CHAPTER 1

INTRODUCTION

The nesting behaviour of domestic fowl (*Gallus gallus domesticus*) is of interest for several reasons. Firstly, the behaviour patterns involved in the selection of a nest site and construction of a nest, regardless of how meagre the architecture, have both biological and ethological significance. While something is known of the motor patterns involved in the search for and establishment of a nest by gallinaceous birds, much less is known of what factors in the birds' environment influence nest site selection or what stimuli from the nest site or nest elicit behaviours appropriate to nesting. Of particular interest is the significance of features of the nest site in the founding of the nest amongst birds in which the site of nest establishment is of greater importance than the actual nest itself. Gallinaceous species would seem to belong to such a group of birds.

Further, the nesting behaviour of domestic fowl is of greater academic interest, for the domestication of the species is likely to have in some ways, either directly or indirectly, altered the form or expression of the behaviour patterns or to have altered their relevance. Some components may have remained constant in form or expression although they have been rendered superfluous or non functional in the context of the environment in which domestication has placed the species today. Others may have been altered and possibly even eliminated through selection of the species for its productive characteristics. However, as pointed out by Kretchmer and Fox (1975), most basic motor patterns resist modification under domestic conditions. Selective breeding tends to have greatest effect on the frequency and intensity of the more maleable behaviour patterns through changes in the thresholds of stimulation required to elicit responses. Therefore, elimination of certair of these patterns is unlikely and activities which no longer have adaptive value under domesticated conditions may not be removed but appear instead as apparently functionless activities.

The behaviour of the reputed progenitor of today's domestic breecs, the Red Junglefowl (*Gallus gallus*), has been studied in considerable detail both in captivity (Kruijt, 1964) and in its natural habitat (Collias and Collias, 1967), but, unfortunately, with little reference to the behaviours related to nesting and nest selection. Aspects of the social organisation of these birds and of domestic breeds has generated most interest in the past. Selection of domestic fowl on the basis of productive characteristics, to which egg laying and nesting are obviously related, has probably taken place relatively recently in the process of domestication (see Wood-Gush, 1959), but certainly evolutionary processes would have operated to achieve some adaptability to the nesting environment provided during domestication. The relatively rapid and recent changes in intensification and housing associated with the introduction of laying caging may, on the other hand, have allowed insufficient time for evolutionary processes to have exerted an influence on certain behaviours, including nesting, through adaptation to these particular environments. This introduces a further consideration of bird welfare, which although of great importance, is not the subject of the research conducted and reported herein.

From a practical or economic viewpoint, the behaviour of hens associated with nest selection, nest construction and oviposition, is relevant in a number of respects. A close physiological relationship exists between ovulation and nesting behaviour and in fact nesting behaviour may provide a better indication of ovulation rate than does actual production (Wood-Gush and Gilbert, 1965). The rate of egg loss through internal laying may represent a considerable proportion of a hen's total ovulations, and nesting frequency may be useful, not only as an index of ovarian activity and therefore of productive potential, but of the rate of loss of productivity through this source (Wood-Gush and Gilbert, 1970a).

Furthermore, in situations in which hens are housed at range or on deep litter,it is important that hens lay in particular places which facilitate egg collection. In commercial egg or fertile egg production in deep litter systems, failure to lay in provided nesting facilities can constitute a serious problem. Eggs which are laid on the shed floor rather than in provided nests are more liable to microbiological contamination. Harry (1963) showed that the total number of potential egg spoiling bacteria in the shell and membranes of eggs from deep litter systems was about 15 times that of battery eggs, the bacteria from the litter presumably being transferred to the nest linings on the feet and feathers of the laying birds. Smeltzer *et al.* (1979) also found statistically significant differences between nest and floor eggs for the percentage of eggs which were penetrated by bacteria. Eggs taken from three different farms in south-eastern Queensland, Australia, were found by this group to average bacterial penetrations of 10.5% and 15.3% for nest and floor eggs respectively. Floor eggs are therefore more predisposed to problems associated with reduced egg hatchability and chicks hatched from them are more likely to have reduced viability, increased incidence of omphalitis and may contain a higher proportion of Salmonellae shedders.

Another major consideration in such situations is the labour cost involved. Floor eggs are time consuming and often difficult to collect and clean and often have to be handled separately to nest eggs. It is interesting to note in this respect that nests provided in commercial situations are usually positioned so as to facilitate egg collection and handling. They tend to be situated at a comfortable height for the collectors, rather than at a level determined by hen preferences.

Floor-laying is also suspected of being associated with egg breakage and egg-eating problems in flocks, as eggs which lie about on the floor are liable to damage and are easily visible targets for potential egg-eating birds. These problems probably apply to an even greater extent in shedding with slatted floors where breakage is even more likely. Vent-pecking is another vice which may be encouraged by floor-laying habits, since hens laying in floor sites tend to be more exposed during oviposition than are hens in nest-boxes. Furthermore, where individual records of production are required in a trap-nesting situation with pedigree stocks, floor-laying leads to difficulties in record collection.

In addition, hens may spend a large part of each laying day actively engaged in the activities associated with nesting. The energy expenditure of hens resulting from this may be considerable (Van Kampen, 1976). This may represent a substantial waste of energy, and therefore of feed, particularly in some situations such as in laying cages, in which the active component of nesting behaviour may be extended and the nesting or sitting component reduced as a result of the hen's response to the environment (Fölsh, 1980). Also, the position of the hen in the cage and her orientation and activity during oviposition may influence the rate of egg loss through breakage, as suggested by Wood-Gush and Gilbert (1969a). Even slight cracking of eggs on impact at ovipositon may, in turn, create additional problems of egg-eating in laying cage situations (Anon., 1976).

In an early report, Turpin (1918) pointed out that the tendency of hens to lay on the poultry house floor causes serious losses to poultry keepers. The reasons given are that this tends to increase the labour input involved in finding and gathering eggs, it can cause the entire loss of eggs and a deterioration in the quality of many others and it can be directly responsible for fowls acquiring the egg-eating habit. Recommendations as to the provision of adequate numbers of nests, type, size, location and elevation of nests and type of nesting material have been forthcoming from a number of sources despite little experimental evidence (see, for example, Turpin, 1918; Smith, 1963; Anon., 1972). The approach to nest and shed design as it applies to minimising floor-laying tendencies has, in fact, largely been empirical. A large component of trial and error and individual farmer ingenuity has been relied upon in the past in the determination of acceptable nest designs and such information gained has been shared throughout the industry. Despite this, the problems encountered in the production of eggs from floor housed poultry are much the same today as they were 65 years ago when Turpin (1918) produced his report. Hill (1980) reiterates the importance of developing a nesting system which accommodates as many of the requirements of hens for nest site as possible. She states "From both a management and an economic point of view it is imperative that the majority of eggs are laid in the nests provided. Floor eggs are difficult to collect and soiled or broken eggs represent an economic loss. Eggs that are laid on slats or on wire floors can be lost in seconds by being trodden on. Furthermore, broken floor eggs can lead to egg eating problems". Apparently, therefore, previous approaches to the design and provision of appropriate nesting facilities have done little towards reducing the floor-laying problem of the last half century.

In order that such problems associated with nesting in commercial situations can be at least understood, and possibly even overcome, a more complete knowledge of the behavioural patterns associated with nesting and the stimuli from the nesting environment upon which nest site selection is based would seem invaluable. Nest usage habits appear to be formed early in the laying history of a flock or even of an individual hen and yet little is known of the development of behaviours and responses to features associated with the nest during this phase. Similarly, nest and floor-laying tendencies would appear to have a genetic basis (McGibbon, 1976) and yet we have only limited information available on the factors influencing nest selection tendencies in different breeds or strains of hen. The domestic fowl is a highly social animal and it seems possible that selection of nest site might also be influenced by social factors.

The present research was initiated in an effort to elucidate the possible influence of age, experiential, genetic, environmental and social factors on nesting behaviour and nest site selection of domestic hens. Studies of the 'preferences' of hens for certain features of potential nest sites were also conducted in order to establish the nature of the stimulus/stimuli upon which nest site selection is based. It was hoped that such investigations could indicate the hens' requirements for nesting which may be applied in the design of facilities provided for nesting in a range of environments. In addition, the nest and floor usage habits of hens was studied in conditions approximating those found in commercial deep litter systems to provide some information on the floor-laying phenomenon and how it changes over time in a maturing flock, and to access the likely value or success of application of nest design of some factors believed to be important to the nest seeking hen.

It should be noted that the investigation of nest site selection and floor-laying at the University of New England was to be carried out in two stages. The research effort recorded in this dissertation was considered to be the first stage of this investigation and its objective was to study nesting behaviour, principles of nest site selection and floor-laying tendencies. It was not intended that the design and assessment of improved nesting facilities, using such information, also be attempted in the current research. This more applied research was to be conducted in the second phase of the overall investigation, and in the course of ongoing studies.

It is envisaged that the results of the studies conducted and reported in this dissertation may suggest avenues of research which will lead to the design of environments, facilities and management principles which may be acceptable to both the poultry husbandryman and the laying hen.

