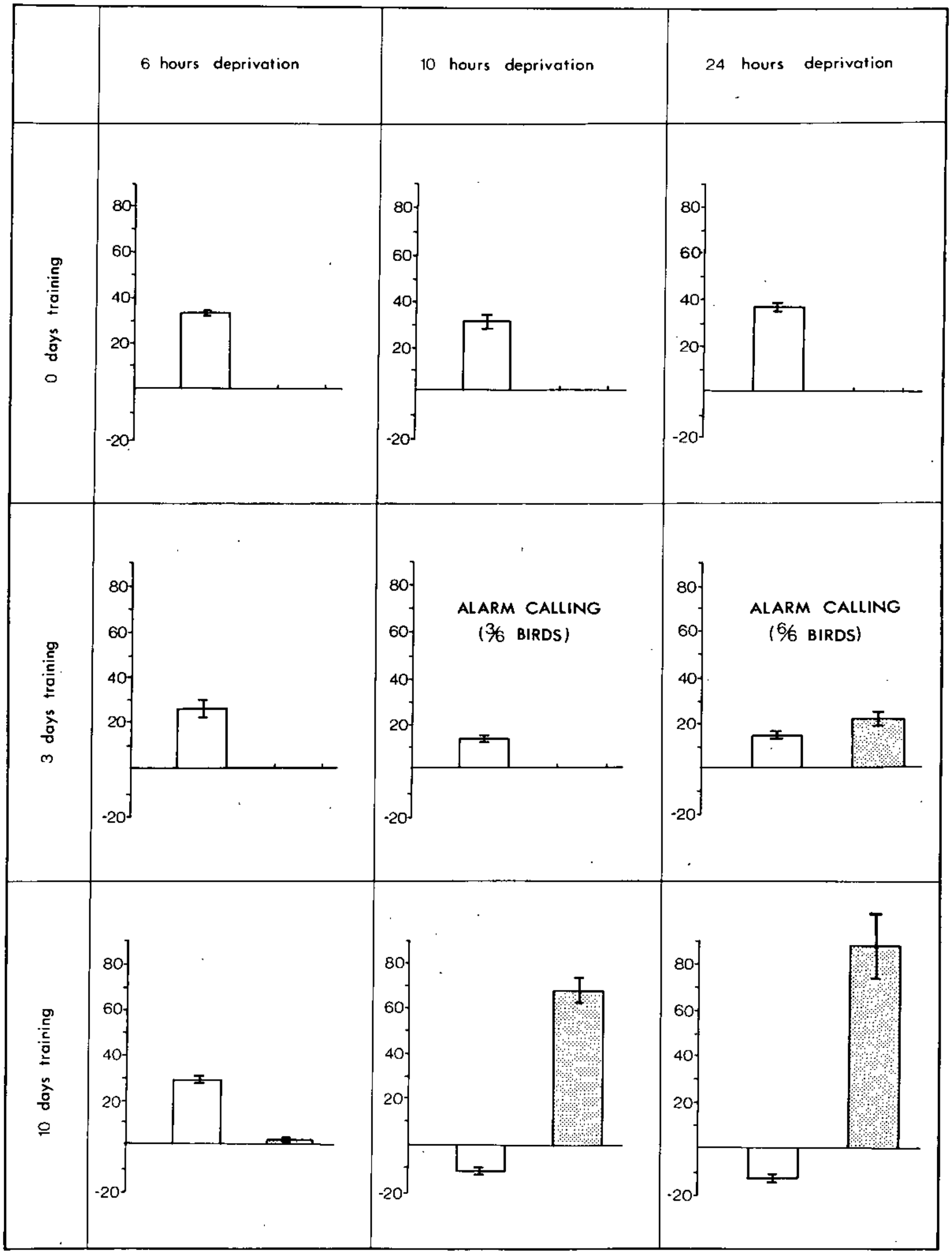

6 hours deprivation
10 hours deprivation
24 hours deprivation
0 days training
3 days training
10 days training
80
60
40
20
-20
ALARM CALLING (3/6 BIRDS)
ALARM CALLING (6/6 BIRDS)

Figure 11.1. The mean increase (or decrease) (± S.E.) in number of preens (white columns) and stereotyped movements (shaded columns) in a frustrating situation compared to a not hungry/no food situation after different lengths of food deprivation and training. An increase is shown by a column rising above the x-axis and a decrease by one falling below it.

be noted that in the 3 days trained/10 hours deprived group there was only a moderate increase in displacement preening and no stereotyped movements shown. This would suggest that it was not necessarily the performance of stereotyped movements which reduced displacement preening in the groups in classes (ii) and (iii).

One very interesting feature of this experiment was that in two of the intermediate groups where neither preening nor stereotyped movements were very frequent, alarm-calling occurred, and this is marked in Figure 11.1. The calling was high-intensity, ground-predator, alarm-calling (Collias and Joos, 1953) and 3 of the 6 birds called in the 3 days trained/10 hours deprived group and all 6 birds called in the 3 days trained/24 hours deprived group.

The two groups which had shown alarm-calling were tested again in the F situation on three consecutive days at the end of this experiment to see if alarm-calling was a common response under these particular conditions. In fact alarm-calling did not occur again and both groups started to show a large number of stereotyped movements and a depression of preening when thwarted.

Discussion

The part played by training in the motivating of responses has been well recognised by those psychologists who use the concept of "general drive". According to this theory, the sort of behaviour which appears depends on the total stimulation impinging on the animal, and on its previous experience in the situation. For example, Hull (1943, 1952) and Spence (1956) considered the excitatory potential (${}_{S}E_{R}$) to be the multiplicative function of drive (D) and habit (${}_{S}H_{R}$). In this formula "habit" was the major associative variable linking the response to the stimulus and was acquired gradually as a function of reinforced trials. Also, as mentioned earlier, (p24) Bindra (1959a) thought that the occurrence of every response was completely determined by four sets of factors, one of which was habit strength.

Ethologists, on the other hand, have, in the past largely ignored habit strength as a motivating factor. Because they have generally adopted "specific drive" theories of motivation, classical ethologists would no doubt account for training effects in terms of extinction of competing tendencies such as fear responses in the sort of situation used in these experiments.

In the present experiment increasing training appeared to have a similar effect to increasing food deprivation on the responses which occur during frustrated feeding. For example, when the birds had been trained for 3 or 10 days a progressive increase in food deprivation from 6 to 24 hours resulted in a decrease in displacement preening and an increase in stereotyped pacing movements. Similarly when the birds had been deprived for 10 or 24 hours a progressive increase in training from 0 to 10 days resulted in a decrease in preening and an increase in stereotyped pacing movements.

The great advantage that was gained in this experiment by having two variables to manipulate was a fine control over the strength of the thwarted tendency. Presumably the same results could have been obtained by holding training constant and varying the length of food deprivation. However, this becomes awkward when one wishes to deprive birds of food for a length of time of about between 12 and 24 hours when there is the complicating factor of a dark period to take into account.

The most interesting feature of this experiment is the fact that in two of the situations alarm-calling was elicited. This was the first time in any of the thwarting experiments that alarm-calling had been heard (except once in Experiment 2 when it was given in response to other birds alarm-calling). However, the two groups which called, were otherwise rather different in their response to thwarting. One response they both showed was a moderate increase in displacement preening in the F situations compared to the NH/NF situation. However, the 10 hours deprived group showed practically no stereotyped pacing whereas the 24 hour deprived group showed quite a lot. A closer examination of the data does not clarify the matter. Three birds, (P, P/P and P/Br) of the 10 hours deprived group called in the first F test and one of them (P/P) called again in the second F test. A common feature of these birds was that they showed less displacement preening in the tests in which they called than the other birds in the group. The tests in which calling occurred averaged 11.5 preens per test compared to 30.5 preens per test for the others. All 6 birds from the 24 hours deprived group called in the first F test and one of them Br/Y called again in the second. Once more there was a tendency for the tests in which birds called to have less displacement preening than those in which they did not (12.8 preens per test compared to 27.8 preens per test). This may have been because alarm-calling and preening are incompatible responses and so when a bird spent time calling there would be less time available for preening. However, it seems unlikely that this was the case because in the two groups the figures for preens per test both with and without calling were very similar and yet the 24 hour deprived group in addition performed on average 23.4 stereotyped movements in tests in which calling occurred and 31.0 movements in tests in which it did not. It seems more probable that these two groups of hens were in a state intermediate between that which gives rise to displacement preening and that which leads to escape and stereotyped movements. Moreover the alarm-calling suggests that this state was in some way frightening or distressing. Since in later thwarting tests the birds showed no alarm-calling but a high frequency of stereotyped pacing then either stereotyped pacing is an index of greater fear or distress or the performance of stereotyped pacing helps to reduce the level of distress or fear or anxiety.

This was the first time that stereotyped movements could be linked to a state of fear or distress. In all the previous experiments although it was shown that stereotyped pacing was probably derived from escape or avoidance movements, this did not necessarily imply fear. A human analogy is that certain stimuli, such as bad smells, may produce avoidance behaviour without in any way producing fear.

If, in fact, the stereotyped pacing movements are motivated by fear or distress it should be possible to reduce their incidence by means of drugs. There are two types of drugs which could be useful in this respect, (a) a central nervous system depressant such as a barbiturate which would produce lethargy, sedation or sleep depending on the dose and (b) a tranquillizing agent which would relieve anxiety.

The next experiment to be described is a short pilot experiment which examined the effects of one barbiturate and two tranquillizers on stereotyped movements. It was hoped that this would help selection of one drug for more detailed studies.

Experiment 12

Material and Methods

The four hens from Experiment 2 were used in this experiment. In the former experiment they had been thwarted 16 times after a 24 hour period of food deprivation and had all shown a large number of stereotyped pacing movements. They had been placed in their home cages with *ad libitum* food for 4 months and tested again. After this interval they were still performing stereotyped movements at a high rate. The present experiment started 2 weeks after the tests described above.

The drugs used in this experiment were Nembutal, Oblivon-C and Pacitran. Nembutal (Abbott) is a solution of pentobarbitone sodium (60mg/ml) and therefore an intermediate-acting barbiturate and a central nervous system depressant. Pacitran (Ciba) is a solution of methyl 18-epi-O-methylreserpate hydrochloride (5mg/ml). It is a derivative of Reserpine and therefore a tranquillizer of the Rauwolfia alkaloid type. Oblivon-C (British Schering) is 3-carbamoyloxy-3-methylpent-1-yne in tablet form, each tablet containing 10mg. It is a derivative of methyl pentynol with short lasting hypnotic and anxiety-reducing effects.

Since little is known about the effects of these drugs on chickens the choice of dosage was arbitrary. Some preliminary observations had shown a dose-level with each of the drugs which resulted in slightly less reaction to handling and to strange visual and auditory stimuli which normally result in alarm responses. These doses were administrated as follows. Nembutal was injected intra-muscularly at the rate of 20mg per kg body weight 30min. before testing. This is about two-thirds of the dose required for full anaesthesia when given intra-venously. The hens showed occasional signs of slight ataxia on this dosage. The Pacitran was injected intra-muscularly at the rate of 1mg per kg body weight 2 hours before testing. Oblivon was given orally at the rate of 20mg per kg body weight 2 hours before testing. As a control 1ml of saline was injected intra-muscularly 1 hour before testing.

Training: These birds of course were well trained to the situation and they were only given 3 days training mainly to accustom them to the 24 hour food deprivation schedule again.

Testing: Eight testing situations were used as shown below:-

	Nembutal	Oblivon	Pacitran	saline
NH/NF	1	2	3	4
F	5	6	7	8

Each hen was exposed to each of these eight test conditions in a randomized order every third day. It was hoped that this spacing of the tests would reduce the probability of the drugs exerting residual effects. On days when tests did not take place the birds were given training sessions in the experimental cage. The numbers of stereotyped pacing movements were counted.

Results

The number of stereotyped pacing movements that occurred during frustrated feeding are shown in Table 12.1A and an Analysis of Variance of these results is shown in Table 12.2A. The drug effects on this behaviour pattern are given in summarized form in Table 12.1. None of the drugs used eliminated the stereo-

Table 12.1. Statistical analysis of drug effects on stereotyped movements.

Treatment	Mean no. of stereotyped movements		Differences between treatments. P.
Drugs	Saline	48.2	p ∠0.01
(n = 24)	Oblivon	29.0	
	Nembutal	* 28.5	* p ∠0.001
	Pacitran	11.8	p ∠0.05

typed pacing movements shown in the F situation. The birds in fact showed the to-and-fro pacing even when ataxic after the fairly large dose of Nembutal. However all the drugs, and in particular the Pacitran, did reduce the frequency of the movements significantly. Apart from this reduction in stereotyped movements there were no other, very obvious, behavioural changes.

It was decided to repeat the experiment using a larger number of birds, keeping a more detailed record of the behaviour shown and using only the drug Pacitran.

Experiment 13

Material and Methods

Eight experimentally naive hens aged between 8 and 9 months and of similar breed and strain to those in Experiment 12 were used. They were put on a 24 hour food deprivation schedule and fed every day for 20min. in the experimental cage for 16 days to ensure that they would all exhibit stereotyped movements. They were then frustrated and fed on alternate days for 20min. on each day for a total of 30 days. Each bird was then tested four times in the F situation, twice after an injection of Pacitran and twice after an injection of 1ml of saline. Both injections were given intra-muscularly 2 hours before the test, the Pacitran at the rate of 1mg per kg body weight as in Experiment 12. The F tests were carried out every third day and on any one day 4 birds received the drug and 4 the saline. On the days between tests the birds had a 20min. training period in the experimental cage.

The F tests lasted 20min. and a record was kept as before of the behaviour patterns which occurred. Particular attention was paid to preening, stereotyped movements and also bouts of thwarted pecking to the perspex cover as it was thought that this might have reflected changes in the tendency to feed. A bout of thwarted pecking was judged to have ended when the bird withdrew its head from the hole in the side of the cage after pecking the perspex.

Results

The numbers of stereotyped movements, preens and bouts of thwarted pecking are given in Table 13.1A and an Analysis of Variance of these results in Table 13.2A. The summarized results for these three activities are shown in Figure 13.1.

It can be seen that the administration of Pacitran significantly decreased stereotyped movements from an average of 218.5 to 125.4 per test (p ∠0.05). Also preening was increased significantly from 3.2 to 15.2 preens per test (p ∠0.001) when the birds were tranquillized. Some of this increased preening was frantic and noisy and clearly displacement preening, but the rest appeared to be fairly normal. The birds had on average 17.6 thwarted feeding bouts per test when under the influence of Pacitran compared to 20.6 bouts after saline injection; the difference was not significant. There were no other obvious changes in behaviour patterns.

Discussion

Although the tranquillizing drug, Pacitran, reduced the incidence of stereotyped pacing, the birds still performed the movement at a high rate. In fact the drug seemed to have less effect in this experiment than the last one. However, the overall level of stereotyped movements was much higher in this

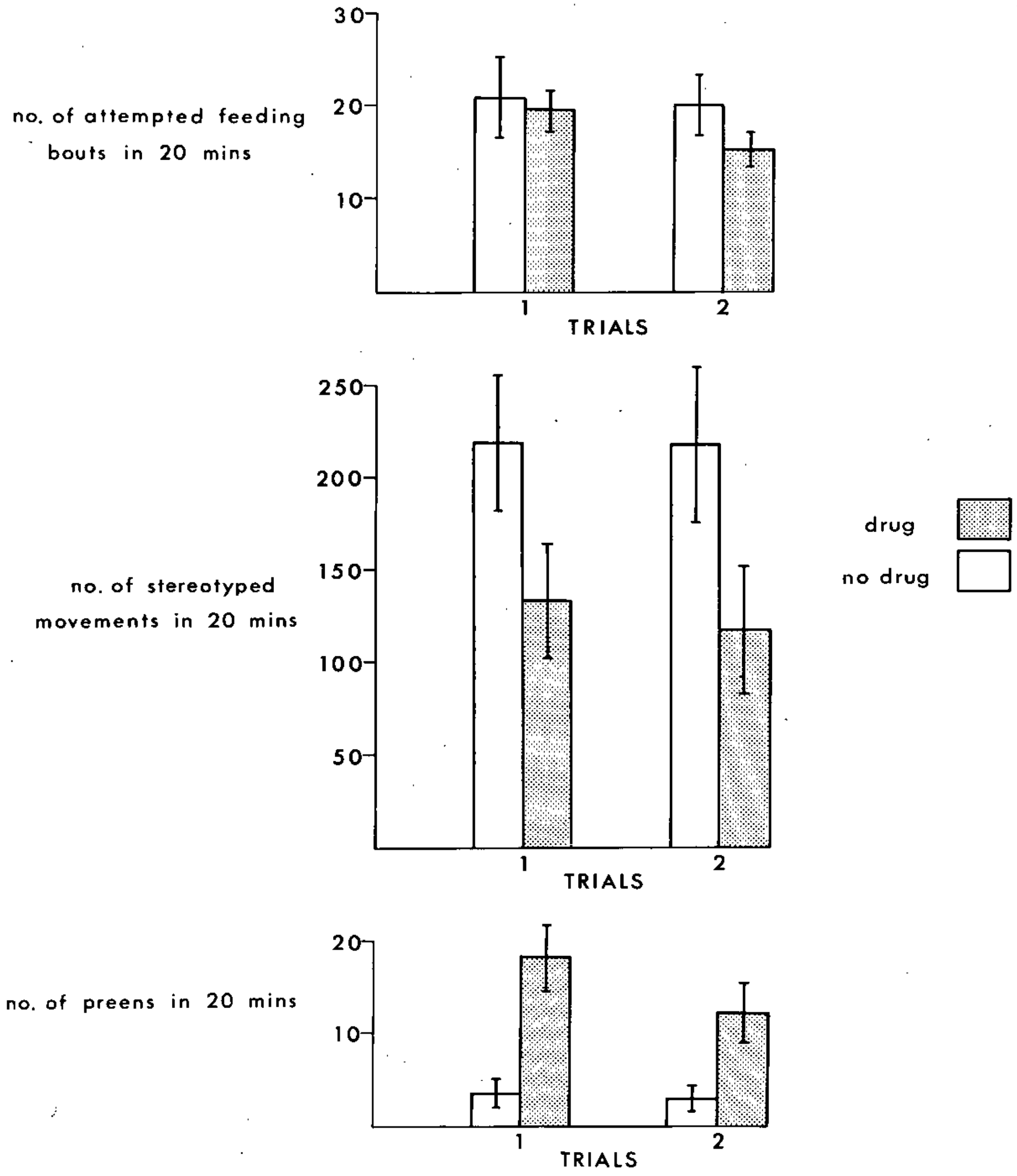

30
20
10
no. of attempted feeding bouts in 20 mins
1
2
TRIALS
250
200
150
100
50
no. of stereotyped movements in 20 mins
1
2
TRIALS
drug
no drug
20
10
no. of preens in 20 mins
1
2
TRIALS

Figure 13.1. Numbers of attempted feeding bouts, stereotyped movements and preens occurring during frustrated feeding after injections of saline or Pacitran.

experiment and it may be that under these conditions the drug is less efficacious. There were several differences in procedure which could explain the higher frequency of pacing movements in this experiment compared to Experiment 12, such as the long training period and lack of a NH/NF situation in the present experiment.

The failure of the Pacitran in this experiment or any of the drugs in the previous experiment to eliminate the pacing movements casts doubt on the theory that they are directly motivated by fear or distress.

There have been no carefully controlled behavioural studies on the effects of Pacitran on the chicken. However, in two studies it was reported that when drinking water was replaced by a 0.015% solution of Pacitran for about 4 hours, pullets were docile, non-excitable and easier to catch and handle than controls (Belloff and Hsu, 1963; Champion, Zindel, Ringer and Wolford, 1966). Pacitran does therefore exert a tranquillizing effect on the fowl. The drug reserpine (of which Pacitran is a derivative) has also been shown to increase the resistance of birds to heat-stress (Burger, Van Matre and Lorenz, 1957; Weiss, 1960) and it has been suggested that the drug exerts this effect through its action on the sympathetic nervous system (Burger and Lorenz, 1960) or adrenocortical tissue (Newcomer, 1962).

There is the possibility, mentioned earlier (p 106) that at first the back and forward movements were attempts to escape and perhaps at this early stage they were motivated by fear or distress. It should be possible to test this theory by giving the tranquillizer before the first F test and in fact this was done in the next experiment.

The increased preening that was observed when the birds were tranquillized in the present experiment may have been a displacement activity. Some of it undoubtedly was, since it was frantic and noisy, but the rest may have occurred simply because there was less pacing and therefore more time available.

There were fewer thwarted feeding bouts when the birds were drugged and, although the difference was not significant, the effect of Pacitran on the feeding tendency should be examined more carefully in case it acts directly on hunger.