CHAPTER 2

LITERATURE REVIEW

Introduction

The nesting behaviour of domestic fowl in deep litter pens has been studied in some detail. Wood-Gush (1975a) has provided an excellent report of nest construction by solitary domestic hens in small litter pens without nest-boxes. The behaviour of hens in laying cages during the pre-laying phase has also received considerable attention, particularly over recent years (for example, Wood-Gush and Gilbert, 1969a; Brantas, 1980). The extent of our knowledge of possible control mechanisms for nesting behaviour has been greatly expanded in the last few decades also (see Section 2.1.3).

In contrast to the quite well researched areas of behaviour of nesting hens in floor pens and laying cages and the control of the behaviour pattern, much less is known of the stimuli upon which nest site selection is based. Further, reports of nesting behaviour and nest site selection in junglefowl, the wild progenitors of today's domestic breeds, and in related gallinaceous birds, are few and usually do not rise above the anecdotal. An understanding of the nest selection process and criteria determining selection in the wild species would be invaluable in establishing the basis of nest site selection in domestic fowl.

Finally, attempts at manipulation of nest site selection characteristics in the provision of suitable nesting facilities for commercial purposes have only infrequently been documented. Research in this area has generally looked at specific characteristics of the nest site and not the total nesting environment.

The extent of our current knowledge of the areas of nesting behaviour of domestic fowl and their wild relatives, nest site selection and characteristics in these species, control of the behaviour pattern and means of providing appropriate nesting facilities for domestic fowl and so of reducing productivity loss associated with poor nest usage will now be reviewed.

2.1 Nesting Behaviour

2.1.1 Nesting behaviour in a natural habitat

Detailed reports of behaviour of domestic hens in natural habitats or even in the backyard situation are not often encountered. However, some information on the behaviours related to nesting and oviposition of feral fowl populations, and of the wild ancestors of domestic breeds or of their close relatives in natural habitats is available. This may be useful in establishing the nature of the nesting response and the significance of particular behaviours in the environments in which they initially evolved.

(i) *Junglefowl*

The Red Junglefowl (*Gallus gallus*), believed to be the ancestors of today's modern breeds (Kimball, 1954; Wood-Gush, 1959) are seasonal breeders in their native habitat, laying and nesting in the months corresponding to the spring and early summer there (Baker, 1930). Very little indeed is known of the behaviour of junglehens during nesting. Henry (1959) reports that the Ceylon Junglehen (*Gallus lafayettei*) when about to lay 'krarks in a similar manner to a domestic hen but in a higher key. These hens do not appear to announce the laying of their eggs by cackling and, in fact, Henry describes the hen's actions in connection with the nest to be silent and furtive in the extreme. The hen is said to approach her nest with the utmost caution and when on the nest, sits very close. She will even suffer an approach to within a couple of metres but when compelled to leave, runs or flutters away quietly. Henry notes, however, that the hen is capable of producing alarm calls in some situations. He also reports that Ceylon Junglefowl x domestic hen hybrids in captivity will also sit very close on the nest but when forced to leave, will dash off, cackling excitedly.

Baker (1930) describes some of the behaviours of Red Junglefowl on the nest. When incubating, the hen is said to sit very close and when forced to leave creeps away silently through the jungle. Wood-Gush (1954, citing Hume and Marshall, 1878) indicates that the junglefowl hen goes silently to nest but cackles after laying. However, Baker (1930) asserts that, having made careful investigations of this fact, he did not find that the junglefowl hens cackled and called after laying.

Kruijt (1964) describes some aspects of the nesting behaviour of captive Burmese Red Junglefowl (*Gallus gallus spadiceus*) in pens. Laying of the egg is preceded by restless behaviour of the female. She walks from corner to corner, sometimes settling and scratching for short intervals in each of them. She calls often throughout this activity and this calling is not dependent on the presence of the male. Her restlessness sometimes attracts an adult male who will corner with her, or accompanies her when she enters a nest-box. The cock may stand or sit close to her until the egg is laid. The male and female apparently cooperate when a nest is founded, the male seeming to assist in the selection of a site. Kruijt (citing Beebe, 1918) notes that a male junglefowl may stand guard near an incubating female and alert her of danger so that she can leave the nest unnoticed before a potential predator gets close to her. Hens nesting in the presence of the cock may perform complete cornering. Kruijt discusses the possibility that cornering by the male may not only function in the selection of a nest site but may also function in the construction of a nest.

(ii) *Other Gallinaceous Species*

Little information is available on the nesting habits in the Phasianidae. Kovach (1974) reports that nest building in Japanese Quail (*Cortunix cortunix japonica*) is performed by the hen alone. Very little nesting activity is performed before the first egg is laid in a shallow depression in the ground. The hen starts to add material to the nest only after the first egg is laid and continues nest building until the cessation of laying. Similarly, Stevens (1961) indicates that nest construction in this species is minimal. A depression is scratched out and some dead vegetation added during each egg laying visit.

Rothstein (1967) attempted to document the nesting behaviour of Japanese Quail in outdoor coops. He was unable to record any attempts by the hen to construct a nest and, in fact, camouflage provided for artificial nests was repeatedly destroyed by the birds.

In the case of the Bobwhite Quail (*Colinus virginianus*), a rather more complex structure is built. The birds still excavate a saucer shapped depression, but the nests are usually domed, spheroidal structures with an oval entrance on one side (Klimstra and Roseberry, 1975). Nests with incomplete or no canopy are more common in the early season. These researchers believed that both males and females took part in nest building in this species.

Indeed, Kendeigh (1952) reports that amongst the species in the family Phasianidae, the male takes part to different extents in nest building. Beebe (1936), commenting on nesting of pheasants in the tropics, reports that males do not share in nesting duties except to stand guard over the female and young.

The extent of elaboration of the nests also varies considerably. Hamerstrom (1936), describing the nests of Ring-necked Pheasants (*Phasianus colchicus*) indicates that the scooped out depression forming the nest may be lined with whatever materials are at hand, but that roof building, as often seen in the nests of Bobwhite Quails, is not generally evident. Baskett (1947) was not able to describe the possible nest building activities of Ring-necked Pheasant at the nest, but did note that nests were usually quite bare under the first egg, but an accumulation of plant debris and feathers appeared as new eggs were laid. In incubated nests the lining was often between ¼ and 1½ inches thick, suggesting that hens may have actively added to the nest.

Baker (1930) reports that most pheasant hens are very close sitters but when approached, sneak away quietly and stealthily. Kuck *et al.* (1970) were able to report that Ring-necked Pheasant hens spent successively more time on the nest as the number of eggs in the clutch increased. Presumably the hens then started to incubate the clutch.

Considerably more information is available on the nesting behaviour of members of the family Tetraonidae. According to Peters (1934) these species are closely related to the Phasianidae. Nest construction is quite well documented in grouse and ptarmigan. Maxson (1977) reports that Ruffed Grouse (*Bonasa umbellus*) have little or no opportunity to construct nests prior to the onset of egg laying, since hens seldom visited the nest site before then. Hens spent from one to several hours on the nest for each egg laid and the time on the nest increased as a clutch approached completion, although a clutch sometimes consisted of several laying sequences. Hens tended to remain inactive on the nest during their egg laying visits.

Bump *et al.* (1947) also describe the nests of Ruffed Grouse. They could find no evidence to suggest that any of the components of the nest are transported to the nest from a distance. The nest is lined and the edges built up of materials that are within the reach of the hen sitting in the depression. Although some feathers are found in the nest, they express doubt that the hen placed them there deliberately. A nesting hen was noted to pick at objects about the nest, but without moving her body.

Watson and Jenkins (1964) report that Red Grouse (*Lagopus lagopus scoticus*) may make nesting scrapes for up to a fortnight before laying. Cocks, even if unmated, also make scrapes. Hens will, however, lay in nests even if no cocks are present. While the hen is laying, the cock remains close to the nest until the hen comes off. These authors also report that the hen usually covers its eggs with vegetation when it leaves the nest, particularly as the clutch nears completion. Some nests were left uncovered, while others would be completely covered with dead grass and other material from around the nest. This tendency to cover the eggs with litter on leaving the nest prior to incubation, which is by the hen alone, has also been reported for Red Grouse by Jenkins *et al.* (1963).

McCourt *et al.* (1973) also record this behaviour in Spruce Grouse (*Canachites canadensis*). Up to incubation the nest was found to be extremely simple, consisting only of a hollow scraped in the forest floor. It then became a more elaborate structure, composed of an orderly arrangement of fallen leaves and other vegetation. Usually, the female covered the eggs with litter upon leaving the nest.

After laying, a Willow Grouse (*Lagopus lagopus lagopus*) hen has also been reported to cover her eggs (Pulliainen, 1978). Materials used to do this, a variety of vegetative types, were gathered with the bill in the immediate vicinity of the nest-cup. The nest itself was a simple hollow scraped in the litter on the ground. The hen only visited its nest in order to lay and on arrival did not remove the material covering the eggs. Such material gradually fell to the bottom of the nest. Whilst on the nest, the hen settled, resettled, ruffled and preened its feathers and shifted the eggs with its feet or bill. The hen would also peck at different objects on the rim of the nest. Most of the time, however, the hen sat motionless on her eggs. The final few minutes spent at the nest were in covering the eggs. Covering of the eggs only occurred until the beginning of incubation.

Allen (1934) describes this covering behaviour of female grouse briefly. He reports that it is first indicated by "feeble attempts at tossing leaves over her shoulder or onto her back as she sits or even as she walks". This 'leaf-throwing' activity he found was continued during the egg laying period and for several days into incubation. The hen would at times be left sitting with her back almost completely covered.

Nesting behaviour of ptarmigan has been well documented by several researchers. Watson (1972) describes the behaviour of adult ptarmigan at the nest in some detail. The nest is formed within 50 metres of the cock's main lookout usually. The cocks first start making scrapes two weeks before the hen lays. One male made many scrapes in the one session, sitting in some and scratching with his feet for several seconds or sitting for longer and digging out a nest hollow. He was accompanied by the hen during this activity but she did not sit on any of the scrapes. Nearer to the time of egg laying hens may make scrapes and be accompanied by the cock.

After laying, the hen covers the eggs partly or completely with assorted vegetative matter. This is accomplished as she sits on the nest, placing material onto the nest on either side of her body (MacDonald, 1970). The extent to which eggs are covered varies. Wild birds usually only cover the eggs partly. While laying, captive hens sometimes call.

Giesen and Braun (1979a) provide more information on the behaviour of White-tailed Ptarmigan (*Lagopus leucurus*) during the nesting season. Prior to egg deposition hens would actively forage in the males' territories, accompanied by the males, in the egg laying period. As the time of laying approached, hens ran or walked directly to their nests, which were generally located some 100-300 metres from the cocks' territories. On reaching the nest, the hens would remove vegetation covering the eggs with the bill before settling on the clutch. As also reported by Giesen *et al.* (1980), almost immediately upon settling, the egg would be laid. Hens would remain, fairly inactive, for some time on the nest after laying. The time spent on the nest after laying increased as the clutch neared completion.

Giesen and Braun (1979a) noted that the ptarmigan hen, before leaving the nest, would begin to peck at vegetation and place it at the rim of the nest or throw it over her back. This behaviour lasted up to 64 minutes in one case. Vegetation was deposited on the nest at the rate of 20 pieces per minute. When the rim of the nest was built up, the hen would stand near the nest and drop vegetation on the eggs, all vegetation being gathered within 10 cm of the nest. After eggs were completely covered the nest was left.

One particularly interesting observation recorded by these workers was the occurrence of displaced egg covering activity when a hen was accidentally flushed from the nest after depositing an egg. After flying about 8 m from the nest she spent about 20 minutes placing vegetation around her as if on the nest. The form of the behaviour pattern was identical to that performed in actual egg covering.

Giesen and Braun (1979a) suggest that egg covering may also function as insulation from low temperatures, and it is interesting in this respect to note that the species for which covering is observed to the greatest extent tend to be those species found in cooler climates. The hens also ate white feathers displaced from the nest, possibly rendering nests less conspicuous, but not feathers actually in the nest.

(iii) *Attachment to the Nest*

In all gallinaceous species, after a nest site is selected, a nest built and eggs laid in it, hens will usually return to the same nest to lay until the completion of the clutch. However, there is some indication that at some stages of the season, some hens may lay in more than one site or lay in another hen's nest for one or several eggs in a sequence.

Baskett (1947) states that Ring-necked Pheasant hens, like many other game birds, may drop eggs promiscuously, particularly early in the season. These 'singles' were sometimes placed in scooped out bowls, but usually there seemed to be little preparation for their deposition. He also indicates that higher incidences of single eggs and of community nests, in which more than one hen has contributed eggs to the nest, occurred in years when nesting density was highest. In such years, the incidence of eggs laid in odd places,such as in manure piles and straw stacks,was also highest. Baskett concludes that this sort of behaviour was perhaps symptomatic of crowding.

A similar conclusion was reached by Einarsen (1942) who also found that as population increased in his study area single pheasant eggs dropped at random were frequently found. In these situations also, hen pheasants established community nests which resulted in egg wastage, as no attempt was made to incubate them. This situation did not occur when pheasant populations were smaller. However, it is possible that insufficiency of adequate nest sites rather than crowding itself may have been involved in this relationship.

Random egg laying or laying in dump nests is also reported for pheasants by Linder *et al.* (1960) and by Seubert (1952), who also noted a tendency for dump nesting to occur early in the season and for nest adoption to be associated with high population seasons. Dumke and Pils (1979) also indicate that although random egg laying or laying in dump nests is common in pheasant hens, the birds may utilise most of such eggs by adopting clutches that were abandoned or in dump nests. This suggests a mechanism for utilisation of most eggs. More dominant hens may appropriate nests from subordinate hens in these cases. These workers also indicate that some hens were more inclined towards promiscuous egg laying before settling down to incubate a clutch than were others.

Evidence of nest 'sharing' in Ruffed Grouse also exists. Bump *et al.* (1947) report that although nests of different hens are usually a distance apart, evidence of cases in which two hens contributed to the one nest was found.

Hens which lost a clutch may also renest in the one season. Evidence for this is provided later in relation to characteristics of the nest and nest site. As evidenced in that section, hens tend to avoid the area in which they first nested in establishing re-nests.

(iv) *Nesting Behaviour of Feral Fowl*

The nesting behaviour of hens from a population of feral fowl found on North-West Island off the coast of Queensland, Australia, is described in some detail by McBride *et al.* (1969). A group of these fowl were captured and released in large outdoor pens in light eucalypt forest for the purposes of behavioural studies.

When approaching oviposition, a feral hen would call and move out of the flock with her tail raised and closed and she would soon be joined by a male. The male then apparently led the hen to examine nest sites, tidbitting strongly when approaching a suitable nesting site. The hen would respond by approaching to about 75 cm and would then pause. The cock would continue scratching and crouch to give a dust-bathe routine, encouraging the hen to approach closer. The result of such scratching activity was the formation of a shallow nest. Where the nest site was off the ground the cock continued this activity on the ground beside it and would then stand with neck stretched upward towards the site. The hen would then hop up and examine the potential site. McBride *et al.* (1969) equate the activity of the cocks to cornering. A description of cornering by Red Junglefowl is provided by Kruijt (1964) who also notes that cornering by the male functions in the selection of a nest site and possibly also to some extent in the formation of the nest-scrape.

The feral hen was never observed to accept the first nest shown to her by the male. Instead she would examine it and move away, usually followed by the male who tried to attract her back to the nest by tidbitting and waltzing. She would sometimes return and re-examine the nest, which was often the site eventually selected. However, if the hen persisted in walking away, she would be joined by the cock who would lead her to another nest until finally one was accepted. The male would stand beside the nest for a minute or two before rejoining the flock.

During the search for a nest, the hen often called with beak wide open. The call appeared to attract a male if she was away from the flock area. When a hen accepted a nest, she squatted, covered the eggs and moved eggs under her with her beak. She would sit for some time and then leave the nest, giving the egg cackle. If she had not yet laid, the hen would stand within one metre of the nest, cackling and throwing twigs and leaves onto her back. Some of these which remained on her back would fall off when she returned to the nest and squatted. While on the nest the hen sometimes threw twigs toward the nest and onto her back. The possible connection between this behaviour and head zig-zagging during cornering in male junglefowl (Kruijt, 1964) is noted. Kruijt (1964) theorises that twig-quivering seen in other bird species may be an analogue of this head zig-zagging behaviour.

When the feral hens studied by McBride *et al.* (1969) had finished laying they would leave the nest, again cackling, and move away. This cackle appeared to attract a male who would join her and return with her to the flock, sometimes mating with her on the way back. The egg cackle given resembled an alarm cackle, but it did not disturb nearby hens. Both cackles attracted the dominant male. Different postures were associated with the two types of cackle. The authors suggest that the whole routine associated with oviposition ensures that the hen is escorted to and from the nest. The role of the cock in selecting the nest is unclear. However, it seems unlikely that the cock is important in the individual decision. The cock would need to recognise each individual hen's nest site if this were the case and, anyway, it is not always the same cock who escorts the hen in her search, but presumably the hen still uses the same nest.

Feral hens were noted to change nests after a few days laying, forming a clutch in a second nest. This was most likely if she had been disturbed by another female while laying.

In an effort to replicate these studies, a group of scientists attempted to establish a population of feral fowl on an uninhabited island off the coast of Scotland (Wood-Gush and Duncan, 1976). Subsequent behavioural studies (Duncan *et al.*, 1978) indicated certain differences in the nesting behaviour of these hens from that described in the Australian study.

Nesting behaviour of these feral birds was not often observed on the island and the amount of time that hens spent in selecting nests was not known. Often, the first indication of nesting was the hen's absence from the flock. The activity of hens in relation to the nest was characterised by secrecy. Many of the behaviours which are exhibited by domestic hens in pens were apparent, but seemed to occur at a reduced intensity. It is unfortunate, in this respect, that observations of a control population, which had been established and was maintained in the pen situation, were not also reported.