Experiment 14

Material and Methods

Twelve experimentally naive hens of similar age, breed and strain to those in Experiment 13 were used. They were put on a 24 hour food deprivation schedule and were trained for 16 days to feed in the experimental cage. They were then divided randomly into two groups of 6 birds, a drug group which received 1mg Pacitran per kg body weight, and a control group which received 1ml saline. The injections were given intramuscularly 2 hours before each frustrating (F) test.

On Day 1 of the experiment all the birds were subjected in turn to 20min. in the (F) situation; the order of testing was such that the birds receiving Pacitran alternated with the birds receiving saline. On Day 2 all had a 20min. training session, and testing and training days alternated thereafter. On Day 21 the injections of Pacitran were changed to saline and the experiment continued with F tests every other day and training sessions on the days between until Day 37 when the experiment ended.

Observations were made on Days 7, 17, 27 and 37. The behaviour of the birds was recorded as before with a careful note being taken of stereotyped movements and preening.

Results

The numbers of stereotyped movements and preens are given in Table 14.1. It can be seen that the birds receiving saline showed a high frequency of stereotyped pacing movements and a low frequency of preening throughout the experiment. On the other hand the to-and-fro movements were almost entirely absent from the tests of the tranquillized birds up to Day 17. These birds also preened at a fairly high rate and the preening was generally hurried and noisy, typical of displacement preening. However, by Day 27, six days after the Pacitran had been replaced by saline, one bird (B/Y) was performing a lot of back and forward movements and another bird (B/B) a moderately high number. On Day 37 five birds were showing a high frequency of stereotyped movements and a low frequency of preening while the sixth bird (B/O) was not pacing at all and was preening at a fairly high rate.

Discussion

This experiment provided conclusive evidence that Pacitran could prevent the onset of stereotyped pacing if given before the start of the first thwarting test. The fact that most of the birds started to show a high frequency of to-and-fro pacing when injections of the drug ceased, is evidence that it was only exerting a temporary effect while being injected. In the tranquillized state the birds behaved as they did in Experiment 3 when thwarted after a 6 hour food deprivation, that is, they showed few stereotyped movements and a lot of

Table 14.1. The numbers of stereotyped movements and preens occurring during frustrated feeding when Pacitran was given from Day 1 to Day 19.

		Day 7		Day 17		Day 27		Day 37	
		s.m.	pr.	s.m.	pr.	s.m.	pr.	s.m.	pr.
Birds receiving saline	W/R	25	16	200	16	186	0	227	0
	W/P	13	12	89	21	92	9	125	0
	W/O	30	12	186	0	150	7	218	0
	W/G	51	8	163	0	141	20	158	11
	W/W	54	9	129	6	89	10	76	8
	W/M	35	10	116	10	113	11	106	5
Means		34.7	11.2	147.2	8.9	128.5	9.5	151.7	4.0
Birds receiving Pacitran	B/R	0	20	2	19	4	8	135	13
	B/B	0	37	6	73	90	7	199	3
	B/G	0	18	0	38	21	68	97	5
	B/M	0	29	0	33	0	107	55	21
	B/O	0	47	0	45	0	107	0	68
	B/Y	9	25	0	46	159	6	233	0
Means		1.5	29.3	1.3	42.3	45.7	50.5	119.9	18.3

s.m. = stereotyped movements

pr. = preens

displacement preening. This could be interpreted in two ways; either (a) the Pacitran reduced the original feeding tendency to equal a 6 hour deprivation, or (b) the Pacitran reduced the escape or avoidance tendency while the feeding tendency remained high.

The first interpretation can be easily tested by measuring the effect of Pacitran on hunger motivation and this was done in Experiment 15.

The second interpretation is supported by the evidence mentioned in the Review of the Literature (p 64), that reserpine can reduce fear of aversive stimuli and lower avoidance (Sidman, 1956; Wenzel, 1959; Feldman and Liberson, 1960). Also the results from this experiment are remarkably similar to those of Feldman (1962) who found that chlordiazepoxide (C.D.P.) greatly reduced the number of rats which formed fixations when placed in an insoluble problem situation if given before the responses became fixated but had no beneficial effect if given after they had been established. Feldman and Green (1967) interpreted these results by saying that when given from the start of the insoluble phase, C.D.P. caused an overall decrease in avoidance components and, therefore, led to less frustration and so less fixated behaviour. In addition they stated that if C.D.P. has fear reducing qualities, the findings that once fixations are established they cannot be eliminated by it, fails to support the hypothesis that fixated behaviour is maintained by self-generating fear reduction.

Exactly the same conclusions must be drawn from the results of the present experiment. The evidence is that Pacitran reduces fear of aversive stimuli and it prevented stereotyped movements appearing when given from the start of testing, therefore, these movements were probably motivated by fear at this time. However, once the movements were established, the drug was only moderately effective in reducing their frequency, therefore, something other than fear must have been the motivating factor at this later stage.

Before accepting the above conclusions, the effect of Pacitran on the motivation of feeding should be tested and this was done in the next experiment.

Experiment 15

There are several ways of measuring the feeding tendency (see for example, Wood-Gush and Gower, 1968) and it was decided to follow Miller's (1956) suggestion to use more than one method. The following three measurements were recorded after 24 hours of food deprivation and after injections of saline or Pacitran; (a) the amount of food consumed, (b) the rate of key-pecking in an operant situation and (c) the rate of back and forward pacing movements when this was involved in an operant response. It was thought that this last measurement would assess the effect of the drug on the birds' motor co-ordination in addition to its feeding tendency. All these measurements were made over a 20min. period since this was the length of the thwarting test.

Material and Methods

The hens used in this experiment were all experimentally naive and of similar age, breed and strain to those used in Experiment 14. Six birds were used to test the effects of Pacitran on food consumption. They were put on a 24 hour food deprivation schedule and trained to feed in the experimental cage for 20min. every day for 12 days. The hens were then injected intra-muscularly with either 1ml of saline or 1ml per kg of Pacitran 2 hours before testing.

These two treatments were given in a random order on successive days and the procedure was repeated 6 times. The weight of food consumed in the 20min. test period was recorded.

Another 6 birds were trained to peck for food in a Skinner box, on a variable interval schedule of reinforcement (Ferster and Skinner, 1957). The mean interval was 60 seconds, and the intervals ranged from 0 to 120 seconds in steps of 10 seconds. The reinforcement was access to food for 5 seconds. The birds were deprived of food for 24 hours and then put in the Skinner box on this schedule for 1 hour on 12 successive days. They were given free access to food for 15min. after being removed from the Skinner box. After this training period the hens were injected with either saline or Pacitran 2 hours before testing as before. The 2 treatments were given in a random order on successive days and the procedure was repeated 3 times. During testing the hens were left in the Skinner box for only 20min. They were then removed and given free access to food for 20min. The average rate of responding during each 20min. test was recorded.

Finally, 8 birds were trained to peck for food in a Skinner box on a fixed ratio schedule of reinforcement (Ferster and Skinner, 1957). The ratio was 5 responses to 1 reinforcement of 8 seconds. The Skinner box panel was then placed at one end of the original experimental cage and the key at which the birds pecked was shifted by a small step each day towards the other end. During this time each bird was put on a 24 hour food deprivation schedule and had daily sessions in the cage lasting 1 hour. The hens were given free access to food for 15min. after being removed from the cage. After 1 week the birds were all pecking the key at one end of the cage and walking quickly to the other end to obtain their reinforcement of food. The hens were now walking approximately the same distance for each reinforcement as they would performing a stereotyped movement. They were trained in this situation for a further 12 days and then tested 2 hours after being injected with saline or Pacitran as before. The 2 treatments were given in a random order on successive days and the procedure repeated 3 times. The tests lasted 20min. and were followed by 15min. free access to food. The hens were observed and the numbers of journeys from the key to the food and back to the key were counted.

Results

The amount of food consumed by the birds is shown in Table 15.1A and an Analysis of Variance of these results is given in Table 15.2A. The birds ate on average 75.46gm after saline injection and 73.58gm after Pacitran, a difference which was not significant. Also the drug did not appear to have any cumulative effect since there was no trend in the amounts eaten in successive trials.

The mean rates of key-pecking in the second part of this experiment and an Analysis of Variance of these results are shown in Table 15.3A and 15.4A. There was no significant difference between the rate of key-pecking after saline injection (0.670 responses per second) and after Pacitran injection (0.659 responses per second).

The mean numbers of back and forward movements occurring in 20min. in the third part of this experiment and an Analysis of Variance of these results are shown in Tables 15.5A and 15.6A. An average of 79.58 movements per test were shown after saline injections and 79.25 after Pacitran injections; these differences were not significant.

Discussion

It may be concluded from the above results that Pacitran had no effect on the birds tendency to feed. This being the case, the drug must have prevented the onset of stereotyped movements in Experiment 14, by reducing the escape or avoidance tendency generated by the frustrating situations.

CHAPTER 8

AN INVESTIGATION OF SOME PHYSIOLOGICAL PARAMETERS OF THWARTING

Introduction

It was stated at the beginning of this thesis (p1) that a study of the domestic fowl in frustrating situations is of importance in understanding the effects of modern husbandry practices on production efficiency and the welfare of the chicken. Most of the work in this thesis is devoted to the behavioural effects of thwarting but it is also important to know what the physiological effects are. This is because any definitive definition of production efficienc is most likely to be made in physiological terms, for example, in terms of energ loss and gain. That is not to say that a behavioural study is of no use in this respect. For instance, it is important to know that stereotyped pacing may be the cause of one particular energy loss. On the other hand a behaviour study may be more important in assessing the effect of thwarting on the welfare the fowl.

The physiological reactions of the fowl to adverse conditions in general have been dealt with elsewhere (Draper and Lake, 1968) but that study did not cover reactions to frustrating situations. It is thus important to link up th present study with other physiological studies so that thwarting can be compare to other stressful situations.

Another reason for studying physiological reactions is that they themselve may act as stimuli for subsequent behavioural responses.

It was decided to measure two parameters involved in the General Adaptation Syndrome (Selye, 1952), namely skin temperature and plasma corticosterone level. Selye (1952) developed the idea that any noxious stimulation induces the body to respond with a stereotyped set of metabolic changes; these changes principally involve stimulation of the hypothalamus and increased secretion of adrenocorticotrophic hormone (ACTH) and gluco-corticoids. More recently emphasis has shifted to the acute reactions of the body to stressors, which anticipate the long-term, metabolic changes and which involve the adrenal medullary hormones, adrenaline and noradrenaline (Carlson, 1966; Malmejac, 1964). Among the more important of these changes are circulatory changes in which there is a shift in the flow of the blood from the skin and viscera to the skeletal muscles (Cannon, 1929). This change is reflected in a drop in skin temperature although there may also be an associated rise in skin temperature as parasympathetic reflexes come into play and over-compensate.

Experiment 16

This experiment was designed to measure the skin temperature of birds in situations in which they normally exhibit displacement preening. As mentioned earlier both Andrew (1956a, c) and Morris (1956) suggested that autonomic changes at the surface of the skin may stimulate grooming activity.

Material and Methods

Twelve hens were used in this experiment of similar age, breed and strain to those in Experiment 15. Skin temperature was measured by means of a thermocouple. One side of the thermocouple, protected in very fine polythene tubing was passed through the top of the experimental cage and stuck with a small piece of P.V.C. tape to an area on the birds back which had been bared of feathers one week previously. The area on the bird's back measured 2cm^2 and was on the immediate left hand side of the second and third thoracic vertebrae. The other side of the thermocouple was passed into a mixture of ice and water in a thermos flask to give a big temperature differential and thus a substantial electrical current. The current changes were amplified and recorded on an ultra-violet oscillograph. With this apparatus it was possible to measure changes of 0.1C^o quite accurately although in practice movement artifacts were of this size and so only changes of 0.2C^o or greater were regarded as significant.

The birds were put on a 6 hour food deprivation schedule and trained to feed in the experimental cage for 4 days with a dummy lead stuck on their backs. All the birds were then tested in 3 situations, hungry/food present (H/F), not hungry/no food present (NH/NF) and frustrated (F), in a random order on successive days. They were observed from a hide and their behaviour recorded as before. Each test lasted 20min. and skin temperature was recorded continuously.

Results

One of the problems of this experiment was that the birds tended to peck the lead and remove it and about a third of the tests had to be started again for this reason. The F tests were much worse in this respect than the others. In every test skin temperature rose on average 1.64 ± 0.60C^o from a mean of 38.60^{o}C to a mean of 40.24^{o}C. It rose steadily throughout the 20min. periods regardless of the testing situation or the birds' behaviour. In about one half of the cases it looked as though the temperature rise was flattening off towards the end of the test period. It was thought that perhaps this rise was a response to handling when the birds were placed in the experimental cage. To test this theory four of the hens were put in the cage in a NH/NF condition and the skin temperature recorded. When the temperature stopped rising (after about 15-25min.) the birds were left for another 20min. and then handled just outside the cage for about 4min. with the thermocouple in position. No change in skin temperature resulted from this manipulation. As another test four birds were left in the cage as long as possible with the temperature being recorded all the time. The lead remained on one bird for one hour 40min. and on the others for about one hour before being pecked off. In this time none of the temperatures changed by more than 0.3C° apart from the usual rise in the first 20min. It therefore seemed likely that the initial rise in temperature was a local reaction to the lead being stuck in position. A certain amount of pressure had to be applied to the skin during this operation and it is quite possible that the rise in temperature was simply due to the blood returning to the area that had been compressed.

The original experiment was repeated but this time the birds were kept in complete darkness in the experimental cage until the initial temperature rise had taken place. The lights were then switched on and the 20min. testing period started. Once again only slight temperature changes were recorded (0.2-0.3C°) and none of them could be related to behavioural changes that were taking place.

Discussion

The results suggest that the skin temperature of chickens does not change very much in a variety of situations and they are probably very different from mammals in this respect. In fact the skin of the fowl is poorly vascularized apart from certain localized areas such as the comb and wattles and seasonally the brood-patch. This is well demonstrated during surgery when the skin may be incised with very little bleeding. Draper and Lake (1968) suggested that in the fowl the shunt of blood from the viscera to the musclature during stress may be much more important than that from the skin.

In fact physical thermoregulation in birds is accomplished mainly through vasomotor control in the skin of unfeathered areas, respiratory changes and alteration of the arrangement of the feathers. Vasomotor control is relatively unimportant in feathered areas of the skin (King and Farner, 1960). This means that it is possible for the bird to regulate heat loss through the layer of feathers without much temperature change occurring at the skin surface.

Andrew (1956a) drew attention to the possible importance of the production of metabolic heat by adrenaline during fear. Many studies have now demonstrated the calorigenic effect of the catecholamines and the subject is well reviewed by Griffith (1951), Ellis (1956) and Lundholm, Mohme-Lundholm and Svedmyr (1966). The mechanism may differ in the bird since the ratio of noradrenaline to adrenaline is higher than in the common laboratory animals (Draper and Lake, 1968). This may mean that the calorigenic effects are lipolytic rather than glycogenolytic. However, although the lipolytic effects of noradrenaline have been shown to occur in mammals (Steinberg, 1966), they have not yet been demonstrated in birds (Carlson, Liljedahl, Verdy and Wirsen, 1964). Nevertheless, even if considerable metabolic heat was produced by the catecholamines in the present experiment, it would have been largely dissipated by one of the three routes mentioned above and would have affected skin temperature very little.

Finally, it should be pointed out that the fight or flight syndrome is not primarily a thermoregulatory mechanism and the pilomotor or, in the case of birds, pteromotor, response is under independent autonomic control from the vasomotor response of the vessels in the skin (Strom, 1960). Therefore, it need not necessarily be a reflex response to a change in skin temperature following a vasomotor response, although it can act in this way.

An interesting fact from this experiment was that the birds pecked the lead off more often in the F tests than in the control tests. McFarland (1966b) suggested that thwarting could induce a switch of attention and this may have happened in the present experiment; the thwarting may have caused the birds' attention to switch from the unobtainable food to the presence of the foreign object on the skin.

In summary it can be said that if thwarting elicits the fight or flight or defence reaction in the chicken we would expect pteromotor activity (probably raising of the feathers) and vaso-constriction of the skin vessels but, as was discussed, this latter response may be slight. Secondarily, we would expect sympathetic activity to stimulate release of catecholamines from the adrenal medulla and for these to produce metabolic heat. Amongst other routes, this heat would be lost by the bird lowering the insulating value of the feathers (sleeking) but again this need not mean much change in skin temperature.

The experiment was therefore unsuccessful in demonstrating a change in skin temperature following thwarting, but it did not rule out the possibility that other changes, such as pteromotor responses, could act as stimuli for displacement preening.

Experiment 17

This experiment was designed to measure the plasma corticosterone levels of hens which had been thwarted in feeding behaviour and which had developed stereotyped pacing movements.

Material and Methods

The hens used were aged between 7 and 8 months and of the same strain and breed as those in Experiment 16. They were trained to expect food in the experimental cage after food deprivation of 24 hours and then thwarted by placing a perspex cover over the food. The training and testing periods lasted 20min. each day, and during the testing periods the number of back and forward pacing movements were counted. 5ml blood samples were taken from the wing vein at various times during this procedure.

The level of corticosterone in the plasma was measured by J.W. Wells and J. Culbert of the Reproduction Section of the Poultry Research Centre by a standard method which had been modified by them. This method involved extraction with a solvent, purification using column chromatography, treatment with sulphuric acid and assay by a fluorometric procedure. The assay measured 11, 21-dihydroxypregn-4-ene-3, 20 dione (corticosterone) which is the glucocorticoid present in by far the greatest amounts in the fowl (J. Wells personal communication). The one disadvantage of this technique is that it is very time-consuming and very few samples could be analysed.

Results

In the first part of this experiment four birds, B, W, R and Y, were trained for 12 days and then subjected to frustrating (F) tests and not hungry/no food (NH/NF) tests on alternate days for a further 26 days. Blood samples were taken from birds B, W, R and Y on day 10 of training, from B and R on day 11 of training, and from W and Y on day 12 of training. All these samples were taken 30min. after feeding. Samples from all the birds were again taken on days 12 and 26 of testing. F tests occurred on both these days and the blood was taken 30min. after the birds had been fed after a variable delay.

The plasma levels of corticosterone are shown in Table 17.1. These values are all within the normal range; only values of above 8μg/100ml plasma could be considered abnormally high (J. Wells personal communication).

The numbers of stereotyped back and forward movements which occurred in each of tests on sampling days are also shown in Table 17.1. It can be seen that stereotyped movements developed in the usual manner when the F tests started.

In the next part of this experiment blood samples were taken from 3 birds (W/R, W/O, and W/G) from the control group in Experiment 14, which had shown a high frequency of stereotyped pacing. These samples were taken immediately after the last F test in that experiment (Day 37). Samples were also taken from 3 birds (M, P and G) of similar age, breed and strain which had been kept in individual battery cages and had not been used in any other experiment.

The results from these samples are shown in Table 17.1. Once again there are no abnormally high values.

Finally, in the third part of this experiment four hens (M/P, W/B, O and

Table 17.1. Levels of corticosterone (µg/100ml plasma) in hens subjected to frustrated feeding.

Part One	Bird	Corticosterone level	No. of stereotyped movements
Day 10 of training	B	6.5	0
	W	0.4	0
	R	3.1	0
	Y	2.5	0
Day 11 of training	B	0.3	4
	R	1.4	0
Day 12 of training	W	0.1	1
	Y	0.0	0
Day 12 of testing	B	1.6	87
	W	1.0	116
	R	0.2	201
	Y	5.0	127
Day 26 of testing	B	5.7	103
	W	4.6	136
	R	3.7	152
	Y	2.2	148
Part Two			
Frustrated birds	W/R	0.7	227
	W/O	3.6	218
	W/G	3.6	158
Control birds	M	2.4	-
	P	1.8	-
	G	0.9	-
Part Three			
	M/P	1.8	-
	W/B	5.9	-
	O	5.7	-
	G/Y	1.0	-

G/Y) were trained for 12 days and then placed in the F situation for one hour each without being observed. Blood samples were taken immediately each test had finished and these results are shown in Table 17.1. Again the corticosterone levels fall within the normal range.

Discussion

An increase in plasma corticosterone is generally accepted to be part of the General Adaptation Syndrome to stress (Selye, 1952; Brown, 1967). It is known that certain physical stresses, such as exposure to cold, can increase the plasma level of corticosterone in poultry (Brown, 1961, 1967). There is also some evidence that other related parameters such as adrenal size and adrenal cholestrol level, show a typical stress reaction to crowding in poultry (Siegel, 1959; 1960; Flickenger, 1961) although recent work has shown that these changes may not be so clear cut as was first supposed (Siegel and Siegel, 1969). It has also been shown that handling birds can change another index of adrenal cortical activity, namely adrenal ascorbic acid level (Freeman, 1967).

The hens in the present study did not show any increase in plasma corticosterone. This can either mean that (a) thwarting, which is severe enough to alter the birds' behaviour permanently, does not stress the birds sufficiently to elicit the General Adaptation Syndrome, or (b) the General Adaptation Syndrome is not so generalized as in mammals and different reactions occur to different stressors.

B External Factors

CHAPTER 9

FACILITATION OF DISPLACEMENT PREENING

Introduction

It was pointed out in the Review of the Literature (p7) that Tinbergen (1952) considered that one of the main characteristics of displacement activities was the absence of the external stimulation normally associated with them. However, the external stimuli normally eliciting preening are likely to be continuously present at the surface of the skin as suggested by Andrew (1956b). If this is the case what happens if these stimuli are increased or added to? Is preening increased in both thwarting and non-thwarting situations? Van Iersel and Bol (1958) investigated the facilitating effect of rain on preening in various conflict situations. They found that the increase in preening frequency in rain was not equal in the various situations and depended on the intensity and duration of the conflict.

Gallinaceous birds do not bathe in water so the use of rain or a water spray or the damping of the plumage with water in any way was ruled out as being too unnatural. The addition of dry material to the surface of the skin in order to facilitate preening would be very difficult but it was thought that the same effect might be gained by preventing the bird from preening for a period of time. This might allow a build-up of foreign material, skin debris and feather dissaray which normally induce preening.

Experiment 18

Material and Methods

Sixteen hens aged between 11 and 12 months and of similar strain and breed to those in Experiment 17 were used. They had been kept in individual battery cages since before sexual maturity and their plumage was in good condition. Preening was prevented by means of round collars 25cm. in diameter made of celastoid, which is a stiff but not rigid material. Each collar had a central hole 4cm. in diameter which could be slipped over the bird's head and down the neck where the downward lie of the neck-feathers kept it in position. When the collars were on the birds could not reach any part of their plumage with their bill apart from the neck feathers above the collar; neither could they scratch their heads with their feet.

The hens were randomly divided into two groups of 8, one group to receive collars the other to act as a control. They were put on a 6 hour food deprivation schedule and trained to feed for 20min. in the experimental cage for 6 days. During this time the birds in the "collar" group had their collars put on over the 6 hour deprivation and 20min. training period to get them used to wearing them. They were then trained for another 2 days without collars. Two testing situations were used, frustrated (F) and not hungry/no food (NH/NF). Each bird was subjected to each test for 20min. separated by a training day. Four birds in each group had the F test first and four the NH/NF test first. The "collar" group had their collars put on 24 hours before testing and removed immediately before each test.

The birds' behaviour during the 20min. tests was recorded in the usual way with particular attention being given to preening.

Results

The number of preens occurring in the test periods are shown in Table 18.1.

Table 18.1. Numbers of preens occurring during frustrated feeding after birds had been prevented from preening for 24 hours. Numbers in brackets refer to the minute of the test in which the first preen occurred.

	Control birds			Birds with collars	
	NH/NF	F		NH/NF	F
R	15 (6)	27 (7)	Y	146 (1)	104 (5)
R/R	0	27 (14)	Y/Y	104 (11)	116 (8)
R/W	0	29 (14)	Y/W	14 (7)	70 (9)
R/B	0	30 (16)	Y/B	64 (8)	114 (1)
R/G	4 (9)	17 (16)	Y/G	77 (3)	85 (9)
R/O	27 (2)	64 (12)	Y/O	68 (9)	70 (2)
R/P	24 (7)	49 (16)	Y/P	73 (14)	66 (10)
R/M	0	25 (9)	Y/M	111 (8)	151 (5)
Means	8.7	33.5		82.1	97.0

't'-values 8.28 1.29

P. <0.001 n.s.

't'-values 5.24 5.38

P. <0.001 <0.001

The various averages were compared by 't'-tests and the 't' and P values are shown in Table 18.1. It can be seen that far more preening occurred in the group which had worn collars than in the control group.

The control group showed the usual increased frequency of preening in the F situation compared to the NH/NF situation and the preening in the former situation was hurried and noisy, typical of displacement preening. On the other hand there was no significant difference in the number of preens occurring in the F and NH/NF situations in the group which had worn collars. Also the preening shown by this group was very thorough in both situations; once it started it tended to last a long time. At times it also looked rather hurried and, generally speaking, there was not much difference between the preening in the F and NH/NF situations after the birds had worn collars.

The fact that there was no difference in the frequency of preening in the F and NH/NF situations in the group which had collars, is not because the birds were preening all the time. The latency of the first preen in each test is shown in Table 18.1 and it can be seen that preening by no means started immediately the birds had the collars removed. However, there was no difference in latency between the F and NH/NF situations. There was a difference in latency to preen on the other hand between the control group and the group with collars. They were compared (in the F situation only, since preening did not occur sufficiently often in the NH/NF situation) by ranking the latencies and applying the Mann-Whitney U test. It was found that on average the birds which had worn collars started preening after 6.1 minutes and the control birds after 13.0 minutes, the difference being statistically significant ($U = 6$: $p = 0.002$).

Discussion

The results suggest that a preening deficit can be built up by preventing the birds from preening with a collar. This is illustrated by the fact that the birds which had been wearing collars preened more and preened sooner than birds which had not. The results also show that preening is facilitated to an equal extent in both thwarting and non-thwarting situations. It is assumed in this discussion that the increase in preening was due to an accumulation of peripheral stimulation. However, the psycho-hydraulic model of Lorenz (1950) could also be used to explain the results in terms of "damming-up" of a "preening drive". This latter possibility was rejected as being unlikely since it was obvious to the observer that the feathers of the birds did become dishevelled while they were wearing collars and there was thus almost certainly a change in peripheral stimulation during this time.

These results have certain implications for the Disinhibition Hypothesis. Van Iersel and Bol (1958) suggested that peripheral stimulation plays only a minor part in displacement grooming and most of the observed variation in grooming is due to the degree of disinhibition given by the strength of the conflict. If this was the case in the present experiment then one would expect the birds to preen more in the F situation whether or not there was increased peripheral stimulation, since the strength of the "conflict" was the same in both cases. Andrew (1956a, b), on the other hand, laid more emphasis on the part played by peripheral stimulation and more particularly he suggested that autonomic changes at the skin surface may stimulate grooming in conflict and thwarting situations. Now if this was the case in the present experiment it is possible that one day's preening deficit might be enough to mask the effect of any peripheral autonomic changes.

The evidence from Experiment 18 therefore suggests that displacement preening can not be accounted for in terms of disinhibition alone.

CHAPTER 10

THE EFFECT OF SOCIAL STIMULI

Introduction

In the Review of the Literature a whole section was devoted to frustration and aggression. It is clear that certain psychologists (Dollard et al, 1939; Scott, 1958) would expect aggressive responses to be fairly common in frustrating situations. Yet in only one of all the previously described experiments in this thesis were any aggressive responses seen following thwarting. This was in Experiment 1 in which some hens, thwarted in nesting behaviour, threatened pullets in a neighbouring pen. In none of the other experiments was there any sign of aggression. For example, when feeding was thwarted, pecking at the perspex cover and redirected pecking were not accompanied by raising of the hackle feathers. However most of the experiments described so far have involved individual birds. The exceptions have been Experiment 4, in which a dominant bird feeding was used to thwart a hungry submissive bird, Experiment 8, in which chicks were present when hens were thwarted and Experiment 10, in which hens were present when cocks were thwarted.

In the next experiment it was decided to frustrate birds in a social situation and observe their behaviour, paying particular attention to any agonistic interactions which might occur.

Experiment 19

Material and Methods

The birds used in this experiment were aged between 14 and 16 months and of the same breed and strain as those in Experiment 18. A similar experimental cage was used but it was slightly larger ($70cm^3$) and had a second feeding hole measuring $8cm^2$ cut in the side directly opposite the original hole. A removable food trough could be attached to the cage outside the hole. The layout of the cage was otherwise the same as shown in Figure 2.1 (p 90).

The experiment was carried out in 5 parts and the experimental details of each part are included in the Results section.

Results

In the first part a pair of hens which had been together in a home cage for about 6 weeks were placed in the experimental cage for 3 days to settle down. Food was available from both food troughs. On the fourth day the pair were observed for 20min.

Aggression seemed to consist almost entirely of four easily distinguishable components:-

1. Threats; a threat occurs when one bird raises its head above another in a characteristic manner and this usually evokes an avoidance or submissive response from the threatened bird.

2. Pecks; pecks to the head and neck region only were scored.

3. Grips; the comb or hackle feathers of another bird are held and sometimes shaken in the beak.

4. Chases; when one bird actively runs after another threatening it.

The numbers of threats, pecks, grips and chases were counted and their direction noted. Further 20min. observations were made (a) after removal of the food troughs (b) 24 hours later (c) after replacing the troughs with a perspex cover over the food and (d) after removal of the cover.

The 5 situations were therefore:-

1. Not hungry/food present (NH/F)
2. Not hungry/no food (NH/NF)
3. Hungry/no food (H/NF)
4. Hungry/frustrated (H/Frustrated)
5. Hungry/food present (H/F)

The experiment was repeated using 5 different pairs of hens. The results are shown in Table 19.1. In every case all components of aggression were in one direction. As can be seen the thwarting alone appears to be responsible for a large increase in aggression.

In the second part of this experiment, four pairs of birds were put on a 24 hour food deprivation schedule and trained to feed for 20min. in the experimental cage for 6 days. Only two testing situations, H/Frustrated and NH/NF, were used because there was little difference between the results from four of the situations in the previous part. Also the H/NF situation could have frustrative properties with repeated food deprivation since there would be an expectancy of food after 24 hours built up. The hens were placed in the 2 situations used (H/Frustrated and NH/NF) in a random order every other day, with a day of training in between. The tests lasted 20min. and each pair was tested three times in each situation. The results are shown in Table 19.1A and

Table 19.1. Numbers of aggressive responses occurring during frustrated feeding.

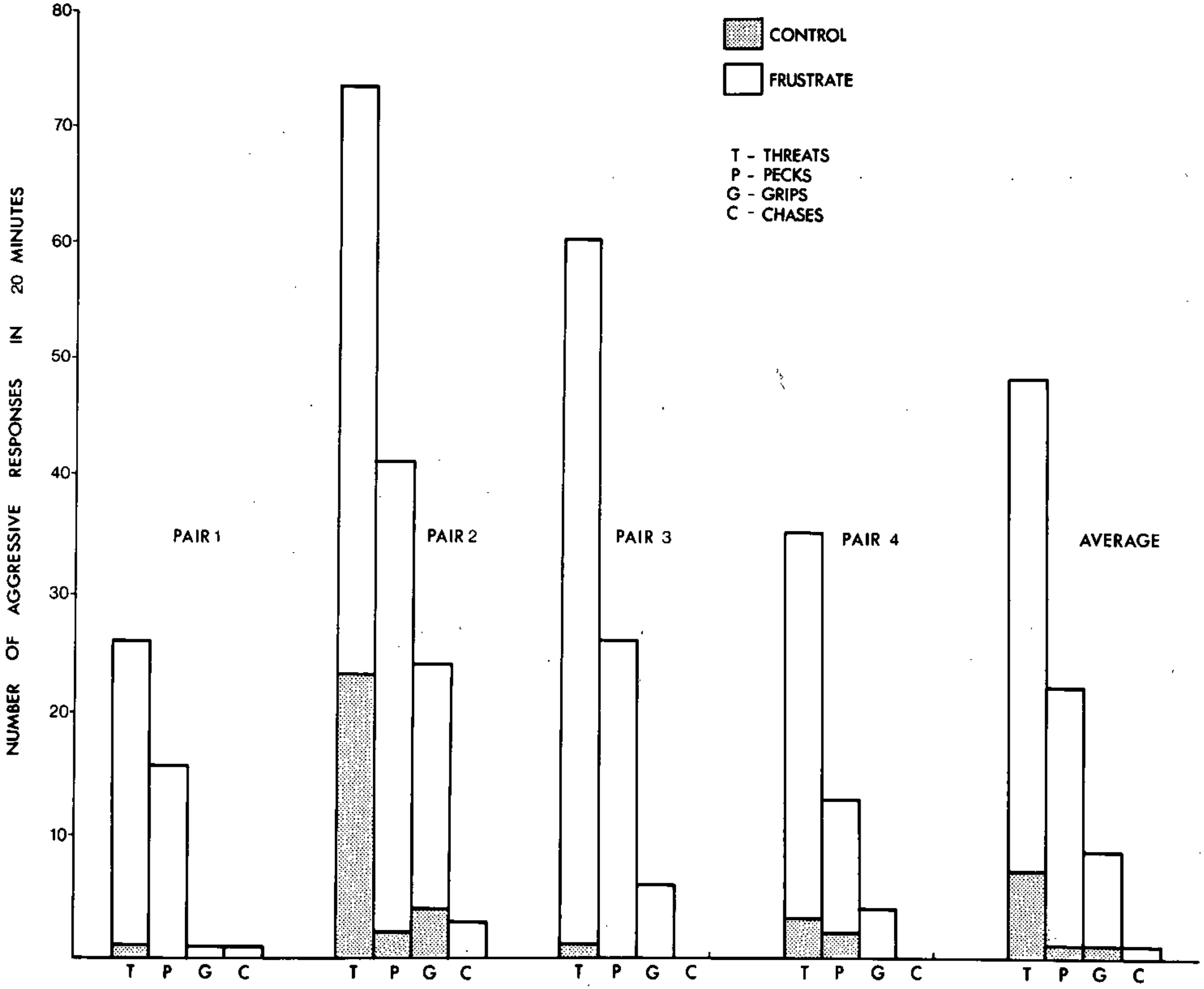
		Threats	Pecks	Grips	Chases	Total aggressive responses
	NH/F	4	0	0	0	4
	NH/NF	0	0	0	0	0
Pair 1.	H/NF	4	0	0	0	4
	H/Frustrated	24	8	0	0	32
	H/F	2	0	0	0	2
	NH/F	0	0	0	0	0
	NH/NF	0	0	0	0	0
Pair 2.	H/NF	0	0	0	0	0
	H/Frustrated	36	19	3	2	60
	H/F	2	0	0	0	2
	NH/F	0	0	0	0	0
	NH/NF	1	0	0	0	1
Pair 3.	H/NF	1	1	0	0	2
	H/Frustrated	32	12	0	0	44
	H/F	1	0	0	0	1
	NH/F	1	0	0	0	1
	NH/NF	0	0	0	0	0
Pair 4.	H/NF	0	0	0	0	0
	H/Frustrated	15	11	0	2	28
	H/F	0	2	0	1	3
	NH/F	0	0	0	0	0
	NH/NF	0	0	0	0	0
Pair 5.	H/NF	0	0	0	0	0
	H/Frustrated	12	6	0	0	18
	H/F	4	1	0	0	5
	NH/F	1.0	0	0	0	1.0
	NH/NF	0.2	0	0	0	0.2
Mean.	H/NF	1.0	0.2	0	0	1.2
	H/Frustrated	23.8	11.2	0.6	0.8	36.4
	H/F	1.8	0.6	0	0.2	2.6

summarized in Figure 19.1. Once again all the aggression was in one direction and there was a large increase in aggression in the frustrating tests compared to the control tests. There was no difference between the three trials.

The third part of this experiment was designed to test birds which are dominant in one situation and submissive in another. Four groups of three hens were used and each bird was tested with the other two birds in its group three times. That is, the birds were living in groups of three in the home cage, and the three possible pair combinations were each tested three times in the experimental cage. This part was otherwise similar to the second part. The four groups all had linear hierarchies with aggression shown in one direction only, and the birds were called A, B or C depending on their position in the hierarchy.

The results for total number of aggressive responses are shown in Table 19.2A and summarized in Figure 19.2. The A birds all showed more aggression in the frustrating situation compared to the control situations; this was to both the B and C birds. The B birds when tested with their C companion showed more aggression when frustrated than in the control period. However, they showed no aggression whatever when tested with the A bird in their group. The C birds showed no aggression. In this part of the experiment less aggressive responses occurred in the third trial than in the first trial ($t = 3.38$: $p \angle 0.01$) or second trial ($t = 2.61$: $p \angle 0.05$).

The fourth part of this experiment was similar to the second part except that pairs of hens and cockerels were used. Cockerels usually dominate hens



CONTROL
FRUSTRATE
T - THREATS
P - PECKS
G - GRIPS
C - CHASES
NUMBER OF AGGRESSIVE RESPONSES IN 20 MINUTES
80
70
60
50
40
30
20
10
PAIR 1
PAIR 2
PAIR 3
PAIR 4
AVERAGE
T P G C
T P G C
T P G C
T P G C
T P G C

Figure 19.1. Numbers of aggressive responses occurring during frustrated feeding (mean of 3 trials).

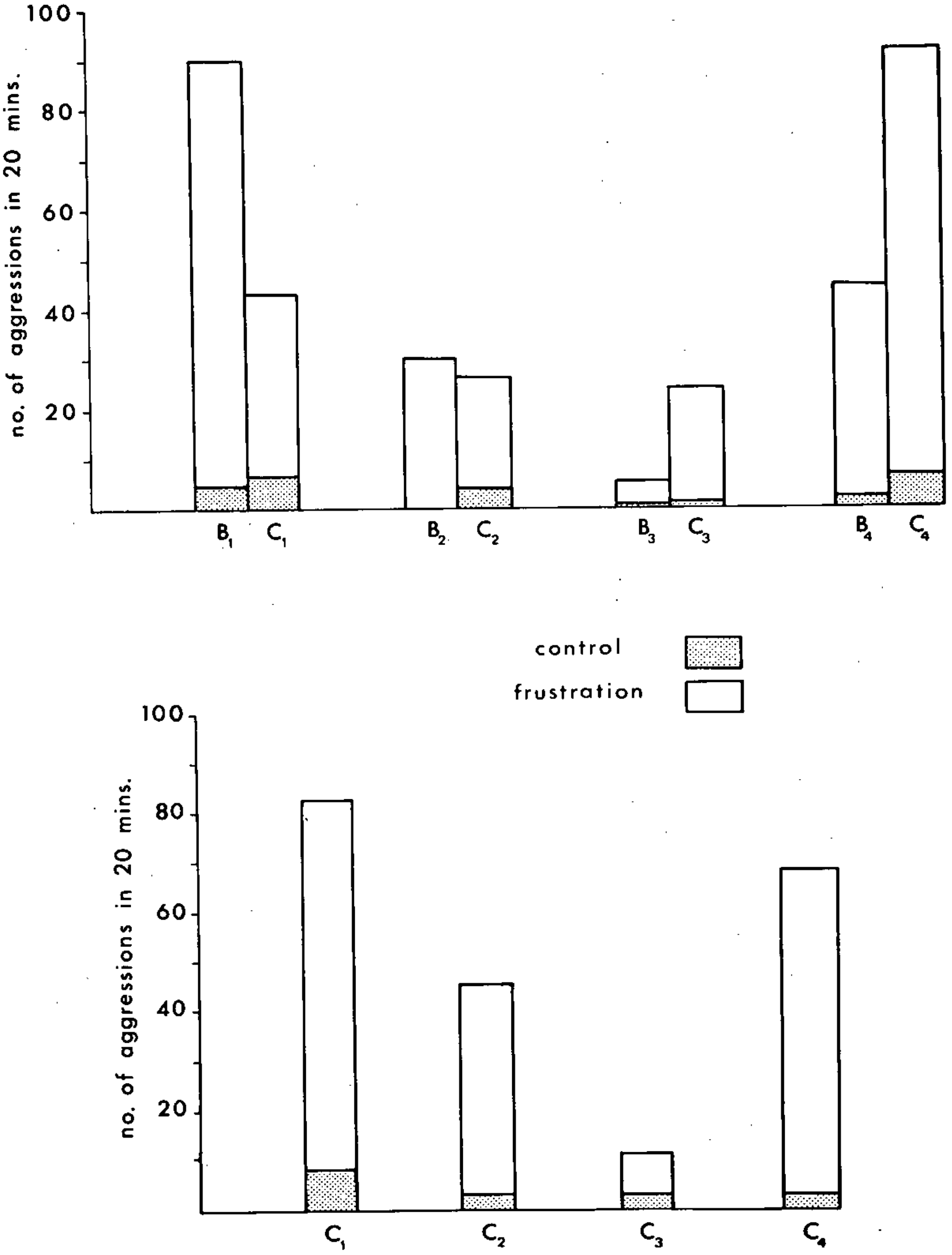

no. of aggressions in 20 mins.
100
80
60
40
20
B1
C1
B2
C2
B3
C3
B4
C4
control
frustration
no. of aggressions in 20 mins.
100
80
60
40
20
C1
C2
C3
C4

Figure 19.2. Numbers of aggressive responses shown by A birds towards B and C birds (above) and B birds towards C birds (below) during frustrated feeding (mean of 3 trials).

passively with no overt aggression shown (Guhl and Fischer, 1969). Eight pairs were tested three times. The results for total aggressions are shown in Table 19.2. In 7 out of the 8 pairs the cockerels showed a large increase in aggression during the frustrating tests compared to the control tests. In the other case it is possible that the female was dominant to the male. In 8 hours total observation time of control periods only 15 threats and 3 pecks were seen to be given by cockerels to hens compared to 546 threats and 260 pecks in 8 hours observations of frustrating tests.