A pre-laying call was sometimes heard from the feral hens, although it was never loud or persistent. Similarly, increased locomotion occurred but often took the form of the hen moving towards the nest. When the hen was seen to enter a nest, she did so without obviously examining other sites. She did, however, approach the nest by a circuitous route and often retraced her steps. Hens spent about one or two hours on the nest when laying, but examination of the nests failed to indicate whether or not nest construction had taken place. Participation by the males in the nesting sequence was not noted and, unlike the Australian study, post-lay cackles were not heard.

2.1.2 Nesting behaviour of domestic hens in provided housing

The nesting behaviour of the domestic hen has been studied in greatest detail in the environment provided by deep litter floor pens. As a result, the description of nesting behaviour of domestic hens in the following sections will be as applies in that environment and comparisons with the behaviours shown in other environments will be discussed later.

(i) *The Onset of Nesting Behaviour*

The onset of nesting behaviour has been reported to be expressed in several ways. Wood-Gush (1954), when describing the behaviour of young hens about to lay their first egg, reported that such birds became extremely restless and apparently nervous and they called persistently. These young, untrained pullets would 'wander' about the sides of the pen as if looking for a way out. The behavioural display of an older hen approaching oviposition was rather less obvious or 'ostentatious'. Such hens, experienced in the use of trap-nests, would visit and examine the nests several times, sometimes calling, and eventually select and enter a nest.

In later reports, nesting behaviour of experienced Leghorn hens in litter pens provided with trap-nests is reported to be indicated initially by restlessness (Wood-Gush, 1963), or restlessness and/or calling (Wood-Gush and Gilbert, 1969b; Wood-Gush, 1971a; Wood-Gush and Gentle, 1978). In the case of Rhode Island Red hens experienced in the use of litter pen floors for nesting and placed into small litter pens from individual cages for observation, the onset of nest site selection was "often heralded by vigorous wing flapping" as well as restlessness and calling (Wood-Gush, 1975b).

The 'restlessness' which has in many instances been reported to occur at the onset of nesting behaviour has not been described in much detail. However, Wood-Gush and Gentle (1978) in their summary of the types of pre-laying behaviours in pens with or without artificial nests suggested that hens commenced their nesting activities by investigating the environment and calling. Presumably, this apparent investigatory behaviour could be equated with the restlessness previously reported. Perry *et al.* (1971), when observing the pre-laying behaviour of broiler hens in a large, windowless, controlled environment shed found that if a bird was to lay on a particular day its diurnal activity pattern was likely to change sometime from its customary early morning feeding time onwards. This, of course, depended on the stage in that particular sequence of eggs which the bird had reached. For hens which were laying the first egg of a clutch, morning preening activities were usually deleted and the hens would be found in areas of the pen other than those in which they usually fed or idled at that time of day. The individual bird initially appeared to be pursuing a food search. However, on closer examination they found that the bird was actually walking around with its head near to the ground and was not, in fact, eating or pecking. The speed at which the hens would proceed in this way increased over time until "on occasion, birds were actually running". They also noted that encounters with other birds increased during this phase and that birds sometimes moved through the entire pen area while involved in this activity.

The behaviour described by Perry *et al.* (1971) could possibly be equated with the 'examination' of walls by the nesting Rhode Island Red hens observed by Wood-Gush (1975b) in small, individual litter floor pens. When 'examining' walls, the hen's posture was described as one in which the keel was kept up very high, giving the impression that the hen wanted to fly away. The 'head down' posture described during this restless phase in the studies conducted by Perry *et al.* (1971) could perhaps be a similar form of this activity which was redirected, since, the shed being windowless, the environment provided no sense of an area beyond which the bird could fly away to.

The calling reported to generally accompany the initial restlessness of the pre-laying phase in a number of studies has been described in some detail. It has variously been termed a "pre-laying call" (Wood-Gush and Gilbert, 1969b; 1970b), a "nesting call" (Wood-Gush, 1971b; 1975a; Wood-Gush and Gentle, 1978), or simply "calling" (Wood-Gush, 1954). Wood-Gush (1954) likened this call to that given by birds in a motivated state, such as that generated when birds in nearby pens are being fed. He suggested that the call was probably not only a sign of excitement, but also an alarm call of low intensity in some situations. Konishi's (1963) "laying call", which is noted to be uttered not only before egg laying but in other situations, such as when a hen is isolated from its cage mates, may be equivalent to the "nesting call" described in the studies conducted by Wood-Gush.

In a later report, Wood-Gush and Gilbert (1969b) show the audiospectrographs of nesting calls given early in the nesting sequence and also when nest entry behaviour was further advanced. When performing the call, the hen's bill was described as being well open and when given at a high intensity, the abdomen was noted to move. The rate of calling varied from 8 to 14 calls per second and a bout of calling lasted, on average, 3.5 seconds, although some bouts lasted for 7 to 10 seconds. They describe the nesting call when given at a high intensity as sounding like "Qwa-a-a-a" and at a low intensity, "Qwa-Qwa-Qwa".

In the same study, Wood-Gush and Gilbert (1969b) also recorded the orientation of adult laying hens in floor pens when calling. Similarly, the orientation of pullets induced to call by hormonal treatment was also scored. The majority of calls in both groups of birds was performed with the caller oriented away from its pen-mates (71 away from: 17 towards, for treated pullets; 147 away from: 22 towards, for adult laying hens). They also noted that many of the calls given by the adult hens (296 out of 420) were accompanied by locomotion, restlessness tending to replace calling as nest entry became imminent, and that they all showed some form of escape behaviour.

Wood-Gush and Gilbert (1969b) and later Wood-Gush (1975a) have stated that nest calling can sometimes be performed by young pullets several days before the first egg is ever laid. However, in Wood-Gush's (1963) description of nesting behaviour, which is often quoted in reference to this area of knowledge, no mention is made of calling as an integral component of the pre-laying behavioural sequence, although in the same paper persistent calling is said to be an idiosyncrasy of one particular bird. Perhaps, the description of nesting behaviour furnished in this article does not mention calling because it related to the sequence displayed by experienced adult hens, in which the tendency to call may be considerably reduced. Similarly, Perry *et al.* (1971) in their description of the pre-laying behaviour of broiler hens housed in controlled environment shedding, do not mention any particular call.

The times at which nesting behaviours are first displayed are, in most studies, referred to only in vague terms and rarely quantified. Wood-Gush (1954) noted that the time from commencement of nesting behaviour to oviposition was quite variable. The early restlessness and calling reported by Wood-Gush and Gilbert (1969b) was said to occur some one or two hours before the hen entered a nest. Perry *et al.* (1971) also indicated that the sequence of activities from the initial movement into pre-laying behaviour until the time at which the hen settled in a nest could last up to two hours.

Brantas (1980, citing Martin, 1975) reported results of observational studies which indicated that the whole egg laying procedure in a hen house with laying nests lasted on average 16.4 minutes. However, these results would seem to underestimate the actual length of time from onset of the initial behaviours to oviposition as indicated by other research (e.g. Turpin, 1918; Perry *et al.*, 1971). This suggests that the determination of initiation of nesting may have been inconsistent with that in other studies which, as will be discussed later, often show times spent in sitting or other component activities in the nesting sequence which exceed this value.

(ii) *Activities Related to Selection of a Nest*

After the initial period of restlessness and calling, most observers have recorded that the hen will enter a phase of nest site examination, gradually showing more and more interest in potential nesting areas such as corners of the shed or nest-boxes. In Wood-Gush's (1975a) study of the pre-laying behaviour of Rhode Island Red hens in small, individual pens with litter floors and no artificial nests, he describes the hen as passing from a phase of "wall examination" to one in which the hen began to pay more attention to pen corners. At this stage, the hens he studied tended to fixate on corners. A hen fixating on a nest stood with neck held out straight in a horizontal position towards the site. When walking, the hen would raise her feet high and "gave the impression of moving with stealth". He noted that hens in the early stages of nest site selection tended only to fixate for a few seconds at a time and that full fixation would only take place when the hen was very near the potential nest site. Wood-Gush then went on to describe the activities of hens once a nest had been selected.

Hens housed in deep litter floor pens provided with artificial nests are reported to move from restlessness and calling into a phase of attention to and approaches to the nests. In his earliest reported study of pre-laying behaviour, Wood-Gush (1954) observed that hens experienced with the use of provided trap-nests would pay several visits to nests, usually between three and five, before entering a nest. The birds are described to "examine" most of the nests during these visits. Wood-Gush found that these preliminary visits gave no indication of the nest which was to be ultimately used.

Wood-Gush (1963) again referred to the hen as "examining" the various nests that it visits by peering into them. He also stated that other activities such as feeding, preening or sleeping, may be resumed between such visits to the nest. In the study reported in that paper, Wood-Gush collected data on the number of nests examined by 13 Brown Leghorn hens on a number of occasions. However, only the data gathered for one henwere presented. The records presented for this one hen indicate that the number of nests examined per oviposition varied from four to as many as 48.

In another report, Wood-Gush and Gentle (1978) also described the apparent examination of trap-nests by hens as they stick their heads into the nests on visiting them. Wood-Gush (1963) interpreted the apparent nest examinations, in ethological terms, as intention movements to enter the nest, since the hen initially only moves a bit of her head into the nest but as time goes on, gradually inserts more and more of her body into the site.

The posture and general attitude of the hen 'examining' nests has certainly caused most authors who have studied the pre-laying activity of hens to attribute considerable 'consciousness' to the hen engaged in this particular activity. It prompted an early researcher (Turpin, 1918) to write that "it was noted especially that most of the hens appeared to consider their selection of a nest a serious matter and that they spent considerable time and apparently deliberated in choosing it". Thus, it is not surprising that the term 'examination', suggestive of conscious assessment, has gained acceptance.

The time which hens spend in examining nests appears, like time of onset of nesting behaviour, to be quite variable. Wood-Gush (1954) found that nest examination in mature, laying Brown Leghorn hens could commence up to three to four hours before a trap-nest is finally chosen. Sometimes, however, visits to the nests commenced only some ten minutes prior to entry. Furthermore, he could find no indication of any relationship between the time taken to choose a nest and the time to lay after entry. Similarly, the data presented by Wood-Gush (1963) for a single Brown Leghorn hen showed a great variability in the time from first nest examination to nest entry by that hen, ranging from 12 minutes to over four hours.

After several visits have been made to potential nests, whether floor sites, open nests or trap-nests, a nest is usually eventually entered. The mature broiler hens studied by Perry *et al.* (1971), which were given access to a nest-tube, were observed to enter a nest unit or sit in a floor site very abruptly following their previously described locomotory activities about the shed. In their study, once the nest-tube was entered the hen would usually remain in it until she had laid. If, however, a floor site was occupied, then the hen would sometimes leave the site several times before finally settling.

Turpin (1918) also noted that individual hens quite frequently visited and entered at least three or four nests in his studies of the nesting habits of Rhode Island Red and White Leghorn hens in floor pens provided with banks of artificial nests. The time spent by an individual hen in these nests varied from "a fraction of a minute to as long as two hours or more on each one before she selected the nest in which she finally laid". He also noted cases of other hens which would walk directly to the nest in which they would eventually lay and settle down in it "without any apparent hesitation, even though the nest, sometimes, was already occupied". Unfortunately, Turpin made no attempt to record these entries for individual birds.

The use of trap-nests in the pre-laying studies conducted by a number of researchers has precluded the gathering of much information on nest entry habits and frequencies in such studies. Little is known about if and how trap-nesting influences nest examination and nest entry characteristics of experienced hens. However, Turpin (1918) recorded times on the final nest for Rhode Island Red and White Leghorn hens given access to open nests and also the times spent on the nest by a smaller group of experienced trap-nesters of both breeds when placed in pens equipped with trap-nests. For both breeds, the results for time on the final nest in open nests and time in the trap-nests were very similar. The Rhode Island Reds spent on average 1 hour 45 minutes per egg laid on the final nest for common (open) nests and 1 hour 49 minutes on the nest for trap-nests. Corresponding results for White Leghorns were 1 hour 35 minutes for both common nests and trap-nests.

Thus, it appears likely that the final nest entry of a hen into an open nest is equivalent to the eventual entry into a trap-nest. If this is so, a hen's drive to enter a number of nests prior to her final selection and entry must be overridden by experience in the case of trap-nested hens which may learn to avoid superfluous nest entries before a final selection is made. However, since "time on the nest", as measured by Turpin (1918), incorporates times spent on the nest both before and after laying, these deductions may not necessarily hold. It may be possible, although unlikely, that while the total time spent on the final nest is very similar for both open and trap-nested hens, the length of time on the nest before laying is longer, and the time on the nest after laying shorter, for example, for trap-nested hens, than for hens in open nests.

Considerably more information is available on the timing of nest entry in relation to oviposition than on the time of onset of behaviours preceding nest entry. This is probably because, particularly in the case of trap-nested birds, these activities are well defined and more easily identified.

Wood-Gush (1954) recorded times from nest entry to egg laying which varied from just over an hour to 3 hours 40 minutes. However, he pointed out that these intervals are also difficult to measure accurately by observational techniques because frequent examination of the nests, conducted to determine whether hens have laid or not, may disturb the nesting hen and cause her to delay oviposition. He cites the report of Patterson (1910), who was able to delay oviposition for nearly 20 hours by continually disturbing the hen when she was about to lay.

Turpin (1918) also found a wide variation in the time which different hens spent on the nest for each oviposition. Although he recorded times spent on the final nest in laying for a number of Rhode Island Red and White Leghorn hens in common nests, and both these breeds plus White Plymouth Rocks in trap-nests, he did not distinguish time on the nest before lay from time on the nest after lay. Only in the case of eight hens did he observe and record the lengths of time that the hens spent on the nest both before and after the egg was delivered. The relative times on the nest before and after oviposition were very different in each of these hens.

A significant contribution to the understanding of the temporal relationships which exist between components of the nesting sequence was made by a study conducted by Wood-Gush (1963). He recorded the time spent on the nest, measured from nest entry to oviposition, the time taken for examining nests, measured from the first examination to nest entry, and the number of examinations performed by 13 Brown Leghorn hens in floor pens provided with trap-nests. He also recorded the time of day at which each oviposition took place, the position of the egg in the clutch and the clutch size, and for each oviposition, determined whether the 'lag' for that particular oviposition was positive or negative. Lag refers to the period by which the time between laying of successive eggs differs from 24 hours. If successive eggs in a sequence are laid more than 24 hours apart, then the lag is said to be positive. This is usually the case, particularly in small clutches, since successive eggs in a clutch are generally laid later in the day. However, negative lags are sometimes recorded, and these occur where successive eggs are laid less than 24 hours apart (Wood-Gush, 1963).

Details of times spent on the nest are provided for one laying hen in this study conducted by Wood-Gush (1963) and these varied considerably, ranging from 47 minutes to over two hours. However, when Wood-Gush looked at the two temporal measurements, "time on the nest" and "nest examination time", in relation to the lag for each oviposition, a trend became apparent. Where lag between successive eggs was positive, time spent on the nest for the second egg, compared with the previous day's egg, tended to have increased. Where the lag was negative, the hen tended to spend less time on the nest. When Wood-Gush analysed the data further he found a mean increase of 35.55 minutes in the time spent on the nest for the later egg as compared with the earlier egg where the lag between them was positive. In cases of negative lag, there was a mean decrease of 21.5 minutes in the time spent on the nest from the earlier to the subsequent egg in the clutch.

A similar relationship also held for nest examination time. For this parameter, positive lag was associated with an increase of 26.75 minutes in the time spent in nest examination from the earlier to the subsequent egg in the clutch and negative lag was associated with a mean decline in the examination time of 139 minutes. In the same study, Wood-Gush was unable to find a relationship between lag and the number of nests examined. These studies throw some light on the mechanisms governing the timing of several phases of the nesting sequence and these will be discussed later in relation to the control of nesting behaviour.

The broiler hens studied by Perry *et al.* (1971) had access to open nests and so details of sitting behaviour quite apart from nest entry were extracted. In this study, the time from final sitting to laying, which the researchers call the "latency of laying", varied markedly for nest-tube or floor layers. The nest-tube layers remained sitting in the nest for an average of 94 minutes before laying, while floor layers remained seated only 43.5 minutes, on average, before laying. This is probably explained by the observation that the two types of layers displayed different levels of attachment to the nest sites they had entered, nest layers generally remaining in the nest they first entered, while floor-layers would often leave the nest several times before settling, although both nest and floor-laying hens tended to return to the same nest for consecutive nestings.

(iii) *Activities on the Nest*

Following selection and entry of a trap-nest, a hen will settle down in the nest and remain sitting until oviposition, occasionally changing position (Wood-Gush, 1963; Gilbert and Wood-Gush, 1965). Once sitting in the nest, nesting birds are difficult to disturb, and it is this characteristic which Wood-Gush (1971a) maintained enabled the observer to distinguish a nesting hen from a bird that has entered a nest in order to escape from others. Wood-Gush and Gilbert (1965) used this criterion for classifying hens as nesting or otherwise in their studies. A hen was regarded as nesting only if it was in a firm sitting position, kept the legs pressed up to the body when picked up from the nest and pecked the observer when disturbed in the nest.

Whilst sitting on the nest, the hen often performs a number of 'nest building' activities. Van Kampen (1976) reported the tendency for hens to pick up wood shavings and drop them around the tail whilst sitting. Wood-Gush (1975a) studied these behaviours in some detail. He observed the pre-laying activities of seven Rhode Island Red hens when placed alone in a 2.4 metre square pen with litter on the floor but no artificial nests. After choosing a corner in the pen the hen would usually half crouch in it and perform a number of activities. She would lower her body into the site so that the chest was in contact with the ground and the hind part of her body was raised. The keel of the body, as a result of this positioning, formed an angle with the ground. The hen would rotate herself in the nest site and push her feet out sideways as she did so. When these activities were not being performed, the stationary bird would often pick up litter or feathers and either drop them at her chest, throw them over one shoulder, or place them on her back. On other occasions the hen would rake material towards her. Any one of these movements was recorded as a gathering.