Finally, the fifth part of this experiment was carried out to test the effects of frustration after short deprivation times and also to see whether aggression increased with deprivation time. One control situation (NH/NF) and three frustrating situations (H/Frustrated) were used, after 2.5, 5.0 and 7.5 hours of food deprivation. Nine pairs of hens were used and each pair was subjected to each of the four situations in a random order every other day. On the intervening days each pair had a 20min. training session in the experimental cage.

The total numbers of aggressive responses are shown in Table 19.3. Paired 't'-tests were carried out between the results for each situation and the 't' values are given in Table 19.4. It can be seen that significantly more aggressive responses occurred when the birds were frustrated after 5.0 and 7.5 hours of food deprivation than in the NH/NF situation. There was also an obvious tendency for aggressive responses to increase with food deprivation time.

In all the parts of this experiment, apart from the aggressive responses,

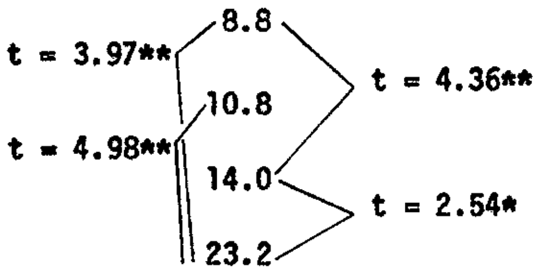
Table 19.2. The increase in total numbers of aggressive responses shown by cockerels towards hens in the H/Frustrated situation compared to the NH/NF situation.

Cockerels	Trials		
	1	2	3
W	41	31	20
P	2	0	0
R	92	55	23
M	41	42	37
Bk	37	58	54
Br	23	38	23
G	69	42	20
Y	20	41	22

Table 19.3. Total numbers of aggressive responses occurring during frustrated feeding after different lengths of food deprivation.

Birds	Situation			
	NH/NF	H/Frustrated (2.5 hours deprivation)	H/Frustrated (5.0 hours deprivation)	H/Frustrated (7.5 hours deprivation)
R	4	3	10	3
P	6	11	6	18
G	0	3	11	11
M	3	0	4	12
Y	7	2	12	14
W	3	0	8	16
Bk	14	21	24	48
O	9	5	13	22
Br	33	52	38	65
Means	8.8	10.8	14.0	23.2

Table 19.4 Differences between means; 't'-values.



** = $p < 0.01$

* = $p < 0.05$

the dominant birds spent most of their time pecking at the perspex cover. A few of them started to show pacing behaviour when they were thwarted after 24 hours food deprivation. However, this never lasted very long and was usually interrupted by the submissive bird getting in the way whereupon the dominant bird would stop and direct aggressive responses towards it. The submissive birds also spent a lot of time pecking at the perspex cover. The rest of their time was spent in avoiding the attacks of the dominant bird and it should be stressed that the aggressive responses of the dominant bird always preceded the avoidance responses of the submissive bird. Pacing behaviour was more common in the submissive birds but it was difficult to tell if this was in response to the thwarting or simply escape behaviour from the dominant bird. Preening seldom occurred at all in this experiment.

Discussion

It would appear from the results of this experiment that frustration may be one of the causes of aggressive responses in the domestic fowl. However, the stimulus of a bird lower in the social hierarchy seems to be necessary before aggressive responses are elicited. For this reason the results fit with the suggestion of Scott (1958) that one of the reasons why frustration may lead to aggression is because it leads to a high degree of excitation and in this state the organism will respond to stimuli, including aggression-inducing stimuli, to which it would not normally respond.

PART FOUR

SYNTHESIS

CHAPTER 11

GENERAL DISCUSSION

The results from the experiments described in this thesis have shown that the domestic fowl may respond to frustrating situations in several ways. Displacement preening, stereotyped back and forward pacing and increased aggression were the commonest responses to thwarting. That is not to say that they are the only possible responses; under different conditions to the ones described, different responses may be elicited. Even under the present conditions other responses were seen; for example, in Experiment 2 there was a higher frequency of feather-raising in the thwarting situation, and in Experiment 10 the cockerels showed a higher frequency of wing-flapping when sexually frustrated.

Displacement preening occurred during frustrated nesting, feeding (when the feeding tendency was fairly weak) incubation and brooding behaviour and was therefore perhaps the most prevalent of the responses to thwarting. This preening showed two of the three features which Tinbergen (1952) stated were characteristic of displacement activities:-

1. The movements shown did not belong to the executive motor patterns of the activated drive. i.e. the drive which was thwarted.
2. An incomplete or frantic performance.
3. Irrelevance or absence of the external stimulation normally associated with the action.

In the case of preening it is almost impossible to prove the presence or absence of the stimuli which normally elicit it, but it has been suggested that they will be continually present (Andrew, 1956b).

Concerning the first characteristic above, McFarland (1966a) has argued convincingly that frustration switches attention and an activity appears which has motor patterns belonging to the newly activated system (because of the switch of attention) and this activity is entirely relevant to its own causal factors. The evidence McFarland gives is good and there is no contradictory evidence to his theory in the results from this thesis.

On the other hand there has been no satisfactory explanation given of the second characteristic namely a frantic or incomplete performance. The supporters of the Disinhibition Hypothesis (van Iersel and Bol, 1958; Sevenster, 1961; Rowell, 1961) paid more attention to the fact that displacement activities are often "normal" in appearance and tended to ignore the fact that most of the previous descriptions emphasised the frantic nature of displacement activities. The explanations that they did give for the frantic nature of displacement activities have been criticised in the Review of the Literature.

The displacement preening described in the present experiments was generally frantic and noisy. It was shown in Experiment 5 that this was due to individual preening movements being of shorter duration than "normal" preening movements and the difficulty of explaining this in terms of disinhibition has been discussed. There would appear to be only two other possible explanations; either (1) the peripheral stimulation present during thwarting is not the same as during normal preening or (2) the frustration state in some way affects the motor patterns of the activities which follow it. There was some evidence to show that a change in peripheral stimulation does affect the pattern of preening which follows.

For example, the preening which occurred in Experiment 18 after the birds had been wearing a collar was more hurried than normal, also in Experiment 1 when there was a hard shelled egg in the uterus, there was more preening than normal of the belly region. The preening in the latter case was probably in response to muscle or feather movements in the abdominal region since it has been shown that distension of the hen's vagina and cloaca evokes bearing-down contractions of the skeletal muscles and erection of the feathers surrounding the vent (Sykes, 1955b). A change in peripheral stimulation would also occur if thwarting elicited the physiological defence reaction. Although this reaction was not demonstrated by a change in skin temperature (Experiment 16) there is a distinct possibility that it did occur and that the displacement preening was a response to pteromotor activity.

There is some evidence that motor patterns could be affected by a state of frustration. For example, Brown and Farber (1951) suggested that frustration may affect overt behaviour by increasing the general level of motivation, and Amsel and Roussel (1952) were able to demonstrate experimentally that this was true. However, as was pointed out in the Review of the Literature this affect has not been demonstrated when an "irrelevant" activity occurs in response to thwarting. In fact there is some slight physiological evidence which shows that motor patterns could be affected by a state of frustration. Electromyograph studies have shown that muscle activity levels are often higher in patients under stress (Goldstein, 1964; Malmo and Smith, 1955; Sainsbury, 1964) so if frustration results in a physiological stress reaction it is possible that motor activity could be affected.

The results from the experiments in Chapters 4 and 5 suggested that displacement preening may have an important function, apart from the obvious one of tending to the body surface. In these experiments displacement preening took place after the bird had avoided the frustrating stimulus. The preening was accompanied by a calming down of the birds and followed by a move back to the frustrating stimulus. It was postulated that displacement preening may function to allow a highly aroused bird to calm down again. Chance (1962) suggested that displacement preening may function to "cut-off" a disturbing stimulus and Wilz (1970a,b) showed that the performance of a displacement activity allowed a change from aggressive to sexual behaviour to occur. The evidence from Experiment 7 was that the mechanism in the present study probably involves a mood change and so is more likely to be of the latter type since preening occurred even when the birds cut themselves off visually from the frustrating stimulus by moving into the other room.

The stereotyped back and forward pacing occurred in bouts during thwarted nesting and to a greater extent during thwarted feeding when the feeding tendency was strong. There was evidence that it started (at least in the feeding situation) as an escape response. This implies that the frustrating situation was in some way aversive and this was supported by the fact that the birds showed active avoidance of frustrating situations in other experiments. However, in Experiments 6, 7 and 8 in which the incubation and brooding tendencies were thwarted, avoidance occurred and was followed by displacement preening without the development of stereotyped pacing behaviour. This suggests that frustration is probably a variable state which is a function of the strength of the frustrated tendency. Displacement preening appears to be associated with mild and short-term frustration (what ethologists would probably prefer to call thwarting) and stereotypy with long-term and intense frustration. A frustrating situation is probably always aversive and leads to an avoidance tendency, and, because of the autonomic changes, to a tendency to preen. Both of these activities were allowed expression when the broody birds were frustrated in the pen. However, in the experiments in which a cage was used the birds could not properly avoid the situation and so they preened when the frustration was mild or attempted to escape from the situation when the frustration was severe. The tendency to preen was probably elicited in both cases but the avoidance tendency was greater in the latter and so it occurred and inhibited preening. The fact that a tranquillizer which reduces fear of aversive stimuli prevented the onset of stereotyped movements is further evidence that they were at first escape movements. However, the nature of the movements changed with repeated exposure to frustrating situations and it was argued that at this later stage, something other than fear must have been the motivating factor. This behaviour pattern had some of the characteristics of "fixated responses" described by Maier (1949) and in many ways it resembled the stereotyped movements often shown by animals in zoos and pet shops. No adequate explanation has yet been given as to why any of these responses should become so fixated into the animals' behavioural repertoire. All that can be said is that presumably their performance has some reinforcing value. It is possible, as was pointed out in Chapter 7, that they help to reduce fear or anxiety or at least hold it at an acceptable level. In any case birds which had been performing these movements for a long time did not show physiological signs of chronic stress as measured by plasma corticosterone level (Experiment 17). It was therefore probable that they had adjusted to the frustrating situation.

As mentioned above there was ample evidence from the experiments that thwarting generated an avoidance tendency but there was no indication that this at any time conflicted with the original approach tendency. If there had been a conflict between approach and avoidance one would have expected the animal to take up a position where the approach and avoidance tendencies were balanced. In this position a move towards the "goal" would result in the avoidance tendency increasing in strength more quickly than the approach tendency and so a withdrawal would follow. On the other hand a move away from the goal would result in the avoidance tendency falling more quickly than the approach tendency, and this would lead to the animal returning to its original position (Miller and Murray, 1952). Also if there had been a conflict present between approach and avoidance, one might have expected ambivalent postures or compromise behaviour to have taken place at the point where the tendencies were in equilibrium. However, with one exception this did not happen. The exception was in Experiment 10 where cockerels showed an increase in wing-flapping when frustrated sexually. As was mentioned previously this behaviour pattern is thought to be a compromise between approach and avoidance so it probably indicated that a conflict was present in this experiment. In all the other experiments there was no sign of a conflict and the birds showed both approach and avoidance in discrete bouts. In Experiment 2 bouts of thwarted pecking were interspersed with bouts of pacing along the door. In Experiments 6, 7 and 8, bouts of attempted approach to the eggs or chicks alternated with bouts of preening as far away as possible from the cage. This is not what the proponents of the disinhibition hypothesis predicted would happen in a thwarting situation; they maintained that thwarting would always lead to a conflict (van Iersel and Bol, 1958; Sevenster, 1961; Rowell, 1961). However, supporting the present results are the findings of McFarland (1966a) that thwarting does not lead to much conflict. He found that a stationary ambivalent posture, thought to be a compromise between approach and retreat, was much more common in an approach-avoidance conflict situation than in a thwarting situation in which retreat was not directly induced. Also Wood-Gush and Guiton (1967) found that a physical thwarting situation led at first to escape behaviour then to an increase to irrelevant activities with little sign of conflict. On the other hand when food was presented to hungry birds in association with an aversive stimulus the birds showed ambivalent movements to and from the source of food and noxious stimulus. From these results it appears that physical thwarting does not lead to an approach-avoidance conflict to the same extent as when avoidance is directly induced. The alternation from one activity to another and from approach to avoidance in the present results also fit into McFarland's theory that frustration leads to a switch of attention.

The increase of aggressive responses during thwarting occurred only when a bird lower in the social hierarchy was present. Again one could say that this was due to the bird switching its attention from the frustrating stimulus to the potentially aggression-inducing stimulus of a submissive bird. However, when cocks and hens were frustrated simultaneously (Experiment 10) the cocks did not show sexual responses towards the potential sexual stimuli of the females. The aggressive responses therefore appear to be more specific than can be explained by a simple switch of attention mechanism. Scott (1958) stated that frustration is likely tp lead to aggression because it results in a high degree of excitation and in this state the organism will respond to stimuli, including aggression-inducing stimuli, to which it would not normally respond. In this respect Scott's explanation is very similar to the attention-switching explanation. However, he gave other reasons why aggression should often follow frustration. These were that aggressive responses may be useful in removing the source of frustration and so they may be reinforced but, more important to the present argument, the physiological and emotional symptoms of frustration do not conflict with those of anger. Thus, if frustration results in the physiological fight or flight response then this means that the sympathetic nervous system will be aroused and the bird will be prepared to make aggressive or escape responses. On the other hand sexual responses, which depend to a large extent on parasympathetic activity, will be inhibited. The results from the present study therefore appear to agree with Scott's explanation.

CHAPTER 12

FRUSTRATION AND POULTRY HUSBANDRY

It was stated in the Introduction (p 1) that a study of the domestic fowl under frustrating conditions might help in understanding the effects of modern husbandry practices on the fowl. It was suggested in the Brambell Report (Her Majesty's Stationery Office, 1965) that intensive husbandry systems often lead to frustration but, as was pointed out earlier, this was a subjective impression only. In the light of the results reported in this thesis is there any evidence that these husbandry practices do lead to frustration? Unfortunately the evidence is meagre. There have been very few behavioural studies made of chickens in these sort of conditions. However, some recent work on the pre-laying behaviour of hens in battery cages has demonstrated that frustration responses do occur in practice. Observations have shown that a great deal of stereotyped pacing may occur in the hour before laying (Wood-Gush and Gilbert, 1969; Wood-Gush, 1969). However, it should not be thought that this behaviour pattern is completely unnatural for in the case of hens in pens there is a gradual build-up of internal stimuli in the period before laying and the search for a nest begins. This period is characterised by a general restlessness, examination of suitable nest sites, intention movements to enter these sites and displacement activities such as preening. This latter pattern suggests that there is normally a conflict present at this time - probably to nest or not to nest (Wood-Gush, 1954a). The evidence from feral chickens in natural conditions is that they too examine many potential sites before choosing one (McBride, Parer and Foenander, 1969). However, once the nest is entered the hen sits fairly quietly until oviposition. In cages, on the other hand, stereotyped pacing may continue right up until laying. In fact, some stereotyped pacing does occur in pens but not generally to the same extent as in cages.

Thwarting situations probably arise on many other occasions under intensive conditions but they are unlikely to be of the type envisaged by Professor Brambell. For example, broodiness has been almost totally bred out of the modern hybrid so that the incubation or brooding tendency is unlikely to be thwarted. For other reasons fowls are unlikely to be frustrated sexually. In the first place sexual behaviour is closely controlled by visual releasers and if these are absent (as they are likely to be in commercial conditions) there is little possibility of sexual behaviour being initiated. Secondly, if the birds generalize to sub-optimal stimuli, any sexual responses they may show are likely to extinguish quickly because they are not reinforced. If the responses do not extinguish, and there is occasional evidence of this when homosexuality occurs, presumably the birds concerned are being reinforced and so are not frustrated. It would seem that frustrating situations are much more likely to arise when a bird has a tendency to approach one of the facilities such as food trough, drinking fountain or nest-box and there is none available, or there is activation of an avoidance tendency because of fear of a dominant bird or because of some aversive property of the surroundings. Assuming that frustrating situations do occur in industry, are the birds given a chance to respond in the normal manner, that is, by performing displacement preening or stereotyped pacing? There seems no reason why these responses should not take place in pens and battery cages containing one or two birds. However, in crowded multiple-bird cages there could be interference with the performance of responses to frustration by other birds. It is not known what the birds would do instead in this situation and many more observations need to be taken of birds in commercial conditions to see exactly what the incidence of frustration responses is and what particular situations elicit them.

If frustration responses occur in practice (and the available evidence suggests that they do) do they imply anything about the welfare of the birds showing them and do they affect production efficiency? The experimental evidence from this thesis would suggest that although certain of the responses to thwarting do nothing to solve the immediate problem and in fact waste energy, there is no evidence that they are symptomatic of a pathological state. There is some slight evidence in fact that their performance may reduce or at least keep distress to an acceptable limit. For this reason the significance of frustration with respect to the welfare of the chicken kept under intensive conditions is difficult to assess.

However, with regard to production efficiency, the effects of frustration responses are much more obvious. For example increased aggression may result in a wastage of energy and physical injury. Also if dominant birds in a group increase their aggressive responses it may mean that fear is increased in submissive birds. This could lead to submissive birds being frustrated through an "approach food or water or nest-box - avoid dominant bird" conflict building up. The whole process would thus be aggravated. Stereotyped pacing must also waste considerable energy and it would seem that the main deleterious effect of frustration responses will be on productivity and in particular on the food conversion ratio rather than production. On the other hand displacement preening, which in itself is not harmful, could provide a very useful warning of the presence of frustration. When it occurred steps could be taken to avoid prolonging the situation so reducing the risk of stereotyped pacing and increased aggression with their more serious consequences. The problem is one of recognising displacement preening. Although the movements tend to be more frantic and noisy than in normal preening this would only be apparent to a trained eye.

As well as behavioural responses, thwarting may stimulate physiological responses such as the defence reaction as discussed in Chapter 8. These physiological changes always mean a net increase in energy expenditure and in the end this means a higher food conversion ratio. This is over and above any direct effect these changes may have on the process of egg formation (Draper and Lake, 1967).

What can be done to eliminate the undesirable responses to thwarting? There would seem to be three ways of attacking the problem. Firstly the environment could be changed to reduce the possibility of frustrating situations developing. The lay-out of facilities is particularly important, in battery cages as well as pens. Since the fowl is territorial in nature (McBride and Foenander, 1962) facilities should be arranged so that each bird has easy access to them and is not frustrated by having to pass into another bird's territory where it is at a disadvantage (Collias, 1943). Also it may be necessary to provide some sort of secluded area for nesting in battery cages. Secondly, an investigation should be made into the possibility of selecting strains of poultry which do not show undesirable behaviour patterns when thwarted. For example, Wood-Gush

(1969) has shown that there is a great deal of within and between strain variability in the amount of pre-laying pacing shown by caged birds. It may be that some birds require specific stimuli for nesting which the cage does not provide. On the other hand there may be an overall variability in frustration threshold, with birds which show undesirable responses in one frustrating situation more likely to show them in another. In either case more research is required to find out if this is a heritable trait which will respond to selection. Further evidence of between strain variability in responses to frustration is the fact that the Brown Leghorn and broiler-type birds in the present study showed different responses when feeding was frustrated after 24 hours food deprivation (Experiments 2 and 9). Also there was a difference between the responses shown by the birds thwarted by Wood-Gush and Guiton (1967) and the birds in the present study. Thirdly, there is the possibility of treating birds with tranquillizers. It would probably not be necessary to dose the birds continuously but only at critical times when frustration was likely to be great as, for example, during transportation or at point of lay.

In conclusion it may be said that frustrating situations do occur in practice and probably lead to some distress, but the responses the bird makes may help it to adjust to the situation. However, from an economic point of view frustrating situations should be avoided or at least kept to a minimum wherever possible.

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APPENDIX 1

Tables of experimental results where these have not been included in the text. These Tables have the prefix 'A'.

Table 1.1A. Numbers of escape movements occurring during frustrated nesting (first hour).

			Birds							
			P	Y	B/W	P/B	P/Y	G	O	B/O
1	Pen	C.	0	0	0	9	4	0	7	10
		F.	14	6	2	2	43	0	11	6
	Cage	C.	0	4	9	0	0	0	3	0
		F.	0	22	0	4	8	0	14	15
2	Pen	C.	0	0	0	3	0	0	10	2
		F.	16	10	3	12	60	31	36	6
	Cage	C.	0	6	7	6	0	0	30	0
		F.	13	35	24	16	20	14	40	37

C = control
F = frustrated

1 = 1st 30min.
2c= 2nd 30min.

Table 1.2A. Analysis of Variance of escape movements (first hour).

Source of variation	Sums of squares	d.f.	Variance estimate	Variance ratio	P
Situation (S)	9.00	1	9.00	-	n.s.
Frustration (F)	2626.56	1	2626.56	23.96	<0.001
Time (T)	930.25	1	930.25	8.48	<0.01
FxT	676.00	1	676.00	6.16	<0.05
Residual	6466.63	59	109.60		
Total	10708.44	63			

S = pen v cage
F = control v frustrated
T = 1st 30min. v 2nd 30min.

Table 1.3A. Numbers of escape movements occurring during frustrated nesting (30min. before laying).

		Birds							
		P	Y	B/W	P/B	P/Y	G	O	B/O
Pen	C.	0	0	0	6.0	2.0	0	8.5	6.0
	F.	16	58	4	0	0	72	0	18
Cage	C.	0	5.0	8.0	3.0	0	0	16.5	0
	F.	28	55	7	13	0	39	22	64

C = control
F = frustrated

Table 1.4A. Analysis of Variance of escape movements (30min. before laying).

Source of variation	Sums of squares	d.f.	Variance estimate	Variance ratio	P.
Situation	148.78	1	148.78	-	n.s.
Frustration	3612.50	1	3612.50	10.94	∠ 0.01
Residual	9574.10	29	330.14		
Total	13335.38	31			

Situation = pen v cage
Frustration = control v frustrated

Table 1.5A. Number of preens occurring during frustrated nesting (first hour).

			Birds							
			P	Y	B/W	P/B	P/Y	G	O	B/O
1	Pen	C.	9	49	33	83	5	29	76	75
		F.	33	7	8	74	19	88	23	29
	Cage	C.	36	12	99	83	2	20	189	33
		F.	71	23	54	41	29	30	104	29
2	Pen	C.	104	43	55	44	3	54	33	79
		F.	29	4	4	75	18	68	13	99
	Cage	C.	23	30	75	154	8	20	102	46
		F.	50	12	38	37	89	43	48	20

C = control
F = frustrated

1 = 1st 30min.
2 = 2nd 30min.

Table 1.6A. Analysis of Variance of preens (first hour).

Source of variation	Sums of squares	d.f.	Variance estimate	Variance ratio	P
Situation (S)	1269.14	1	1269.14	-	n.s.
Frustration (F)	2462.64	1	2462.64	1.78	n.s.
Time (T)	9.76	1	9.76	-	n.s.
Residual	82994.69	60	1383.24		
Total	86736.23	63			

S = pen v cage
F = control v frustrated
T = 1st 30min. v 2nd 30min.

Table 1.7A. Number of preens occurring during frustrated nesting (30min. before laying).

		Birds							
		P	Y	B/W	P/B	P/Y	G	O	B/O
Pen	C.	56.5	46.0	44.0	63.5	4.0	41.5	54.5	77.0
	F.	29	0	1	22	101	34	0	6
Cage	C.	29.5	21.0	87.0	118.5	5.0	20.0	145.5	39.5
	F.	17	0	8	19	0	41	17	1

C = control
F = frustrated

Table 1.8A. Analysis of variance of preens (30min. before laying).

Source of variation	Sums of squares	d.f.	Variance estimate	Variance ratio	P
Situation	3.78	1	3.78	-	
Frustration	9695.28	1	9695.28	8.66	∠ 0.01
Residual	32440.66	29	1118.64		
Total	42139.72	31			

Situation = pen v cage
Frustration = control v frustrated

Table 1.9A. Numbers of litter-pecks occurring during frustrated nesting (first hour).

		Birds							
		P	Y	B/W	P/B	P/Y	G	O	B/O
1	C.	31	24	39	11	68	51	13	24
	F.	29	32	18	18	37	29	52	43
2	C.	17	19	30	66	65	35	42	6
	F.	23	17	12	0	28	39	21	48

C = control
F = frustrated

1 = 1st 30min.
2 = 2nd 30min.

Table 1.10A. Analysis of Variance of litter-pecks (first hour).

Source of variation	Sums of squares	d.f.	Variance estimate	Variance ratio	P
Frustration (F)	282.03	1	282.03	-	n.s.
Time (T)	81.28	1	81.28	-	n.s.
Residual	8786.91	29	302.99		
Total	9150.22	31			

F = control v frustrated
T = 1st 30min. v 2nd 30min.

Table 1.11A. Numbers of litter-pecks occurring during frustrated nesting (30min. before laying).

		Birds							
		P	Y	B/W	P/B	P/Y	G	O	B/O
Pen	C.	24	23.5	43	33.25	43.75	43.6	24	24
	F.	23	3	4	0	0	22	32	41

C = control

F = frustrated

Table 1.12A. Analysis of Variance of litter-pecks (30min. before laying)

Source of variation	Sums of squares	d.f.	Variance estimate	Variance ratio	P
Frustration (F)	1123.93	1	1123.93	6.42	∠0.05
Residual	2448.11	14	174.86		
Total	3572.04	15			

F = control v frustrated

Table 2.1A. Numbers of thwarted pecks occurring during frustrated feeding.

		Birds			
		B	W	R/Y	B/P
Trials	1.	217	739	463	371
	2.	21	122	81	160
	3.	6	44	10	139
	4.	26	48	66	327
	5.	78	266	301	115
	6.	217	238	84	182
	7.	10	357	119	136
	8.	0	100	42	31

Table 2.2A. Analysis of Variance of thwarted pecks.

Source of variation	Sums of squares	d.f.	Variance estimate	Variance ratio	P
Trials	462,955	7	66,136	4.60	∠ 0.01
Residual	344,999	24	14,375		
Total	807,954	31			

Trials = trials 1 - 8

Table 2.3A. Numbers of redirected pecks occurring during frustrated feeding.

Trial	Situation	Birds B	W	R/Y	B/P
1.	H/F	4	6	0	4
	NH/NF	61	17	4	3
	F	10	2	6	5
2.	H/F	18	19	7	14
	NH/NF	11	10	3	4
	F	8	6	15	0
3.	H/F	13	0	0	0
	NH/NF	45	14	0	19
	F	4	38	11	4
4.	H/F	21	11	8	0
	NH/NF	24	20	7	0
	F	3	3	3	0
5.	H/F	23	27	4	0
	NH/NF	20	25	0	3
	F	3	6	0	0
6.	H/F	3	13	0	0
	NH/NF	8	10	8	2
	F	79	23	0	11
7.	H/F	23	14	0	2
	NH/NF	72	24	0	8
	F	9	11	10	10
8.	H/F	9	15	2	5
	NH/NF	112	11	0	2
	F	20	18	9	16

Table 2.4A. Analysis of Variance of redirected pecks.

Source of variation	Sums of squares	d.f.	Variance estimate	Variance ratio	P
Frustration	1325	2	662	2.17	n.s.
Trials	973	7	139	-	n.s.
Residual	26275	86	305		
Total	28573	95			

Frustration = H/F v NH/NF v F
Trials = Trials 1 - 8

Table 2.5A. Numbers of stereotyped movements occurring during frustrated feeding.

Trial	Situation	Birds			
		B	W	R/Y	B/P
1.	H/F	23	2	0	0
	NH/NF	30	6	52	0
	F	144	70	204	56
2.	H/F	0	0	14	0
	NH/NF	0	2	2	9
	F	169	152	149	54
3.	H/F	30	63	91	0
	NH/NF	56	10	8	0
	F	207	83	207	250
4.	H/F	0	0	0	0
	NH/NF	0	86	0	0
	F	204	191	177	121
5.	H/F	7	31	0	0
	NH/NF	48	54	0	2
	F	195	184	113	200
6.	H/F	40	3	48	0
	NH/NF	2	2	0	0
	F	64	191	80	176
7.	H/F	18	12	0	0
	NH/NF	42	128	0	0
	F	183	307	211	121
8.	H/F	18	27	0	0
	NH/NF	40	6	0	0
	F	198	241	173	78

Table 2.6A. Analysis of Variance of stereotyped movements.

Source of variation	Sums of squares	d.f.	Variance estimate	Variance ratio	P
Frustration	449,179	2	224,589	135.46	/_ 0.001
Trials	19,704	7	2828	1.70	n.s.
Residual	142,609	86	1658		
Total	611,582	95			

Frustration = H/F v NH/NF v F

Trials = Trials 1 - 8

Table 2.7A. Numbers of preens occurring during frustrated feeding.

Trial	Situation	Birds			
		B	W	R/Y	B/P
	H/F	14	22	0	0
1.	NH/NF	44	76	51	62
	F	22	48	0	55
	H/F	8	3	0	4
2.	NH/NF	12	90	32	59
	F	2	4	4	45
	H/F	0	10	0	0
3.	NH/NF	21	24	30	19
	F	7	43	10	14
	H/F	5	0	0	7
4.	NH/NF	101	5	3	42
	F	17	30	38	35
	H/F	0	2	2	2
5.	NH/NF	36	30	25	88
	F	32	32	98	45
	H/F	4	1	0	0
6.	NH/NF	43	186	93	18
	F	40	7	13	24
	H/F	7	11	42	5
7.	NH/NF	73	54	49	82
	F	40	0	14	40
	H/F	4	2	6	10
8.	NH/NF	46	25	7	43
	F	12	7	17	9

Table 2.8A. Analysis of Variance of preens.

Source of variation	Sums of squares	d.f.	Variance estimate	Variance ratio	P
Frustration	30,628	2	15,314.0	25.33	/0.001
Trials	6,177	7	888.43	1.46	n.s.
Residual	51,997	86	604.62		n.s.
Total	88,802	95			

Frustration = H/F v NH/NF v F

Trials = Trials 1 - 8

Table 2.9A. Numbers of feather raises occurring during frustrated feeding.

Trial	Situation	Birds			
		B	W	R/Y	B/P
1.	H/F	1	1	1	0
	NH/NF	2	2	3	1
	F	0	5	1	1
2.	H/F	1	0	1	1
	NH/NF	0	1	2	2
	F	2	1	3	3
3.	H/F	1	2	0	0
	NH/NF	1	1	0	1
	F	1	2	1	1
4.	H/F	1	3	1	2
	NH/NF	2	1	1	1
	F	2	3	2	3
5.	H/F	0	1	1	0
	NH/NF	1	3	1	1
	F	1	5	1	2
6.	H/F	1	0	2	0
	NH/NF	0	1	1	0
	F	1	2	1	1
7.	H/F	1	0	2	1
	NH/NF	1	2	0	2
	F	1	7	1	1
8.	H/F	2	0	1	1
	NH/NF	2	1	0	0
	F	2	6	2	1

Table 2.10A. Analysis of Variance of feather raises.

Source of variation	Sums of squares	d.f.	Variance estimate	Variance ratio	P
Frustration	23.69	2	11.84	8.77	/0.001
Trials	6.75	7	0.96	-	
Residual	116.06	86	1.35		
Total	146.50	95			

Frustration = H/F v NH/NF v F

Trials = Trials 1 - 8

Table 2.11A. Numbers of bill-wipes occurring during frustrated feeding.

Trial	Situation	Birds			
		B	W	R/Y	B/P
1.	H/F	9	3	5	0
	NH/NF	3	1	12	3
	F	11	0	0	4
2.	H/F	0	13	1	7
	NH/NF	2	1	1	0
	F	0	0	2	0
3.	H/F	6	1	0	0
	NH/NF	1	6	0	14
	F	0	1	2	0
4.	H/F	4	13	14	0
	NH/NF	1	23	4	3
	F	0	2	3	0
5.	H/F	12	17	17	4
	NH/NF	1	11	0	0
	F	0	0	0	0
6.	H/F	8	7	4	0
	NH/NF	1	0	0	2
	F	0	0	2	0
7.	H/F	2	7	11	1
	NH/NF	10	3	0	4
	F	0	0	0	0
8.	H/F	5	0	2	1
	NH/NF	0	2	0	0
	F	5	0	0	0

Table 2.12A. Analysis of Variance of bill-wipes

Source of variation	Sums of squares	d.f.	Variance estimate	Variance ratio	P
Frustration	315.8	2	157.9	8.14	< 0.001
Trials	205.5	7	29.4	1.51	n.s.
Residual	1670.1	86	19.4		
Total	2191.4	95			

Frustration = H/F v NH/NF v F

Trials = 1 - 8

Table 2.13A. Numbers of minutes spent sleeping during frustrated feeding.

Trial	Situation	Birds			
		B	W	R/Y	B/P
1.	H/F	0	0	0	0
	NH/NF	0	0	0	0.26
	F	0	0	0	0
2.	H/F	0	0	0	0
	NH/NF	0.40	0	0	0
	F	0	0	0	0
3.	H/F	0	0	0	0
	NH/NF	0	0	4.30	0.02
	F	0	0	0	0
4.	H/F	0	0	0	0
	NH/NF	0.55	0	11.16	0
	F	0	0	0	0
5.	H/F	0	0	0	0
	NH/NF	0	0	2.83	0.46
	F	0	0	0	0
6.	H/F	0	0	0	0
	NH/NF	2.63	0	7.65	0.48
	F	0	0	0	0
7.	H/F	0	0	0.93	0
	NH/NF	0	0	1.31	0
	F	0	0	0	0
8.	H/F	0	0	0	0
	NH/NF	0	0	0.95	0.51
	F	0	0	0	0

Table 2.14A. Numbers of minutes spent resting during frustrated feeding.

Trial	Situation	Birds			
		B	W	R/Y	B/P
1.	H/F	0	2	0	10
	NH/NF	1	5	5	12
	F	1	1	2	4
2.	H/F	0	0	0	0
	NH/NF	19	10	16	8
	F	0	0	0	0
3.	H/F	0	0	7	3
	NH/NF	2	18	28	18
	F	0	9	2	0
4.	H/F	3	2	16	3
	NH/NF	11	8	25	23
	F	0	2	4	2
5.	H/F	0	0	10	0
	NH/NF	6	3	21	8
	F	0	0	3	0
6.	H/F	2	1	3	11
	NH/NF	20	12	22	22
	F	2	0	15	0
7.	H/F	2	0	13	0
	NH/NF	3	1	15	10
	F	0	0	1	0
8.	H/F	4	3	14	10
	NH/NF	3	15	24	14
	F	1	0	6	3

Table 2.15A. Analysis of Variance of minutes spent resting.

Source of variation	Sums of squares	d.f.	Variance estimate	Variance ratio	P
Frustration	2185	2	1092.5	37.03	∠ 0.001
Trials	449	7	64.1	2.17	∠ 0.05
Residual	2540	86	29.5		
Total	5174	95			

Frustration = H/F v NH/NF v F

Trials = 1 - 8

Table 2.16A. Numbers of vocalizations occurring during frustrated feeding.

Trial	Situation	Birds			
		B	W	R/Y	B/P
1.	H/F	0	1	0	0
	NH/NF	0	2	0	4
	F	0	5	0	0
2.	H/F	2	0	0	0
	NH/NF	1	2	0	0
	F	0	0	0	4
3.	H/F	0	0	0	0
	NH/NF	0	0	0	1
	F	5	0	0	3
4.	H/F	1	0	2	0
	NH/NF	2	0	0	0
	F	0	0	0	0
5.	H/F	0	4	0	1
	NH/NF	1	1	0	1
	F	4	0	7*	2
6.	H/F	0	0	0	0
	NH/NF	3	0	0	0
	F	2	3	1	0
7.	H/F	0	0	0	2
	NH/NF	0	0	0	1
	F	0	0	0	0
8.	H/F	0	0	0	0
	NH/NF	3	0	4	0
	F	1	0	0	2

* high intensity, ground-predator alarm calls

Table 3.1A. Numbers of preens occurring during frustrated feeding.

6 Hour Deprivation Group

Trials	Situations	P/M	G/R	B/R	P/Y	M	Bk	P/G	R/Y
1.	NH/NF	3	8	12	0	8	0	7	5
	F	5	22	21	17	24	15	42	23
2.	NH/NF	2	9	0	5	6	9	3	0
	F	19	31	32	24	28	31	26	34
3.	NH/NF	0	19	21	7	6	3	0	0
	F	10	59	23	30	38	25	32	39

24 Hour Deprivation Group

Trials	Situations	B/Y	Y/Bk	G/W	G/O	B/M	G/Y	O	B
1.	NH/NF	10	7	0	2	0	8	8	22
	F	15	21	26	14	11	19	17	38
2.	NH/NF	6	6	12	11	2	7	12	15
	F	0	3	2	3	5	3	3	2
3.	NH/NF	9	3	2	6	10	26	6	14
	F	0	7	0	4	5	0	8	6

Table 3.2A. Analyses of Variance of preens occurring during frustrated feeding.

6 Hour Deprivation Group

Source of variation	Sums of squares	d.f.	Variance estimate	Variance ratio	P
Frustration	5568.5	1	5568.5	74.54	< 0.001
Trials	312.9	2	156.4	2.09	n.s.
Residual	3288.9	44	74.7		
Total	9170.3	47			

Frustration = NH/NF v F
Trials = Trials 1 - 3

24 Hour Deprivation Group

Source of variation	Sums of squares	d.f.	Variance estimate	Variance ratio	P
Frustration (F)	6.8	1	6.8	-	n.s.
Trials (T)	559.5	2	279.7	7.08	<0.01
Interaction (FxT)	907.5	2	453.7	11.49	<0.001
Residual	1660.5	42	39.5		
Total	3124.3	47			

Frustration = NH/NF v F
Trials = Trials 1 - 3

Table 3.3A. Number of stereotyped movements occurring during frustrated feeding.

6 Hour Deprivation Group

Trials	Situation	P/M	G/R	B/R	P/Y	M	Bk	P/G	R/Y
1.	NH/NF	0	0	0	0	0	5	0	0
	F	2	5	3	10	4	4	1	9
2.	NH/NF	9	2	0	0	0	0	0	0
	F	1	3	5	4	4	2	4	3
3.	NH/NF	0	1	0	0	2	0	1	2
	F	2	2	16	3	2	3	3	4

24 Hour Deprivation Group

Trials	Situation	B/Y	Y/Bk	G/W	G/O	B/M	G/Y	O	B
1.	NH/NF	0	0	0	0	0	1	0	0
	F	0	5	21	4	5	18	3	21
2.	NH/NF	0	0	2	0	0	2	0	0
	F	24	8	101	22	16	33	17	33
3.	NH/NF	1	0	7	0	0	2	4	2
	F	17	12	161	27	29	34	34	63

Table 3.4A. Analyses of variance of stereotyped movements occurring during frustrated feeding.

6 Hour Deprivation Group

Source of variation	Sums of squares	d.f.	Variance estimate	Variance ratio	P
Frustration	125.5	1	125.50	15.55	∠ 0.01
Trials	1.2	2	0.60	-	n.s.
Residual	349.3	44	7.94		
Total	474.0	47			

Frustration = NH/NF v F
Trials = Trials 1 - 3

24 Hour Deprivation Group

Source of variation	Sums of squares	d.f.	Variance estimate	Variance ratio	P
Frustration	19832.7	1	19832.7	55.97	∠0.001
Trials	3121.9	2	1560.95	4.40	∠0.05
Residual	15590.6	44	354.33		
Total	38545.3	47			

Frustration = NH/NF v F
Trials = Trials 1 - 3

Table 4.1A. Numbers of preens occurring during frustrated feeding.

Trials	Situation	Birds					
	[illegible]	W	G/M	B/W	B/P	Bk	R/M
1.	NH/NF	11	15	7	10	7	0
	F	56	18	15	17	16	20
2.	NH/NF	0	0	7	6	4	0
	F	20	15	18	18	30	17
3.	NH/NF	6	0	7	9	7	0
	F	21	7	15	7	34	18

Table 4.2A. Analysis of Variance of preens occurring during frustrated feeding.