In this study (Wood-Gush, 1975a) nest building activities were occasionally interrupted by short 'forays' off the nest in which the hen might pursue further material gathering activities. These involved the tossing of material over a shoulder or placement of material on the back. Wood-Gush noted that when the material, which was either litter or a feather, was placed on the back it was then carried back to the nest where it would drop off while the hen was engaged in other nest building activities. This activity was the only means by which hens were observed to transfer material to the nest, for a hen was never seen to carry material back to the nest in her beak, or deliberately remove any of the gathered material from her back.

Wood-Gush (1975a) recorded and tabulated the numbers of gathering movements both on and off the nest, rotations, and the time taken to build nests, for each hen on several occasions in his study. The number of gathering movements on the nest varied both between hens and on different occasions for the one hen. A maximum of 574 gathering movements on the nest were recorded for one particular hen for one nesting. The least number of gatherings on the nest recorded for one of the hens was 29. Gathering activities off the nest followed the same pattern but occurred less frequently, only two or three off-nest gatherings being recorded in several cases. Even greater variation in the number of rotations performed by an individual hen on different occasions was indicated. The greatest number of rotations recorded for any one hen during one nesting was 201.

The time taken in building a nest also varied considerably both between hens and for different nests in this study. However, Wood-Gush makes the point that many of these recordingswere probably incomplete because the hen was already in a motivated state before being placed in the pen for observation.

The rotations and foot scraping activity of hens observed by Wood-Gush resulted in the formation of a round depression in the site with a rim of litter. Feathers lining the nest or on the rim of the nest were placed there as a result of the material gathering activities.

In the course of his studies, Wood-Gush noticed several instances in which hens built two nests for the one oviposition. He also observed many cases in which material gathering activities were performed for several minutes after oviposition and refers to instances in which this resulted in the partial destruction of the nest which a hen had constructed for that oviposition and only just vacated.

In a later experiment, Wood-Gush and Gentle (1978) noted that their White Leghorn hens did not make elaborate nests but did exhibit some nest building behaviours, such as scraping the litter and rotations in the site. These activities, which all experimental hens were observed at some time to perform, resulted in the formation of a circular depression in which they would sit.

Duncan (1980) has suggested that the material gathering activities off the nest described by Wood-Gush (1975a) are perhaps more correctly interpreted as nest building motor patterns occurring out of context rather than as true foraging for nesting materials. He points out that the environment provided by the pen in which the birds are placed for observation offers little by way of seclusion and the observed 'forays' off the nest were therefore quite likely to have resulted from disturbance due to lack of seclusion. This interpretation would seem to be quite reasonable, particularly in the light of the observation of Perry *et al.* (1971) that floor-laying hens, as opposed to nest layers, were more liable to leave their selected nest site on occasions for short periods off the nest. It would therefore appear that hens nesting in less secluded sites, such as pen corners, are more prone to disturbance than are nest layers.

The extent and length of time over which hens perform nest building activities will largely depend upon when a nest is entered and sitting is commenced. In the few studies in which nest building activities have been recorded, little information has been given as to when these activities occur in the temporal sequence of events following nest entry and leading up to oviposition. However, Wood-Gush (1975a) inferred that the rotations and 'excavations' associated with the formation of a depression in the nest site take place shortly after a site is selected. He also noted that the time taken to build a nest varied considerably and recorded a maximum time of 4 hours 15 minutes spent in nest building for one nesting.

(iv) *Oviposition and Post-Lay Activities*

In the published studies of nesting behaviour of hens in floor pens with or without open or trap-nests, there is a dearth of information on the behaviour, posture and orientation of the hen at the point of oviposition. In most cases, the hen is simply said to "lay", or is assumed to have 'laid'. However, Wood-Gush and Gilbert (1969a) have documented the position of hens and various stances used by hens when laying in battery cages. Hens in this study were recorded as laying in one of three stances, either standing, squatting or lying down. The hen in a standing position is described as keeping the legs and back straight. When squatting the hen's legs would be bent with the back sloping downward towards the tail. When in a lying position, the hen's breast would be in contact with the cage floor. Hens were rarely observed to lay in a lying position. The most common stance at oviposition was squatting, although most hens used more than one type of stance for different ovipositions. The same stances may be used by hens nesting in nest or floor environments but, unfortunately, no reports could be found which would validate or dismiss such a possibility. However, Fölsh (1980), describing the nesting behaviour of hens in a deep litter system with nests, referred to the laying stance in which the thorax is raised as the "penguin position".

After laying in an artificial nest or floor site in litter pens, the hen would appear to pursue one of a number of possible courses of action. She may sit down again within the nest for some time, begin to cackle or leave the nest, or she may pursue some combination of these activities. Wood-Gush (1963) stated that oviposition, in many cases, does not necessarily coincide with a desire to leave the nest. He reports that after laying, many hens will resume a sitting position and may later cackle before standing ready to leave the nest. Gilbert and Wood-Gush (1965) reported that a hen may immediately cackle after laying or she may sit within the nest for some time following oviposition. Cackling may not necessarily follow immediately upon oviposition, and Wood-Gush (1971a) suggested that the interval between cackling and laying is variable, the hen eventually standing after cackling. Also, as previously noted, Wood-Gush (1975a) observed that Rhode Island Red hens which had nested and laid in pen corners often continued material gathering activities for several minutes after oviposition, presumably both on and off the nest.

The post-lay cackle has been described by Schjelderup-Ebbe (1923) and is equated with a Warning-call, Type 2, in Konischi's (1963) classification of the vocalisations of domestic fowl. Konishi describes this call as consisting of (a) a series of pulse-type sounds having a short duration and a wide frequency range, spaced regularly in time, and (b) a sustained sound of longer duration, with a distinct harmonic structure, which usually follows a series of the pulsed sounds.

After laying, and sometimes before laying, hens will often roll their eggs, or other eggs in the nest, towards the body or manipulate the egg in some way (Wood-Gush, 1975a; Brantas, 1978; Fölsh, 1980). Wood-Gush (1975a) noted that hens nesting alone on the floor in most instances showed interest in their own eggs after oviposition. The egg would usually be rolled to a position in which it would be in contact with the breast as the hen sat. To do this, the hen sometimes had to turn the head so that the comb was on the ground. Egg rolling of an egg in front of a hen was accomplished by placing the bill over the egg and rolling it back towards the breast. Hens often rolled eggs from their previous nestings when they entered an existing nest and the action patterns sometimes occurred in the absence of eggs. Eggs were rolled over distances of up to 1.5 m and cases were observed in which eggs were rolled from previously used nest sites to newly established nests.

The length of time a hen will sit on a nest after laying, if she does so at all, would seem to vary considerably. The limited data for times spent on the nest after oviposition produced by Turpin (1918) show times ranging from three minutes to 189 minutes for eight different hens. Gilbert and Wood-Gush (1965) referred to a previous study in which they had determined that the maximum time which any of a group of 165 normal hens had spent on the nest after lay was about three hours.

Of particular interest is the observation of Wood-Gush (1954) that several Brown Leghorn hens, which had selected and laid in trap-nests, nested shortly afterwards. When these hens were released from the trap-nests, they would re-enter the nests. These hens, which presumably were not becoming broody and which Wood-Gush explicitly stated were not being persecuted, would therefore spend most of their day on the nest. This would tend to suggest that hens which sit on the nest after laying are highly motivated to do so, to the extent that they will re-enter nests from which they have been evicted to continue such sitting activity. This rules out the possibility that hens, or at least those particular hens, which sit on the nest after lay are doing so merely to 'relax', or, in the case of trap-nested hens, to quietly await release.

After the hen has stood and left the nest of her own volition after laying, then presumably she does not engage in any further nest related activities that day. However, cackling and perhaps material gathering activities may continue for a short period of time after the nest is vacated as indicated previously, but beyond these the published descriptions of nesting behaviour cease.

(v) *Factors Influencing the Form of the Behaviour Pattern*

Although the sequence of activities described in the foregoing sections appears to be quite consistent between studies and authors, a number of factors have been shown to influence the behavioural sequence or been implicated as doing so. These include the age or perhaps the extent of 'nesting experience' of the hen, breed effects, individual and social effects and the environment in which the hens are placed. The evidence for such factors will now be detailed.

(a) Age or experience of the hen

Wood-Gush (1954) described the nesting behaviour of young, Brown Leghorn pullets, untrained in the use of trap-nests and compared it with that of older, more experienced hens. The young birds studied would become very restless and nervous when about to lay for the first time and called persistently. They would wander about the sides of the pen and appeared to be searching for an exit from the pen. Older hens, experienced in the use of trap-nests, would pay several visits to the nests initially and might call. The majority of a group of young pullets under observation laid at least their first few eggs in floor sites rather than in the trap-nests.

One particularly interesting observation reported by Wood-Gush (1954) was that one of the young pullets was seen to try and 'nuzzle under' other birds when approaching oviposition. This activity was not noted in any other hens. However, in a later report Wood-Gush and Gilbert (1969b) recorded the same activity being performed by one oestradiol treated, and three other non-treated pullets. It was also seen in four mature laying hens, but the researchers thought that it was most commonly observed in hens about to lay which have had little experience with artificial nests.

Wood-Gush and Gilbert (1969b) also reported that orientation away from pen-mates during nest calling was as marked in adult females as in young pullets.

Little additional information is available on comparative nesting behaviours of young laying pullets and mature laying hens maintained under the same conditions. The extent to which experience is able to modify the behavioural sequence leading up to the selection of a nest and oviposition would not only be of theoretical interest but of practical significance, particularly in the case of floor reared breeder flocks in which nest usage patterns established in the early stages of lay may have a profound effect on patterns of floor-laying throughout their laying history.

(b) Strain or breed effects

Some evidence exists to suggest that different breeds of domestic hen may differ with respect to the behaviour patterns they display prior to laying or in the extent or intensity at which they will perform component activities of the nesting sequence. On the purely anecdotal side, Wood-Gush (1975a) commented that the nesting behaviour of a few intact Brown Leghorns observed in earlier studies had been less complete than that of intact Rhode Island Red hens and that the nests built by the Brown Leghorns were rudimentary in comparison.

On the other hand, Turpin (1918) provided quantitative evidence to indicate possible breed differences in the extent to which hens will perform particular activities associated with nesting. He recorded the number of nest entries for which the hen sat down within the nest and remained for at least one minute without laying, for about 40 Rhode Island Red hens and about 50 White Leghorn hens in litter pens provided with artificial nests. The White Leghorns, as a group, recorded nearly as many entries in one day as the Rhode Island Reds did in two. It should be noted, however, that the figures obtained were whole flock totals, and the numbers of hens which were laying in each flock and so contributing to the nest entry data were not given. It is thus possible that the White Leghorns made more entries in total simply because more of them were laying. However, the existence of a real difference between the two breeds, at least for this parameter, is given credence by the author's observation that the difference in number of nest entries would have been even larger had he recorded entries for which hens remained in the nest for less than one minute. He noted that the Leghorns recorded many more very short visits to the nests than did the Rhode Island Reds.

When Turpin totalled the times spent in the nest by both breeds for each of the recorded nest entries which exceeded one minute in duration, he found that the Leghorns spent 21 minutes in the nest per visit, on average, while the Reds averaged 15 minutes. He also found that the Leghorns spent, on average, 1 hour 35 minutes and the Rhode Island Reds, 1 hour 45 minutes, on the final nest for each egg laid. The total time which hens spent on the nest for each egg laid, which included time on the nest for nest entries occurring without laying and time spent on the final nest both before and after laying, was very similar for the two breeds. The Leghorn hens spent an average of 1 hour 58 minutes and the Rhode Island Reds 1 hour 55 minutes on the nest for each egg produced. Thus, although the total times that hens sat on the nest for each oviposition were much the same for both breeds, the manner in which they distributed their time on the nest may have differed between the breeds. Unfortunately, Turpin did not analyse his data statistically and so it is difficult to reach firm conclusions on this point.

Although several breeds often have been used for the studies on nesting behaviour of domestic hens in floor pens, few other reports of direct comparisons between different breeds or strains with respect to this behaviour pattern in such environments are available. However, several studies comparing the behaviour of hens of different breeds or strains during the nesting phase in laying cages have been provided, and these will be dealt with in the following section.

An interesting report on the pre-laying and laying behaviour of hens of a commercial turkey strain has been furnished by Opel and Proudman (1982). The nesting behaviour of these hens, which were observed two weeks after being moved to a floor pen from individual cages, was remarkably similar to that described for domestic hens in floor pens. The researchers were particularly struck by the hundreds of pacing and escape movements performed by these hens in both cages and floor pens. In some hens, these activities began as early as five hours before oviposition. They report that these pacing movements, when performed by penned hens, were of variable speed and orientation and "tended to occur as far as possible from the final nesting site". They were sometimes accompanied by a distinctive call, although a description of the call is not given. Pre-lay pacing sometimes continued up until one or two minutes before oviposition. Hens sat quietly on the nest for only brief periods of time before oviposition and few, if any, nest building activities were performed. After laying, hens which had performed a great deal of pre-lay pacing tended to stand immobile with wings drooped and held away from the body for several minutes. The researchers attributed the pre-lay pacing activity to frustration but could see no apparent reason why penned hens should be frustrated.

(c) Environmental effects

Obviously, the type of behavioural activities a hen is stimulated to or able to perform will be determined by environmental constraints. The types of pre-lay behavioural patterns which hens will exhibit are therefore likely to be in some respects different in very dissimilar environments. However, even within the same environment a number of nesting environments may be available, and hens using such alternatives may display different nesting behaviours in response to these.

. *Nesting behaviour in nest-box or floor environments - deep litter pens*

Flocks housed in floor pens with artificial nests provided have a number of potential nest sites available to them. It has already been noted that Perry *et al.* (1971) found that broiler hens which chose to lay on the shed floor or in provided nests displayed quite different affinities for their selected sites. Floor-layers often left their sites for periods of time before settling, whereas nest-box layers tended to remain in the first nest entered until oviposition. The time from final sitting to laying in the floor site nesters was almost half as long as that of the nest-box users. Although no further direct comparisons have been found between the nesting behaviours displayed by hens which elect to lay in different nesting environments, the observations of these researchers indicate that the type or extent of activities performed may vary according to the nest environment selected.

. *Nesting behaviour at free range or in the wild*

Few reports of the behaviour of domestic hens during the pre-laying phase at free range or in the 'backyard' situation have been produced. However, the nesting behaviour of feral fowl and of gallinaceous birds in a natural habitat has been studied in some detail and has been reviewed in Section 2.1.[illegible] of this Chapter.

. *Nesting behaviour in laying cages*

The nesting environment provided by a laying cage is a far cry from that available in a natural habitat or even in a litter floor pen. The behaviour of hens in such environments could, therefore, also be expected to be quite different.

Nesting behaviour in laying cages is reported to begin with searching movements, then the hen inspects the cage floor and corners with her neck protruded, while she emits weak calls (Brantas, 1980, citing Martin, 1975). These movements increase in intensity and "sounds of fright" are given. The hen may crawl beneath other hens and appears to attempt to escape from the cage by pushing her head between the cage bars and squeezing her body forward. She may attempt to "climb" up the cage, falling to the floor as if in a state of panic. Suddenly she will cease such activities, sit quietly and lay. Afterwards, apparently exhausted, she may sink to the floor again. Results obtained (Brantas, 1980, citing Martin, 1975) showed that the entire egg laying procedure lasted on average 74.2 minutes per hen, whereas in a hen house with laying nests it had taken 16.4 minutes.

In the course of their studies, Bobr and Sheldon (1977) also described the behaviour of hens when approaching oviposition in laying cages. Its onset is said to be signalled by soft, continuous vocalisations, while the bird stands quietly but alert and facing the front of the cage. This may be interrupted for varying lengths of time by maintenance activities, the frequency of these interruptions depending on the individual bird. The vocalisation would be resumed again to become continuous and gradually increasing in intensity, usually persisting until oviposition. The hen moved into a phase of restless activity after a variable period of vocalisation. The initial cage pacing develops into, or may be intermittent with, 'escape' movements. Nest building or dust-bathing may occur in the final stages. Some birds displayed periods of resting, during which they would sit quietly, between these bouts of restlessness. Most birds cease their activity quite abruptly, assume the laying stance while facing the back of the cage, and then lay. Others may rest for some time before raising themselves quietly to expel the egg. After laying, the hen appears to relax for a period of minutes and then turns abruptly to feed, eating avidly for some time.

Fölsh (1980) reported observations comparing the nesting behaviour of hens in a deep litter system with nests with that which occurs in cages. He found that hens remained in nests in the deep litter system for 54 minutes on average. In the laying cage environment, hens spent, on average, only 17 minutes on comparable activities, which involved sitting quietly and nest building, laying and resting quietly after laying. The remaining time before and after laying, tended to be occupied by pacing or general movement about the cage. The more hens in the cage, the less time was spent lying down in the hour before egg laying and the more time upright.

However, many of the component activities of nesting behaviour as displayed in other environments are also apparent in the nesting sequence in laying cages. Wood-Gush and Gilbert (1969a) recorded a number of behavioural parameters which occurred during the pre-laying phase and during oviposition for two commercial strains of hens in individual battery cages. In general, pre-laying behaviour consisted of calling, preening, sleeping, pacing and escape components.