Source of variation	Sums of squares	d.f.	Variance estimate	Variance ratio	P
Frustration	1965.4	1	1965.4	28.46	$\underline{/}$0.001
Trials	194.0	2	97.0	1.40	n.s.
Residual	2209.8	32	69.06		
Total	4369.2	35			

Frustration = NH/NF v F

Trials = Trials 1 - 3

Table 6.1A. Number of preens occurring during frustrated incubation

Trials	Situation	Birds						
		P/Y	G	B/G	M/Y	M/R	G/Y	Y
	C.	0	3	0	2	4	6	0
1.	FI.	67	72	64	61	65	48	2
	FO.	137	67	56	116	74	39	72
	C.	5	0	0	4	12	9	5
2.	FI.	88	44	0	153	53	60	0
	FO.	49	61	40	99	19	21	59
	C.	2	0	6	0	3	0	0
3.	FI.	106	64	0	129	42	53	0
	FO.	70	57	57	50	89	81	55

C. = Control
FI. = Frustrated/Eggs inside cage
FO. = Frustrated/Eggs outside cage

Table 6.2A. Analysis of Variance of preens.

Source of variation	Sums of squares	d.f.	Variance estimate	Variance ratio	P
Frustration	47288.2	2	23644.1	27.23	< 0.001
Trials	721.3	2	360.7	-	
Residual	50402.9	58	869.01		
Total	98412.4	62			

Frustration = C v FI v FO

Trials = Trials 1 - 3

Table 6.3A. Number of litter-pecks occurring during frustrated incubation.

Trials	Situation	Birds						
		P/Y	G	B/G	M/Y	M/R	G/Y	Y
	C.	4	6	0	0	10	4	7
1.	FI.	7	54	41	11	46	69	52
	FO.	0	16	41	0	24	39	12
	C.	15	8	4	5	0	15	7
2.	FI.	9	89	48	62	92	123	19
	FO.	10	24	26	0	90	60	267
	C.	0	11	0	0	11	8	22
3.	FI.	65	64	7	12	357	84	40
	FO.	94	40	20	11	31	79	54

C. = Control
FI. = Frustrated/Eggs inside cage
FO. = Frustrated/Eggs outside cage

Table 6.4A. Analysis of Variance of litter-pecks

Source of variation	Sums of squares	d.f.	Variance estimate	Variance ratio	P
Frustration	36285.18	2	18142.59	6.23	< 0.05
Trials	9583.46	2	4791.73	1.64	n.s.
Residual	168987.11	58	2913.57		
Total	214855.75	62			

Frustration = C v FI v FO

Trials = Trials 1 - 3

Table 7.1A. Number of preens occurring during frustrated incubation

Trials	Situation	Birds					
		Bk	P	M	W	Br	R
1.	C.	0	15	0	4	0	0
	F/I.	16	10	37	51	48	72
	F/II.	123	15	61	52	52	16
2.	C.	17	0	8	6	6	0
	F/I.	130	41	59	51	65	46
	F/II.	54	47	53	47	47	32

C = Control
F/I = Frustrated/Access to Room I
F/II = Frustrated/Access to Rooms I and II

Table 7.2A. Analysis of Variance of preens

Source of variation	Sums of squares	d.f.	Variance estimate	Variance ratio	P
Frustration	17235.50	2	8617.75	15.10	∠ 0.001
Trials	521.36	1	521.36	-	n.s.
Residual	18259.89	32	570.62		
Total	36016.75	35			

Frustration = C v F/I v F/II
Trials = Trials 1 - 2

Table 7.3A. Number of litter-pecks occurring during frustrated incubation

Trials	Situation	Birds					
		Bk	P	M	W	Br	R
1.	C.	3	6	12	17	0	0
	F/I.	7	67	52	196	31	29
	F/II.	40	170	112	226	75	65
2.	C.	4	13	14	3	8	8
	F/I.	13	182	146	95	102	74
	F/II.	42	117	124	254	134	132

C = Control
F/I = Frustrated/Access to Room I
F/II = Frustrated/Access to Rooms I and II

Table 7.4A. Analysis of Variance of litter-pecks

Source of variation	Sums of squares	d.f.	Variance estimate	Variance ratio	P
Frustration	84340.39	2	42170.19	14.85	< 0.001
Trials	3540.25	1	3540.25	1.25	n.s.
Residual	90886.33	32	2840.20		
Total	178766.97	35			

Frustration = C v F/I v F/II
Trials = Trials 1 - 2

Table 8.1A. The % time spent by the broody birds in different parts of the pen when allowed different types of contact with distressed chicks.

Type of Contact	Part of pen	Birds					
		P/Y	G	B/G	M/R	G/Y	Y
	Near	11	1	0	0	3	9
NC	Middle	67	62	63	57	52	56
	Away	22	37	37	43	45	35
	Near	17	16	18	10	18	13
VC	Middle	33	31	31	23	28	25
	Away	50	53	51	67	54	62
	Near	41	20	23	29	35	30
AC	Middle	17	8	11	9	9	8
	Away	42	72	66	62	56	62
	Near	84	80	81	97	87	92
VAC	Middle	3	0	5	3	4	6
	Away	13	20	14	0	9	2

NC = no contact
VC = visual contact
AC = auditory contact
VAC = visual and auditory contact

Table 8.2A. A comparison of the mean % times spent in the "Near" part of the pen when broody hens were allowed different types of contact with distressed chicks.

Condition		Visual and auditory contact	Auditory contact	Visual contact	No contact
	% time	86.9%	29.6%	15.3%	4.0%
Expected results if hen walked about at random	9.0%	* * *	t = 6.59 * *	t = 4.58 * *	t = 2.54 n.s.
No Contact	4.0%	* * *	t = 11.76 * * *	t = 4.11 * *	
Visual contact	15.3%	* * *	t = 4. 34 * *		
Auditory contact	29.6%	t = 16.12 * * *			

't'- values were not calculated where the level of statistical significance was obvious by extrapolation from other comparisons.

* * * $p \angle 0.001$

* * $p \angle 0.01$

Table 8.3A. A comparison of the mean % times spent in the "Middle" part of the pen when broody hens were allowed different types of contact with distressed chicks.

Condition		Visual and auditory contact	Auditory contact	Visual contact	No Contact
	% time	3.5%	10.3%	28.5%	59.5%
Expected results if hen walked about at random	70.5%	* * *	* * *	* * *	t = 4.94 * *
No Contact	59.5%	* * *	* * *	t = 20.47 * * *	
Visual Contact	28.5%	* * *	t = 14.00 * * *		
Auditory Contact	10.3%	t = 4.13 * *			

't'- values were not calculated where the level of statistical significance was obvious by extrapolation from other comparisons.

* * * $p < 0.001$

* * $p < 0.01$

Table 8.4A. A comparison of the mean % times spent in the "Away" parts of the pen when broody hens were allowed different types of contact with distressed chicks.

Condition		Visual and auditory contact	Auditory contact	Visual contact	No contact
	% time	9.7%	60.0%	56.2%	36.5%
Expected results if hen walked about at random	20.5%	t = 3.49 *	* * *	t = 12.62 * * *	* * *
No Contact	36.5%	t = 5.13 * *	* *	t = 6.19 * *	
Visual Contact	56.2%	* * *	t = 0.86 n.s.		
Auditory Contact	60.0%	* * *			

't'- values were not calculated where the level of statistical significance was obvious by extrapolation from other comparisons.

* * * p ∠ 0.001
* * p ∠ 0.01
* p ∠ 0.05

Table 8.5A. The number of preens occurring when broody birds were allowed different types of contact with distressed chicks.

Situation	Birds					
	P/Y	G	B/G	M/R	G/Y	Y
T	0	7	14	13	0	5
NC	38	85	46	44	40	30
VC	18	36	40	37	35	15
AC	17	46	36	29	27	23
VAC	11	4	15	2	11	0

T = together

NC = no contact

VC = visual contact

AC = auditory contact

VAC = visual and auditory contact

Table 8.6A. A comparison of the mean numbers of preens which occurred when broody hens were allowed different types of contact with distressed chicks.

Condition		Visual and auditory contact	Auditory contact	Visual contact	No contact
	No. of preens	7.2	29.7	30.2	47.2
Together	6.5	t = 0.18 n.s.	t = 6.46 * *	t = 6.62 * *	t = 5.24 * *
No Contact	47.2	t = 4.72 * *	t = 3.70 *	t = 2.48 n.s.	
Visual Contact	30.2	t = 5.35 * *	n.s.		
Auditory Contact	29.7	t = 4.59 * *			

* * p /_0.01

* p /_0.05

Table 10.1A. Numbers of wing-flaps occurring during frustrated sexual behaviour.

Trial	Situation	Birds					
		R/R	B/B	P	G/G	Y	O/O
	C.	4	23	7	1	3	20
1.	S.	4	3	0	0	0	4
	F.	21	9	14	8	18	24
	C.	3	20	4	1	4	20
2.	S.	2	7	1	2	2	6
	F.	8	21	13	9	11	27
	C.	1	10	2	4	7	17
3.	S.	4	3	2	1	2	4
	F.	14	18	9	11	24	41
	C.	3	38	7	6	7	14
4.	S.	4	4	2	1	1	8
	F.	11	27	12	10	22	21

C = control
S = sexual contact
F = frustrated

Table 10.2A. Analysis of Variance of wing-flaps.

Source of variation	Sums of squares	d.f.	Variance estimate	Variance ratio	P
Frustration	2754.25	2	1377.12	29.01	∠ 0.001
Trials	48.11	3	16.03	-	n.s.
Residual	3133.64	66	47.47		
Total	5936.0	71			

Frustration = Control v sexual contact v frustrated

Trials = Trials 1 - 4

Table 11.1A. The numbers of preens and stereotyped movements during frustrated feeding after 0 days training and various deprivation schedules.

Deprivation	Situation	Birds					
<u>6 hours</u>		0	0/0	0/R	0/W	0/P	0/Bk
No. of preens	F1	26	38	53	46	44	43
	F2	45	29	37	37	36	44
	NH/NF	0	0	12	9	5	7
No. of stereotyped movements	F1	0	1	0	0	0	1
	F2	0	0	0	0	0	0
	NH/NF	0	0	0	0	0	0
<u>10 hours</u>		M	M/M	M/R	M/W	M/Bk	M/G
No. of preens	F1	37	28	27	31	33	19
	F2	40	31	29	38	64	34
	NH/NF	10	0	3	7	0	4
No. of stereotyped movements	F1	0	0	0	0	1	0
	F2	0	0	0	0	0	0
	NH/NF	0	0	0	0	0	0
<u>24 hours</u>		Y	Y/Y	Y/R	Y/W	Y/M	Y/Bk
No. of preens	F1	26	42	32	31	42	48
	F2	57	62	58	39	58	28
	NH/NF	7	8	0	0	14	10
No. of stereotyped movements	F1	0	0	0	0	0	0
	F2	0	0	0	0	0	0
	NH/NF	0	0	0	0	0	0

F1 = first frustration test
F2 = second frustration test
NH/NF = not hungry/no food

Table 11.2A. The numbers of preens and stereotyped movements during frustrated feeding after 3 days training and various deprivation schedules.

Deprivation	Situation	Birds					
<u>6 hours</u>		G	G/G	G/R	G/W	G/Bk	G/0
No. of preens	F1	26	24	20	28	20	19
	F2	80	48	27	40	33	40
	NH/NF	7	10	0	17	3	7
No. of stereotyped movements	F1	0	0	0	0	0	0
	F2	0	0	0	0	0	0
	NH/NF	0	0	0	0	0	0
<u>10 hours</u>		P	P/P	P/R	P/W	P/Bk	P/Br
No. of preens	F1	10	9	26	26	24	10
	F2	31	17	31	46	24	36
	NH/NF	10	0	16	17	16	11
No. of stereotyped movements	F1	0	0	0	7	0	0
	F2	1	0	0	0	0	0
	NH/NF	0	0	0	0	0	0
<u>24 hours</u>		Br	Br/Br	Br/R	Br/W	Br/Bk	Br/Y
No. of preens	F1	7	22	13	16	14	0
	F2	39	37	23	17	23	18
	NH/NF	8	11	6	0	7	0
No. of stereotyped movements	F1	19	3	11	30	8	38
	F2	22	14	30	55	34	55
	NH/NF	0	0	0	0	0	0

F1 = first frustration test
F2 = second frustration test
NH/NF = not hungry/no food

Table 11.3A. The number of preens and stereotyped movements during frustrated feeding after 10 days training and various deprivation schedules.

Deprivation	Situation	Birds					
6 hours		Bk	Bk/Br	Bk/M	Bk/P	Bk/O	Bk/Y
No. of preens	F1	37	52	36	41	30	30
	F2	28	33	28	47	32	37
	NH/NF	8	17	3	7	4	5
No. of stereotyped movements	F1	2	2	1	1	8	16
	F2	0	0	1	2	0	4
	NH/NF	0	0	0	3	0	1
10 hours		W/Br	W/P	W/G	W/Y	W	W/M
No. of preens	F1	0	3	3	9	4	3
	F2	0	0	0	5	2	6
	NH/NF	15	16	17	21	7	17
No. of stereotyped movements	F1	77	65	54	39	35	64
	F2	81	129	85	76	74	66
	NH/NF	9	0	0	0	0	0
24 hours		R/G	R/Y	R	R/W	R/M	R/P
No. of preens	F1	0	0	2	9	10	0
	F2	0	0	0	3	3	0
	NH/NF	9	11	10	6	0	3
No. of stereotyped movements	F1	95	48	98	80	33	118
	F2	134	63	102	73	63	176
	NH/NF	0	0	4	0	0	0

F1 = first frustration test
F2 = second frustration test
NH/NF = not hungry/no food

Table 12.1A. Numbers of stereotyped movements occurring during frustrated feeding after the administration of certain drugs.

Trial	Drug	Situation	Birds			
			B	W	R/Y	B/P
1.	Nembutal	NH/NF	0	0	0	0
		F	77	81	61	15
	Oblivon	NH/NF	0	2	0	0
		F	111	59	73	31
	Pacitran	NH/NF	0	5	0	0
		F	51	30	13	14
	Saline	NH/NF	0	7	0	0
		F	152	72	95	43
2.	Nembutal	NH/NF	0	9	5	0
		F	29	48	70	54
	Oblivon	NH/NF	0	4	0	0
		F	63	55	92	23
	Pacitran	NH/NF	2	0	0	0
		F	11	39	29	17
	Saline	NH/NF	0	5	0	6
		F	129	64	135	62
3.	Nembutal	NH/NF	1	2	0	0
		F	85	67	38	42
	Oblivon	NH/NF	0	0	3	0
		F	66	43	50	21
	Pacitran	NH/NF	0	0	0	0
		F	21	14	30	8
	Saline	NH/NF	0	0	0	0
		F	113	93	141	39

NH/NF = not hungry/no food
F = frustrated

Table 12.1A. Numbers of stereotyped movements occurring during frustrated feeding after the administration of certain drugs.

Trial	Drug	Situation	Birds			
			B	W	R/Y	B/P
1.	Nembutal	NH/NF	0	0	0	0
		F	77	81	61	15
	Oblivon	NH/NF	0	2	0	0
		F	111	59	73	31
	Pacitran	NH/NF	0	5	0	0
		F	51	30	13	14
	Saline	NH/NF	0	7	0	0
		F	152	72	95	43
2.	Nembutal	NH/NF	0	9	5	0
		F	29	48	70	54
	Oblivon	NH/NF	0	4	0	0
		F	63	55	92	23
	Pacitran	NH/NF	2	0	0	0
		F	11	39	29	17
	Saline	NH/NF	0	5	0	6
		F	129	64	135	62
3.	Nembutal	NH/NF	1	2	0	0
		F	85	67	38	42
	Oblivon	NH/NF	0	0	3	0
		F	66	43	50	21
	Pacitran	NH/NF	0	0	0	0
		F	21	14	30	8
	Saline	NH/NF	0	0	0	0
		F	113	93	141	39

NH/NF = not hungry/no food
F = frustrated

Table 12.2A. Analysis of Variance of numbers of stereotyped movements occurring during frustrated feeding after the administration of certain drugs.

Source of variation	Sums of squares	d.f.	Variance estimate	Variance ratio	P
Drugs	15881.83	3	5297.27	10.03	$p < 0.01$
Frustration	76953.37	1	76953.37	145.83	$p < 0.001$
Trials	212.31	2	106.15	-	n.s.
Residual	46964.99	89	527.69		
Total	140012.50	95			

Drugs = Nembutal v Oblivon v Pacitran v saline

Frustration = NH/NF v F

Trials = trials 1 - 3

Table 13.1A. Numbers of stereotyped movements, preens and thwarted feeding bouts occurring during frustrated feeding after injection with Pacitran or saline.

Activity	Days	Birds							
		P	P/W	R/M	B/W	G/W	R/W	P/R	M/W
Stereotyped movements	1st	437	150	221	104	170	103	221	69
	2nd	334	260	131	130	43	93	131	219
	3rd	487	139	95	146	129	73	85	199
	4th	350	241	198	44	70	112	233	86
Preens	1st	0	23	0	15	9	27	2	24
	2nd	0	0	7	0	22	8	28	9
	3rd	0	15	31	2	12	12	8	3
	4th	0	0	4	8	12	0	3	11
Thwarted feeding bouts	1st	3	19	36	16	17	22	27	25
	2nd	8	12	18	11	22	35	28	27
	3rd	3	15	15	21	18	18	21	21
	4th	4	18	16	19	15	34	30	16

saline tests not underlined

Pacitran tests underlined

Table 13.2A. Analyses of Variance of stereotyped movements, preens and thwarted feeding bouts.

Stereotyped movements

Source of variation	Sums of squares	d.f.	Variance estimate	Variance ratio	P
Days	1664.84	3	554.946	-	n.s.
Drugs	69285.03	1	69285.03	6.36	p ∠ 0.05
Residual	294257.10	27	10898.41		
Total	365206.97	31			

Preens

Source of variation	Sums of squares	d.f.	Variance estimate	Variance ratio	P
Days	256.59	3	85.53	1.65	n.s.
Drugs	1140.03	1	1140.03	22.07	p ∠ 0.001
Residual	1394.85	27	51.66		
Total	2791.47	31			

Thwarted feeding bouts

Source of variation	Sums of squares	d.f.	Variance estimate	Variance ratio	P
Days	81.13	3	27.04	-	n.s.
Drugs	72.00	1	72.00	-	n.s.
Residual	2066.75	27	76.55		
Total	2219.88	31			

Days = 1 - 4
Drugs = saline v Pacitran

Table 15.1A. Amounts of food (in grams) eaten in 20min. after injections of saline or Pacitran.

Trial	Treatment	Birds					
		M	Y	G	O/W	G/Y	B
1.	saline	85.4	56.1	63.2	55.7	78.5	81.5
	Pacitran	73.0	61.8	63.1	63.7	59.0	73.6
2.	saline	83.2	56.3	60.2	65.9	82.7	107.4
	Pacitran	94.2	48.7	56.6	83.0	77.8	81.4
3.	saline	100.4	67.7	68.1	87.0	94.0	105.1
	Pacitran	110.6	46.0	62.5	66.8	69.8	85.3
4.	saline	78.1	67.3	64.8	61.7	76.7	76.3
	Pacitran	95.3	71.8	82.3	75.6	71.3	91.4
5.	saline	79.3	89.0	69.1	60.9	73.2	88.8
	Pacitran	86.8	64.5	64.5	64.2	88.4	69.7
6.	saline	95.4	64.6	62.3	76.3	68.1	66.3
	Pacitran	62.5	74.3	76.0	69.7	75.6	88.1

Table 15.2A. Analysis of Variance of amounts of food (in grams) eaten in 20min.

Source of variation	Sums of squares	d.f.	Variance estimate	Variance ratio	P
Drugs	63.66	1	63.66	-	n.s.
Trials	975.20	5	195.04	1.03	n.s.
Residual	12250.54	65	188.45		
Total	13289.40	71			

Drugs = saline v Pacitran

Trials = trials 1 - 6

Table 15.3A. Mean rates of key-pecking (in responses per second) after injections of saline or Pacitran.

Trial	Treatment	Birds					
		B/W	R/Y	R/M	G/M	W	R/W
1.	saline	0.84	0.73	0.62	0.75	0.64	0.57
	Pacitran	0.73	0.57	0.52	0.62	0.66	0.63
2.	saline	0.76	0.64	0.51	0.63	0.69	0.68
	Pacitran	0.78	0.65	0.63	0.70	0.71	0.56
3.	saline	0.71	0.74	0.59	0.55	0.74	0.68
	Pacitran	0.81	0.67	0.57	0.75	0.74	0.57

Table 15.4A. Analysis of Variance of rates of key-pecking (in responses per second).

Source of variation	Sums of squares	d.f.	Variance estimate	Variance ratio	p
Drugs	0.001	1	0.0010	-	n.s.
Trials	0.003	2	0.0015	-	n.s.
Residual	0.236	32	0.0073		
Total	0.240	35			

Drugs = saline v Pacitran

Trials = trials 1 - 3

Table 15.5A. Numbers of back and forward movements occurring after injection of saline or Pacitran.

Trial	Treatment	R	R/G	R/B	W/M	W/Y	O	O/M	O/B
		Birds							
1.	saline	77	61	81	74	83	54	72	61
	Pacitran	102	75	94	80	96	66	77	35
2.	saline	98	81	81	89	96	69	60	63
	Pacitran	105	59	80	92	87	64	82	68
3.	saline	106	80	87	91	104	71	82	89
	Pacitran	91	76	82	91	90	68	79	63

Table 15.6A. Analysis of Variance of back and forward movements.

Source of variation	Sums of squares	d.f.	Variance estimate	Variance ratio	P
Drugs	1.34	1	1.34	-	n.s.
Trials	821.17	2	410.58	1.92	n.s.
Residual	9389.16	44	213.39		
Total	10211.67	47			

Drugs = saline v Pacitran

Trials = trials 1 - 3

Table 19.1A. Numbers of aggressive responses occurring after frustrated feeding.

	Trial	Situation	Threats	Pecks	Grips	Chases
Pair 1.	1.	NH/NF	0	0	0	0
		H/Frus.	24	12	2	3
	2.	NH/NF	3	0	0	0
		H/Frus.	23	3	0	0
	3.	NH/NF	0	0	0	0
		H/Frus.	30	12	1	0
Pair 2.	1.	NH/NF	27	2	6	0
		H/Frus.	53	37	23	1
	2.	NH/NF	22	5	4	0
		H/Frus.	98	34	26	6
	3.	NH/NF	19	0	2	0
		H/Frus.	67	51	24	1
Pair 3.	1.	NH/NF	0	5	0	0
		H/Frus.	10	17	5	0
	2.	NH/NF	4	1	0	0
		H/Frus.	54	8	4	0
	3.	NH/NF	4	1	0	0
		H/Frus.	40	15	3	0
Pair 4.	1.	NH/NF	0	0	0	0
		H/Frus.	63	29	9	0
	2.	NH/NF	2	0	0	0
		H/Frus.	69	30	7	0
	3.	NH/NF	0	0	0	0
		H/Frus.	48	18	2	0

NH/NF = not hungry/no food

H/Frus = hungry/frustrated

Table 19.2A. The increase in total numbers of aggressive responses in the H/Frustrated situation compared to the NH/NF situation occurring during frustrated feeding (groups of 3 birds).

	Trial	A birds towards B birds	A birds towards C birds	B birds towards C birds
Group 1.	1.	118	49	97
	2.	96	35	60
	3.	42	25	66
Group 2.	1.	29	29	13
	2.	43	25	97
	3.	18	14	17
Group 3.	1.	3	36	17
	2.	5	10	8
	3.	7	22	1
Group 4.	1.	72	131	129
	2.	38	75	45
	3.	18	50	23

APPENDIX 2

DUNCAN, I.J.H. 1970. Frustration in the fowl. In: Aspects of poultry behaviour, 15-31. Edit. Freeman, B.M. and Gordon, R.F. Br. Poult. Sci. Edinburgh.

Aspects of Poultry Behaviour
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British Poultry Science, Edinburgh

FRUSTRATION IN THE FOWL

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SYNOPSIS

The effects of frustrating situations on the behaviour of an organism have been studied in the past in relation to many dependent variables of which the most important are aggression, fixation and stereotypy, regression and displacement activities. A very brief outline of these studies is given. Experiments are described in which the domestic fowl is frustrated in various ways during feeding, nesting, incubation, brooding and sexual activity. Depending on the severity of the frustration and the stimulus situation, the chicken may show displacement preening, increased aggression or stereotyped behaviour. The relevance of these behaviour patterns to poultry husbandry is discussed. Although none of the patterns needs necessarily be symptomatic of a pathological state in the bird, nevertheless two of them, namely increased aggression and stereotyped behaviour, could be detrimental to production. Increased aggression may result in a wastage of energy or physical injury as well as frustration in other birds, which would aggravate the whole process. Stereotyped behaviour also wastes a lot of energy and it may be possible to prevent stereotypies or reduce their incidence with tranquillising drugs. The occurrence of displacement activities, on the other hand, could act as a warning that a frustrating situation exists. Finally some preliminary experiments on the measurement of physiological parameters during and after frustration are described.

INTRODUCTION

In 1965 the report of the Technical Committee set up by the British government to enquire into the welfare of animals kept under intensive livestock husbandry systems, under the chairmanship of Professor Rogers Brambell, was published (Her Majesty's Stationery Office, 1965). In this report, in the section dealing with the domestic fowl, it was suggested that intensive husbandry systems often lead to frustration. For example the report stated: "Much of the ingrained behaviour is frustrated by caging. The normal reproductive pattern of mating, hatching and rearing young is prevented and the only reproductive urge permitted is laying. They cannot fly, scratch, perch or walk freely. Preening is difficult and dust-bathing impossible. . . . The caged bird, which is permitted only to fulfil the instinctive urges to eat and drink, to sleep, to lay and to communicate vocally with its fellows, would appear to be exposed to considerable frustration." The research reported in the present paper is an attempt to discover exactly how the fowl does behave when frustrated in a carefully controlled situation, and whether this behaviour is the same as, or resembles, that seen in intensive husbandry systems. In the future we hope to measure some physiological parameters, which may be indicative of stress, such as heart rate and skin temperature, to see what bodily changes take place in frustrating situations. In this way it should be possible to assess whether fowls are frustrated and whether the frustration is acting as a stressor in any given situation.

Frustration is the state of an organism placed in an objectively defined frustrating situation. In this paper a " frustrating situation " will be restricted to those situations in which there is interference with a behaviour sequence normally leading to a goal-response. Ethologists often use the word " thwarted " in place of " frustrated " in an attempt to avoid the pathological implications that this latter term has often had in the past.

Until recently the study of frustration has suffered because isolated groups of workers have examined its effects in relation to only one of many dependent variables. The most important of these variables (if importance is judged by the amount of research generated) have been aggression, fixation and stereotypy, regression and displacement activities.

FRUSTRATION AND AGGRESSION

The frustration-aggression hypothesis was introduced by a group of Yale psychologists (Dollard, Doob, Miller, Mowrer and Sears, 1939). They stated that (1) aggression is always the consequence of frustration and (2) the occurrence of aggression always presupposes the existence of frustration. In a later paper the group modified their views to say that frustration can lead to a tendency to perform a number of different types of response, one of which is some form of aggression (Miller, Sears, Mowrer, Doob and Dollard, 1941). The frustration-aggression hypothesis was really remarkable since it was based on very little experimental evidence. However it did provoke a lot of controversy and research in the next twenty years and much of the theory was subsequently substantiated (McKellar, 1949; Haner and Brown, 1955; Otis and McCandless, 1955; Lesser, 1957; Palmer, 1960). Substantiated, that is, by human experimentation; the work on animals was less clear-cut. Frustration seems to play little or no part in the causation of aggression in mice (Fredericson, 1950, 1952) or rats (Hall and Klein, 1942; Seward, 1945). On the other hand chimpanzees show aggressive responses, among others, when frustrated (Finch, 1942). Scott (1948) tested the effects of a frustrating situation on a group of 14 goats of both sexes. He found that frustration, produced by delayed feeding, increased the amount of aggressive fighting in dominant animals while it caused subordinate animals to take more punishment and almost never caused aggression in them. This applied to animals that were dominant in one situation and submissive in another. He concluded that frustration causes aggression in situations in which the animals are in the habit of being aggressive. Similarly King (1965) noted the effects of decreasing the accessibility of food on the peck order of three stable flocks of domestic cockerel. In each case aggression, as measured by the frequency of pecking among members, increased as accessibility was restricted. In general the peck order remained linear, but with severe restrictions disruptions occurred. There is the possibility in the experiments of Scott (1948) and King (1965) that hunger may have an effect on aggression. Andrew (1957) investigated the effects of hunger on aggression in yellow-hammers (*Emberizia citrinella*) and found that there was no direct effect. However hunger did increase general activity and this meant that there were more chance encounters between birds so there was an apparent increase in aggression. Both Scott's (1948) and King's (1965) results could be explained by this " increased encounter " theory of Andrew. Alternatively all three experiments may involve frustration.

Scott (1958), in a useful review of aggression, suggested that there are certain primary stimuli, varying from species to species, which lead to aggressive responses. Among the more important of the factors which generally stimulate aggression are pain, territorial trespass and encounters involving possession of food or females. Furthermore certain stimuli become secondary releasers of aggression through association, conditioning and generalisation.

The evidence for pain, or at least aversive stimulation causing aggression is good and this has been intensively studied by Azrin and his co-workers in Illinois. Aggressive responses have been elicited by tail pinching in mice (Scott and Fredericson, 1951), by electric shock in mice (Tedeschi, Tedeschi, Cook, Mattis and Fellows, 1959), hamsters and rats (Ulrich and Azrin, 1962), squirrel monkeys (Azrin, Hutchinson and Hake, 1963) and cats (Ulrich, Wolff and Azrin, 1964), by intense heat in rats (Ulrich and Azrin, 1962) and by a physical blow in squirrel monkeys (Azrin, Hake and Hutchinson, 1965).

More recently Azrin and his group have changed their aversive stimulation from electric shock, physical blows and intense heat to non-reward. Aggression was shown in a Skinner Box situation when a food reward was no longer given to pigeons for pecking a disc (Azrin, Hutchinson and Hake, 1966) or to squirrel monkeys for pressing a bar (Hutchinson, Azrin and Hunt, 1968). This is of course a frustrating situation although the authors of these last two reports do not use the word " frustration " at all.

Scott (1958) stated that frustration is not a primary stimulus but is likely to lead to aggression for three reasons: (1) frustration results in a high degree of excitation and in this state the organism will respond to stimuli, including primary and secondary aggression-inducing stimuli, to which it would not normally respond; (2) the physiological and emotional symptoms of frustration do not conflict with those of anger; (3) aggressive responses may be useful in removing the source of frustration and so they may be reinforced.

Other people have emphasised the spontaneity of aggression including Konrad Lorenz in his book " *On Aggression* " (Lorenz, 1966).

There have thus been theories of aggression based on frustration as the sole cause (Dollard *et al.*, 1939). Others have accepted either overtly (Scott, 1958) or implicitly (Azrin *et al.*, 1966) that frustration may be one of many causes of aggression. Lastly some theories ignore or pay very little attention to frustration as the cause of aggression (Lorenz, 1966).

FIXATED AND STEREOTYPED BEHAVIOUR

At the same time as the Yale school were investigating frustration and aggression, Maier and his students at Michigan were investigating fixated behaviour (Maier, 1949). Maier's definition of a frustrating situation was very restricted, namely that an animal be very highly motivated to respond to an insoluble problem and if necessary be forced to respond. His apparatus consisted of a platform on which a hungry rat was placed facing a board with two windows. Each window was covered by a card, say one black and one white, and the cards could be locked in position or free to fall. Behind the windows was a shelf on which a reward was placed. The rat was forced to choose one of the windows and jump at it. If its choice was correct, the card fell down, the rat landed on the shelf and received the reward of food. If the choice was wrong the rat bumped its nose and fell into a net some 1 m (3 ft) below. The rat could easily learn to jump to one of the cards, say the black one, if it was rewarded for so doing. However the problem could be made insoluble for the rat by rewarding it for 50 per cent and punishing it for 50 per cent of the jumps it made, no matter which card it chose. When this was done 75 per cent of Maier's rats developed abnormal position fixations. That is to say they jumped consistently to one side. Once established, fixations were very stable. The response continued if a rat with a left fixation was punished every time it jumped left. It remained even if the right-hand card was removed to reveal the shelf and food. Maier insisted that the development of fixations could not be explained by any conventional learning and motivational principles. The sub-title of his book was, in fact, " *The Study of Behaviour without a Goal*," which emphasised what he thought was the abnormal nature of fixations. His theory was attacked by other psychologists who sought to explain the phenomenon in terms of established principles of learning and motivation. There is no need here to enter into the details; the argument continues. All that need be said is that under certain severe frustrating conditions behaviour patterns can emerge which are fixated.

A type of behaviour related to fixations is the movement, or series of movements, which is repeated regularly and which serves no apparent function in isolated and confined animals. These movements are called repetitive stereotypies and are commonly observed in zoos and pet shops (Holzapfel, 1939; Hediger, 1950; Morris, 1964). Some examples are " pacing " in bears, " head swaying " in elephants, " head bobbing " in parrots and trotting over a particular route in wolves, jackals and hyaenas. The causation and function of stereotypies is still obscure but they have been described in the following ways: (1) thwarted intention movements to escape (Lorenz, 1952), (2) activities resulting from movement restraint (Levy, 1944; Hediger, 1950; Draper and Bernstein, 1963), (3) substitutes for normal activities denied expression by the impoverished environment (Levy, 1938; Keiper, 1969), (4) substitutes for stimulation normally supplied to an infant by the mother (Mason and Green, 1962; Davenport and Menzel, 1963) and (5) mechanisms to relieve boredom (Berkson, Mason and Saxon, 1963; Berkson and Mason, 1964) or control arousal level (Berkson and Mason, 1964).

The first four of these descriptions all probably involve a frustrating situation. None of the researchers in this field has looked directly at the relationship between frustration and stereotypies but most have implied that the situations involved are frustrating. For example Morris (1964) states that the characteristic stereotyped pacing to-and-fro of the caged animal may indicate the need for a greater territorial space in which to patrol. However he also says that stereotyped pacing indicates that the animal has come to terms with its restricted space and has developed a rhythmic, modified version of patrolling. To-and-fro pacing may also be a side-to-side ambivalent reorientation of a forward movement and Morris (1964) cites examples of the animal pressing forward and injuring itself through constant rubbing against the side of the enclosure. Keiper (1969) was able to reduce route-tracing in caged canaries by putting them in a much larger flight cage or providing a swinging perch. This had no effect on another stereotypy, spot-picking, which was reduced by making the canaries work for their food.

FIXATION AND REGRESSION

Most of the interest in regression was aroused by the report of Barker, Dembo and Lewin (1941) on the effects of frustrating young children. They stated that 25 out of 30 children showed a decrease in constructiveness of play behaviour when frustrated by being separated from highly valued toys. The behaviour shown was characteristic of an earlier developmental stage. It was a change of behaviour to that of a less mature state and they called this regression. " Instrumental act regression " was shown to occur under frustrating situations in rats (Whiting and Mowrer, 1943) and humans (Barthol and Ku, 1959). This differed from generalised regression in being a regression to a specific, previously acquired response.

Neither type of regression has received much investigation but there is always the possibility that a response of this kind may appear in frustrating circumstances. For this reason it is worthwhile mentioning regression as a possible reaction to frustration.

DISPLACEMENT ACTIVITIES

In ethology one of the most important and certainly the most controversial phenomena associated with frustration has been the concept of displacement activities. However other behaviour patterns have been described in thwarting situations and these should be distinguished from displacement activities. For example when a thwarted tendency is directed towards an object other than the original goal, this is a " redirection activity " (Bastock, Morris and Moynihan, 1953). Thus a hen, frustrated in feeding, may show redirection pecking at surrounding inanimate objects. Also if an animal is thwarted by fear of approaching a desired goal then both approach and avoidance tendencies may be simultaneously activated and " ambivalent postures and movements " (Bastock *et al.*, 1953) and " compromise behaviour " (Andrew, 1956*a*) may be shown. An example of an ambivalent movement is waltzing in the courtship of the domestic cockerel (Wood-Gush, 1956). It is a circular movement and therefore contains elements of approach and avoidance. Another courtship display of the cockerel, the wing flap (Wood-Gush, 1956) is an example of compromise behaviour since it is an intention movement both to approach and to avoid.

The term " displacement activity " was first used by Armstrong (1947) and Tinbergen and van Iersel (1947) to describe irrelevant behaviour patterns which are seen frequently during agonistic or sexual encounters, particularly between birds (Armstrong, 1947) and between sticklebacks (Tinbergen and van Iersel, 1947). They had previously been grouped together and described as acts out of context with the behaviour immediately preceding or following them and which commonly occur in a thwarting on conflict situation (Tinbergen, 1940; Kortlandt, 1940). For example two domestic cockerels in the middle of fighting and threatening each other may suddenly start to peck at the ground and even pick up grains in their beaks. Tinbergen (1952) said that the main characteristics of displacement activities were as follows:

1. The movements shown do not belong to the executive motor patterns of the activated drive.
2. Their irrelevance, or absence of the external stimulation normally associated with the action.
3. An incomplete or frantic performance.

Tinbergen's idea was that when an activity is thwarted there is a build-up of " surplus " energy which eventually " sparks-over " from the activated drive to another drive (Figure 1a). Tinbergen suggested that the primary function of displacement activities is as an outlet for this excess energy and so they form a defence against neurotic disorders.

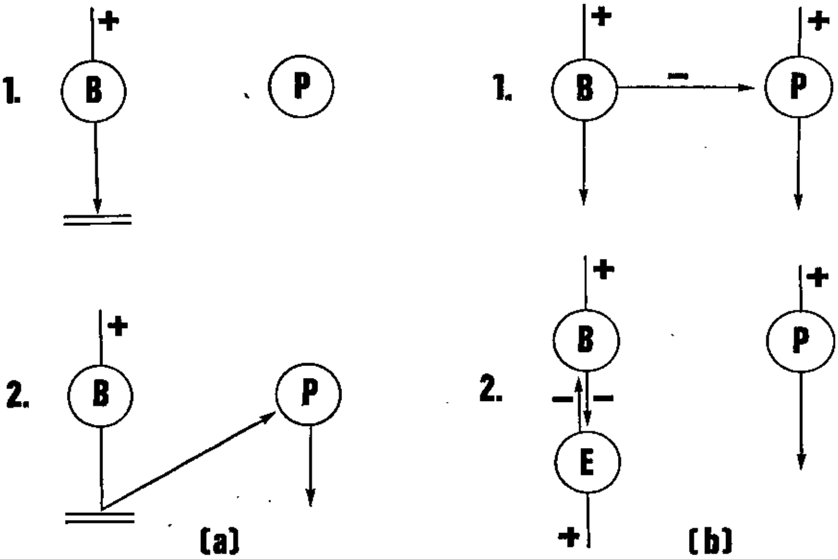

FIG. 1.—A diagram of (*a*) the " surplus " hypothesis and (*b*) the " disinhibition " hypothesis. Centres *B*, *P* and *E* control the performance of brooding, preening and escape respectively. See explanation in text.

However the research that has been done on the subject since has shown that the influence which external stimuli have on a behaviour pattern is the same no matter in what circumstances it is performed (van Iersel and Bol, 1958; Sevenster, 1961; Rowell, 1961; McFarland, 1965). Moreover displacement activities are sometimes performed when the consummatory act can take place and is not prevented, as for example when one egg of a clutch of three is removed from the nest of black-headed gull (*Larus ridibundus*); the bird is not prevented from incubating and in fact does so, but also performs displacement nest building (Moynihan, 1953). In this situation it is difficult to imagine a build-up of energy since the consummatory response (incubation) is actually taking place. Furthermore it was shown that a frantic or incomplete performance is not necessarily characteristic of displacement activities (Moynihan, 1953).

All of these facts, together with the observation that displacement activities may occur at the changeover from one activity to another (Andrew 1956*b*), led to the rejection of Tinbergen's " surplus " hypothesis and the formulation of the " disinhibition " hypothesis (van Iersel and Bol, 1958 ; Sevenster 1961; Rowell, 1961).

This states that when two conflicting tendencies are simultaneously activated they inhibit each other, or cancel each other out, and so a third activity which would normally be inhibited by one of them becomes " disinhibited " and able to be expressed (Figure 1b). For example in breeding terns (*Sterna* spp.) strong activation of the brooding system (*B*) inhibits preening (*P*) and only when *B* is not activated or is reduced and the causal factors for *P* are strong, will *P* become active. Escape (*E*) also inhibits *P*. Now *E* and *B* are also mutually inhibitive (the bird cannot perform both at once), and the theory is that when there is a conflict between *E* and *B*, they will also inhibit each other and so disinhibit *P* (van Iersel and Bol, 1958). It can be seen that this mechanism is dependent on there being a conflict of drives present. In the pure thwarting situation the occurrence of displacement activities can be explained by postulating that an avoidance tendency is generated which conflicts with the approach tendency.

In addition to disinhibition, Andrew (1956*a*) suggested that physiological arousal accompanying thwarting may affect displacement activities. For example a male bunting (*Emberiza* spp.) shows warming and cooling responses when fearful of the female. Andrew suggested that this irrelevant behaviour is caused in the same way as normal heat regulatory responses, since sympathetic neural activity leads to constriction of superficial blood vessels and a fall in skin temperature. Morris (1956) also speculated on the behavioural significance of autonomic changes which accompany intense thwarting. He was particularly interested in piloerection and the possibility of the resultant feather postures becoming social signals.

The disinhibition hypothesis is fairly well accepted but it still leaves some questions unanswered. It does not account for the frantic performance of displacement activities nor for their occurrence when there is a strong activation of a drive and absence of appropriate external stimuli.

THE BEHAVIOUR OF THE FOWL IN FRUSTRATING SITUATIONS

Before going on to describe some of the experimental work on the chicken it is profitable to consider what responses are available to it when thwarted. The American psychologist R. R. Sears stated that there are three possible action sequences which can occur when an animal is placed in a frustrating situation (Sears, 1941):

1. The organism may continue or repeat the *same* instrumental acts leading to the *same* goal response. This response is persistent and non-adjustive and more characteristic of lower animals and children than higher animals and adults. Certain of the stereotyped movements would fall into this category.
2. A *different* set of instrumental acts may be adopted to put the organism in position to perform the *same* goal response. Trial-and-error behaviour appears to be largely of this kind, as do certain types of instrumental act regression.
3. A *different* set of instrumental acts may be instigated in order to put the organism in such a position that it may perform a *different* goal response from that which was originally frustrated. Displacement activities and some aggressive responses would be included in this group.

To these three could be added another group:

4. The *same* instrumental acts may lead to a *different* goal response as happens in a redirection activity.

Which of the four action sequences occurs following frustration will depend, among other things, on how advanced or primitive the organism is phylogenetically, the organism's previous experience in similar situations, the strength of the frustrated drive, the nature of the environment and the organism's perception of the environment at the moment of frustration. For example the chicken is phylogenetically primitive compared to, say, the dog or monkey and so one would not expect it to show responses of the second type. This is in fact the case, and the chicken does not perform well on a simple detour problem where it has to find a way round a barrier placed between it and a goal. It is more likely to show responses of the first or third type such as repeated approaches to the barrier or displacement activities.

Very little experimental work has been carried out on thwarting in the fowl. Wood-Gush and Guiton (1967) frustrated hungry, adult hens by presenting them with food under a glass cover. They found that at first the birds showed avoidance and escape behaviour, but this decreased, along with attempted feeding, with successive tests. At the same time there was an increase in grooming and sleeping behaviour until by the fourth test the birds were not reacting to the thwarting situation but were behaving as they did in the control situation. It seemed that thwarting generated a large amount of avoidance even when the animal was being frustrated for the first time and this could have produced an approach-avoidance conflict. However there was no increase in displacement activities associated with this conflict and in fact they tended to increase with the passing of the conflict. Moreover the level or irrelevant activities did not increase to a level higher than that found in the control situation. It is possible then that the grooming and sleep were not direct responses to the thwarting, but " normal " responses as occurred in the control situation.

The author has carried out some similar experiments with adult Brown Leghorn hens. The hens were deprived of food for 24 h and then trained to feed in the experimental cage measuring 60 cm cubed for 30 min each day. After about 10 d training, testing was started. Three testing situations were used with the birds (1) hungry and food present (2) not hungry and no food present (3) hungry and food present but covered with a Perspex cover. The first two situations were controls and the last one the frustration situation. One trial consisted of exposing each hen to these three treatments in a randomised order on consecutive days. Eight such trials were conducted. The observations were taken from a hide and lasted 30 min in the first experiment but this was reduced to 20 min in the later experiments. Four hens were observed in the first experiment.

The most striking feature of this experiment was the large number of " escape " movements which occurred in the frustration situation. This movement consisted of the hen walking quickly back and forward along one side of the cage (the side with the door). One such double movement without interruption was termed at first an " escape movement " but this was later changed to " stereotyped movement ". The numbers of stereotyped movements are shown in Table 1. During the first few tests these movements were accompanied by circular head movements as though the bird was looking for an exit. They were also variable in speed and orientation, but always occurred towards the door. This is in agreement with the findings of Wood-Gush and Guiton (1967) that physical thwarting generates a large amount of avoidance. However, in contrast to their results the high rate of escaping showed no signs of decreasing by the eighth test. In addition the form of the escape movements changed. In the first test they were variable in such features as number of steps taken, direction of turn, position of head, and orientation. By test 8 they were much more rigid and showed a high degree of stereotypy. It is possible that these movements started as attempts to escape from the frustrating situation and developed into a repetitive stereotypy.

TABLE 1

Mean number of stereotyped movements (with standard deviations) occurring per test (8 tests)

	Birds			
	A	B	C	D
Hungry/food	17±4·7	17±6·0	19±11·1	0
Not hungry/no food	27±7·7	37±15·8	8±16·9	3±1·6
Frustration	170±15·8	177±25·7	164±15·7	132±23·5

Another difference from Wood-Gush and Guiton's results was that after the first test the birds continued to try to feed at a fairly high rate. The mean numbers of pecks at the Perspex cover per test were 447·5, 96·0, 49·7, 116·7, 190·0, 130·2, 155·5 and 43·2 for trials 1 to 8 respectively. Significantly more pecks were given in the first trial than in any of the others ($P < 0·01$). Apart from this initial decline in pecking, therefore, the birds were not habituating to the situation as they did in Wood-Gush and Guiton's experiment.

A further feature of this experiment was that preening, redirected pecking and sleeping, all of which have been observed to occur as displacement activities in frustration and conflict situations in other avian species (Tinbergen, 1952; Andrew 1956*a*, *b*; van Iersel and Bol, 1958; McFarland, 1965), occurred less frequently in the frustration situation than in the not hungry/no food control situation. The results for preening are shown in Table 2.

TABLE 2

Mean number of preens (with standard deviations) occurring per test (8 tests)

	Birds			
	A	B	C	D
Hungry/food	5±1·5	6±2·5	6±4·8	3±1·2
Not hungry/no food	47±9·4	61±19·1	36±9·5	52±8·6
Frustration	21±4·8	21±6·3	24±10·5	33±5·4

If the escape movements are motivated by fear or distress it should be possible to reduce them by means of drugs. There are two types of drug which could be useful in this respect (*a*) a central nervous system depressant such as a barbiturate, which would produce lethargy, sedation or sleep depending on the dose and (*b*) a tranquillising agent, which would relieve anxiety. It was therefore decided to test the effects of three drugs on the original four hens. The drugs were Nembutal (Abbot), which is a solution of pentobarbitone sodium, an intermediate-acting barbiturate and a central nervous system depressant, Pacitran (Ciba) which is a solution of methylreserpate hydrochloride, a derivative of reserpine and therefore a tranquilliser of the Rauwolfia-alkaloid type and Oblivon-C (British Schering) which is a derivative of methyl pentynol and has short-lasting hypnotic and anxiety-reducing effects.

None of the drugs used eliminated the escape behaviour shown in the frustration situation. The birds in fact showed escape behaviour even when ataxic after fairly large doses of Nembutal. However the two tranquillising drugs, and in particular the Pacitran, did reduce escape behaviour significantly. This reduction in escape behaviour was accompanied by an increase in preening. In fact when the birds were injected with Pacitran intramuscularly at the rate of 1 mg/kg body weight 2 h before the test, they preened more when frustrated than in control tests.

The results with Pacitran were confirmed in another experiment on a larger scale. The increased preening that occurred in the frustration situation could be explained in terms of displacement preening. The fact that the stereotyped movements were never entirely eliminated shows just how fixated they had become in the birds' behaviour repertoire. In fact some birds which were frustrated daily over a long period started to show a high rate of stereotyped movements in the hungry/food present control situation. This is similar to Maier's rats which showed fixated responses even when the problem was soluble. Morris (1964) also gives examples of stereotyped movements continuing long after confined animals had been removed to a relatively large enclosure. It would seem that once a response of this type becomes established it is very difficult to remove. Some of the hens were rested for four months and they showed very high levels of stereotyped movements on the very first frustration test and fairly high levels when the Perspex cover was removed even after this long rest period.

In another experiment it was found possible to prevent the onset of stereotypies completely by the administration of Pacitran from the beginning of testing. Pacitran was injected daily before the frustration test and after 20 d no stereotyped movements had appeared whereas they had reached a very high level in a control group after only 10 d. The injections were then stopped and after a further 10 d five of the six birds in the " drug " group were showing stereotyped movements at the same high rate as the control group.

The frustrating situation can be made less severe either by depriving birds of food for a shorter period of time or by giving them less training so that their " expectancy " of food is less when they come to be tested. The results of an experiment are shown in Table 3 in which 9 groups of birds were put on various training and deprivation schedules. It can be seen that when hunger and expectancy of food were low there was an increase in preening in the frustration compared to the control period. On the other hand when hunger and expectancy of food were high preening was depressed and there was an increase in stereotyped movements. One of the most interesting points in this experiment was that in two of the intermediate groups the birds gave alarm calls. This was the first time that alarm calls had been heard in any of the frustration tests and it was probably a sign of fear or distress. When these two groups were tested again they did not give alarm calls but showed a large increase in stereotypies. This would seem to indicate that the performance of stereotyped movements may serve to reduce the level of distress or fear or anxiety.

In none of the experiments so far discussed was there any sign of aggression. For example the pecking at the glass did not look particularly aggressive and neither

TABLE 3

The responses of hens in various frustrating situations compared to control situations

	Length of period of food deprivation (h)		
Training period (d)	6	10	24
0	Increased preening, no stereotypies	Increased preening, no stereotypies	Increased preening, no stereotypies
3	Increased preening, no stereotypies	Slightly increased preening, no stereotypies, 3 out of 6 birds alarm calling	Slightly increased preening, some stereotypies, 6 out of 6 birds alarm calling
10	Increased preening, a few stereotypies	Less preening, many stereotypies	Less preening, many stereotypies

did the few redirected pecks at other parts of the cage. However when pairs of birds were frustrated simultaneously in the same cage the dominant birds showed a large increase in aggression. They threatened, pecked and chased the submissive birds many more times than in a not hungry/no food situation. The submissive birds spent most of their time avoiding the dominants but some did develop stereotypies. The middle bird of a group of three showed greatly increased aggression when frustrated with the bird lower in the hierarchy but no aggression at all when frustrated with its superior. It seems, therefore, that the elicitation of aggression depends entirely upon the presence of an inferior bird. However the birds used in these experiments had formed very stable hierarchies and perhaps with less stable relationships aggression may be shown by both the frustrated birds.

In summary, when the hunger drive of the chicken is physically thwarted in a cage it may show displacement preening, stereotyped back-and-forward pacing or increased aggression depending on the length of food deprivation and its expectancy of food and also on the stimulus situation.

We have also frustrated birds in many other ways, including thwarting the nesting, incubation and brooding drives. The reason for these studies, which probably seem to have no application to the poultry industry, is that it is important to know the full range of responses which the hen makes in every possible thwarting situation.

One situation which probably is important to the industry is thwarting of the nesting drive. Brown Leghorn hens which had been taught to nest in trap-nests in deep litter pens were frustrated by (*a*) closing all the trap-nests in the home pen or (*b*) removing the bird to a cage measuring 60 cm cubed. Control observations were taken of the birds in the same situations, at the same time on a non-laying day. The birds showed increased stereotyped pacing in the hour before laying when frustrated. The pacing in the cage was remarkably similar to that which occurred in the food-thwarting situation, while that in the pen usually took place along the front of the shut nest boxes. It did not occur continuously, but in bouts lasting two or three minutes interspersed with bouts of feeding, preening and other maintenance activities. The amount of pacing increased with the approach of oviposition. There was less preening in the frustration periods compared to control periods for the 30 min before laying. However the preening that did occur in the frustration situation was different, in that the belly and vent regions were preened more than usual. It would be interesting to find out if the hens were responding to uterine movements or neuro-humoral changes in the oviduct at this time. One of the most interesting features of this experiment was that no difference was observed in the stereotyped or preening behaviour of the frustrated birds in the pen and in the cage. One would have expected the pen situation to have interfered less with the nesting responses since it provided a much richer environment including litter to nest in, lighted and shaded regions, and secluded corners, all of which were absent from the cage. However this was not the case, although there was one difference between the situations. Oviposition was delayed in both the pen and cage but it took, on average, an hour longer in the cage situation. This meant that when the birds were frustrated in the cage they performed more stereotyped movements in total than when in the pen but in the hour before laying there was no difference. It has been shown that injections of adrenaline can delay oviposition (Sykes, 1955; Draper and Lake, 1967) and it would be interesting to know if this delay in laying in the present study was due to a release of catecholamines following frustration.

In another series of experiments broody hens of a broiler parent strain were frustrated by placing a wire cage over their nest and eggs when they made a daily expedition for food and water. When this was done the birds showed a great deal of displacement preening. Furthermore 90 per cent of this preening took place at the farthest points in the pen from the nest. Bouts of attempted entry into the nest alternated with bouts of preening at the far ends of the pen. The subjective impression was that during the bouts of attempted entry the hen became very aroused or excited and during the bouts of preening the hen calmed down again. It may be that displacement preening acts in this way to " cut-off " the aversive frustrating situation and allows homeostasis to occur.

Very similar results were obtained when the hens were separated from chicks at a later date. It should be remembered that the incubation and brooding experiments were carried out on a different breed of hen from the rest of the experiments and for this reason are not strictly comparable to them. In fact when these broiler-type birds were tested in a food-thwarting situation they showed an increase in preening where the Brown Leghorns would have shown stereotyped pacing. This may have been because they were larger birds and so a 24-h period of food deprivation had less effect on them than on the smaller Brown Leghorns. Alternatively it could be that they have a different temperament and require to be more severely frustrated than the Brown Leghorns to show the same responses.

One experiment was carried out on another drive in Brown Leghorns. This was an attempt to frustrate cockerels sexually. Each day cockerels were released individually into a pen containing three females and allowed to court and copulate with them for 20 min. After a week the hens were placed under a cage so that copulation could not take place. The cockerels then showed a large increase in wing-flapping compared to that shown when they had access to the hens and also when the hens were absent. Of the other courtship displays (Wood-Gush, 1956), there was less waltzing, and the same amount of tidbitting, sex-calling, cornering, head-shaking, and feather-ruffling in the frustration situation compared to when the hens were present. Very few of these displays occurred when the hens were absent.

There was no increase in preening or stereotyped pacing in the frustration situation and there was no apparent difference in the behaviour of the hens apart from the fact that they approached the side of the cage nearest the cocks in response to tidbitting.

Wing-flapping was mentioned earlier as being compromise behaviour between approach and avoidance. The increase during frustration is further evidence that frustration is aversive and generates avoidance which then conflicts with the approach tendency.

Two experiments involving physiological measurements are currently in progress at the Poultry Research Centre. Firstly, the levels of corticosterone in the blood of frustrated hens showing stereotyped pacing, both before and after it has become fixated and also that in control hens has been measured (I. J. H. Duncan, J. Culbert and J. W. Wells, unpublished observations). An increase in plasma corticosterone is generally accepted to be part of the General Adaptation Syndrome to stress (Selye, 1952; Brown, 1967). It is known that certain physical stresses, such as exposure to cold, can increase the plasma level of corticosterone in poultry (Brown, 1961, 1967) and it has also been established that other related parameters, such as adrenal size and adrenal cholesterol level, show a typical stress reaction to crowding in poultry (Siegel, 1959, 1960; Flickenger, 1961.) The hens in the present study did not show any increase in plasma corticosterone. This can either mean that (*a*) thwarting, which is severe enough to alter the birds' behaviour permanently, does not stress the birds sufficiently to elicit the General Adaptation Syndrome, or (*b*) the General Adaptation Syndrome is not so generalised as in mammals and different reactions occur to different stressors.

Secondly, experiments have been started in which the skin temperature of frustrated birds is recorded continuously. The first impression is that skin temperature rises about 1° C during a 20 min frustration period in which the bird shows displacement preening. So far we have looked at very few birds and these results require verification. However it does seem possible that the birds could have been preening in response to this rise in skin temperature or to an associated change such as piloerection.

FRUSTRATION AND POULTRY HUSBANDRY

It has been seen that in an experimental frustrating situation the hen may show displacement preening, increased aggression or stereotyped behaviour depending on the severity of the frustration and the stimulus situation. Although these behaviour patterns may appear to be maladaptive, there is some evidence that their performance may reduce or at least keep distress to an acceptable level. They are, therefore, not necessarily symptomatic of a pathological state. Nevertheless two of these patterns, namely increased aggression and stereotyped pacing, could be detrimental to production. Increased aggression may result in a wastage of energy and physical injury. Also if dominant birds in a group increase their aggressive responses it may mean that fear is increased in submissive birds. This could lead to submissive birds being frustrated through an " approach food/water/nest box—avoid dominant bird " conflict building up. The whole process would thus be aggravated. Stereotyped pacing must also waste considerable energy. We have no records on the effect of frustration on egg production. In the experiment in which nesting was frustrated, laying was delayed, and it is possible that this might lower production. Apart from this it appears that the main deleterious effect may be on productivity rather than production, and in particular on the food conversion ratio.

In commercial practice, frustrating situations are likely to arise when a bird has a tendency to approach one of the facilities such as a food trough, drinking fountain, or nest box and there is none available, or there is activation of an avoidance tendency because of fear of a dominant bird or because of some aversive property of the surroundings.

Since the fowl is territorial in nature (McBride and Foenander, 1962), facilities should be arranged so that each bird has easy access to them and is not frustrated by having to pass into a stranger's territory where it is at a disadvantage (Collias, 1943).

The fact that frustration responses do occur in practice is best illustrated by the pre-laying behaviour of hens in battery cages. Observations have shown that there may be a great deal of stereotyped pacing in the hour before laying (Wood-Gush and Gilbert, 1969; Wood-Gush, 1969). Now with hens in pens there is a gradual build-up of internal stimuli in the period before laying and the search for a nest begins. This period is characterised by a general restlessness, examination of suitable nest sites, intention movements to enter these sites and displacement activities such as preening. This last pattern suggests that there is normally a conflict present at this time—probably to nest or not to nest (Wood-Gush, 1954). The evidence from feral chickens in natural conditions is that they too examine many potential sites before choosing one (G. McBride, personal communication). However once the nest is entered the hen sits fairly quietly until oviposition. In cages however stereotyped pacing may continue right up until laying. In fact, some stereotyped pacing does occur in pens but not generally to the same extent as in cages.

What can be done to eliminate these undesirable behaviour patterns? There would seem to be three ways of attacking the problem. Firstly, the environment could be changed to cut down the possibility of frustrating situations developing. The importance of the lay-out of facilities has already been discussed, and this applies to battery cages as well as to pens. Also it may be necessary to provide some sort of secluded areas for nesting in battery cages. Secondly, the possibility of selecting strains of poultry with a high " frustration threshold " should be investigated. For example, Wood-Gush (1969) has shown that there is a great deal of within and between strain variability in the amount of pre-laying pacing shown by caged birds. Research is needed to find out if this is a heritable trait which will respond to selection. Thirdly, there is the possibility of treating birds with tranquillisers. It would probably not be necessary to dose the birds continuously but only at critical times when frustration was likely to be great as, for example, during transportation or at point of lay.

So far we have discussed how two of the symptoms of frustration may lower production efficiency. The frustration state itself, however, may lower efficiency, if it is accompanied by the physiological changes known as the defence reaction (Draper and Lake, 1967). These changes always mean a net increase in energy expenditure and, at the end of the day, this means a higher food conversion ratio. This is over and above any direct effect these changes may have on the process of egg formation (Draper and Lake, 1967).

The third symptom of frustration, namely displacement preening, which in itself is not harmful, could be a very useful warning of the presence of frustration. When it occurred, steps could be taken to avoid prolonging the situation and the other two symptoms with their more serious consequences. The problem is one of recognising displacement preening. It was mentioned earlier that a frantic performance was characteristic. This has been confirmed using slow-motion cinematographic techniques. Individual preens are of shorter duration in displacement preening. The differences between ordinary and displacement preening, however, are slight, and would only be apparent to a trained eye. Research is continuing to see if there are any other differences, and until this is completed it would be a mistake to think that the occurrence of preening is necessarily a sign of frustration.

GENERAL CONCLUSIONS

It can be seen from the research reported above that the domestic fowl may respond to frustrating situations in several ways. Some of the responses may lower production efficiency while others may be useful as warnings that frustration exists. The significance of frustration with respect to the welfare of the chicken kept under intensive conditions is difficult to assess. Frustrating situations do occur in practice and probably lead to some distress but the responses the bird makes may help it to adjust to the situation. However, it is obvious that from an economic point of view, frustrating situations should be avoided or at least kept to a minimum wherever possible.

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