Although individual bird effects were felt, the pre-laying behaviour of the two breeds studied, one a White Leghorn hybrid (White strain) and the other a Rhode Island Red/White Sussex hybrid (Brown strain) differed markedly. The onset of pre-laying behaviour of the White strain hens was relatively easy to establish. The hen would stop its current activity, look around for a while, then resume her previous activity for 10-30 minutes before commencing typical pre-laying behaviours. A large restlessness and escape behaviour component was present during the pre-laying phase of these birds, only one of the 15 birds in this group spending less than 45 minutes in very restless activity. The Brown strain hens, on the other hand, preened and slept to a large extent on both laying and non-laying days and exhibited less pacing and escape behaviour. Some of these hens never showed escape behaviour and only one cut of seven hens spent more than 45 minutes in very restless activity. A later experiment (Wood-Gush, 1969) attempted to quantify these differences in restless activity between the two strains. In the case of one strain (presumably the White birds) some hens recorded as many as 1,000 paces in the pre-laying hour. As few as 50 paces were recorded for hens of the other strain.

Wood-Gush and Gilbert (1969a) also found that pre-laying behaviour generally extended for a period of over two hours and seldom occurred for less than one hour. For White Leghorn hybrid hens the duration of pre-laying behaviour rarely exceeded four hours, although for the Brown strain, pre-laying behaviour lasted more than four hours in about 20% of all cases. All birds of both strains showed "nest-building" activities which were not described but which included the performance of litter gathering movements. Although no data are given, the authors indicated that the Rhode Island Red/White Sussex hybrid hens tended to 'nest' more than the White Leghorn hybrids.

In the same study, Wood-Gush and Gilbert (1969a) also found that the position of the hen in the cage at the time of oviposition was non-random and that hens tended to have 'preferred' positions of the cage in which to lay. The back of the cage was most popular. The orientation of the hen in her cage during oviposition was also non-random. Most of the eggs were laid with the hen facing the back of the cage rather than the observer (front of the cage) or facing across the cage. Twenty four of the 31 birds showed an orientational preference and always faced in that direction when laying. Most hens also used more than one type of stance when laying, but for both strains squatting was most, and lying down least, common. No difference was found between the two strains of hen in the frequency of the stances.

In an effort to provide possible explanations for the observed differences in pre-laying behaviour in battery caged White, as opposed to Brown, strain hens, Wood-Gush (1972) conducted a series of experiments comparing the behaviour of the two strains in a number of situations. In floor pens provided with trap-nests no significant difference was found between the two strains when the numbersof paces taken in the half hour up to nest entry were compared. Highly significant differences were, however, found between birds. He suggested that the previously reported differences in pacing by the two strains in battery cages may have been a result of the conditions of the cage.

In an effort to establish whether the relative degree of 'enclosure' could affect the frequency of pacing and time spent sitting in battery cages, Wood-Gush (1972) recorded these parameters for both strains in ordinary wire battery cages and in battery cages with solid metal walls and back. Significant differences were found for these parameters for the hours preceding oviposition as compared to the corresponding hours on non-laying days. White strain hens paced more in the pre-laying hour than in the non-laying hour and this was unaffected by cage type. The Brown strain paced less and sat more than the Whites during the pre-laying hour and paced less and sat longer in the pre-laying hour if in the enclosed as opposed to the open cages. The average times spent sitting during the one hour pre-laying period in open cages were 32.66 minutes and 9.28 minutes for Brown and White strain hens respectively, and in enclosed cages 48.59 minutes for the Browns as opposed to 17.12 minutes for the Whites.

When cages of hens were placed in two pens of differing light intensity in an extension of the previous experiment, both strains paced significantly more in the pre-laying than in the non-laying hour, and,again, Whites paced more than Browns in the pre-laying hour. Brown hens tended to pre-lay pace more in the lighter environment while the reverse was true for the White hens. Brown hens again sat longer than White hens in either pre-laying or non-laying hours. These experiments indicated that neither the provision of additional enclosure nor darkness to the cage, both stimulus components of a trap-nest, resulted in a reduced frequency of pacing or increased time sitting during the pre-laying period of White strain hens.

In a further experiment, Wood-Gush (1972) found that pacing frequency in the half hour before laying was not significantly different from that recorded in a half hour feeding frustration test in the case of the White strain hens, but that Brown hens paced less during the pre-laying phase than during frustration. He suggested that the White strain hens may therefore be frustrated by having to lay in battery cages and their excessive pacing may be a reflection of this. On the other hand, the Brown strain hens would appear not to be frustrated by caging in the pre-laying period. To determine whether this was a result of differential 'drive' strengths of the two strains, Wood-Gush (1972) measured re-entry times for hens removed from the trap-nest after initial entry during the pre-laying phase. Mean times to the second entry were not significantly different for the two strains, indicating that the two strains did not apparently differ in the strength of their nesting 'drive' in pen-conditions. Thus, the possibility that the Brown strain hens may have been nesting in sub-optimal conditions because of a greater nesting urge and a correspondingly enhanced responsiveness to such stimuli provided was not supported.

Wood-Gush (1972) went on to suggest that the minimal sitting behaviour shown by White strain hens in battery cages would therefore be more likely to have resulted from the absence or inadequacy of some key stimulus other than enclosure or darkness, or some necessary stimulus change which would otherwise release sitting behaviour in these hens. The difference observed between strains in this behaviour, he concluded, was probably due to differences in responsiveness to releasers for sitting behaviour rather than to differences in the intensity of the nesting drive. However, Wood-Gush's experiment revealing, non-significant differences in times to second entry for motivated hens removed from trap-nests, is limited and fails to take into account that the initial trap-nest entry time may be influenced by factors other than the hen's 'drive' strength to nest. Individual hen effects in the small sample taken could mask any inter-strain differences with respect to nesting 'drive'. It should also be noted that, as pointed out by Duncan (1980), the hens which Wood-Gush (1972) tested in the more enclosed or darkened battery cages had already exhibited excessive pacing probably indicative of frustration in normal battery cages may have continued to perform these stereotypic pacing movements when placed in the modified environments.

In a further study, Wood-Gush (1975b) investigated the role of the cage floor in eliciting sitting behaviour in the White strain hens. He firstly recorded the number of pacing steps and sitting times for the half hour before lay and the corresponding half hour on non-laying days for hens in cages with floor slopes of either 1 in 6 or 1 in 3. The slope of the cage floor did not affect the trend demonstrated in previous studies in which hens paced more on laying than non-laying days. A trend existed, although non-significant, for hens on less steep floors to sit for longer than those on the steeper floors on laying days. The reverse situation existed on non-laying days. Wood-Gush therefore suggested that steep floors hindered sitting during the pre-laying phase and that the qualities of the floor that elicit sitting in the pre-laying period as opposed to resting periods are different.

In a second experiment (Wood-Gush, 1975b) pacing and sitting were recorded for the White strain hens in cages with conventional wire floors of 1 in 5 slope and in cages in which the floors had been removed and replaced with litter-lined metal trays. Each hen was observed in both situations, so was effectively its own control. Hens laying on the flat litter floors sat significantly longer and paced significantly less than hens laying on the sloping wire floors. Unfortunately, the experiment did not differentiate between these variables of slope and the presence of litter, so Wood-Gush was unable to conclude which of these two stimuli was eliciting sitting. Also, the hens had been kept on litter prior to the experiment and so, perhaps, had not developed frustration induced stereotypic pacing movements that may have been apparent in the caged hens of the earlier studies.

Brantas (1980) reported the findings of studies in which the pre-laying behaviour of hens in cages, in which the birds were either allowed access to nests attached to the cage or were not, were studied. All hens had previous experience of nest-boxes in the deep litter pens from which they originated.

When no access was allowed to the nests, significantly more paces were taken by the hens and less time was spent in sitting. This tendency occurred in both situations in which hens had initially had access to the nests (then nests were closed and opened again over periods of three weeks) and in which the hens had first been prevented access to the nests (then nests were opened, and finally closed again). It is possible, therefore, that hens which in the first period of observation had no access to nests, may have been frustrated by inability to get into the nest which they were accustomed to using in their earlier pen experience. Frustration resulting from exclusion of previously used trap-nests or caging of hens used to laying in trap-nests has been indicated by increased stereotyped pacing in the pre-laying hour in a study reported by Duncan (1970).

(d) Effects of social factors

Not a great deal is known about the influence of other flock members on the nesting behaviour displayed by individual hens, nor about the effect, if any, of the individual's position in the flock social hierarchy. However, the nesting hen does interact with other hens in many situations during the nesting sequence and such interactions may influence the ultimate behaviour pattern displayed. Hens are known to perform most of the previously described nesting behaviours in isolation (Wood-Gush, 1975a). However, one interesting observation is that the presence of other hens is not necessary for the nesting call to be elicited, but the pen-mates may affect the orientation of the calling hen (Wood-Gush and Gilbert, 1969b).

One activity described by several authors which occasionally appears in the nesting sequence of hens close to oviposition is a tendency to crawl under other hens. Wood-Gush (1954) observed this activity in a Brown Leghorn pullet that would not use the provided trap-nests. The pullet made no attempt to lay away from other birds. Wood-Gush and Gilbert (1969b) reported the occurrence of the same activity, which they termed "nuzzling under", in the pre-laying behaviour of a number of oestradiol treated pullets and untreated mature laying hens. This activity is also seen, apparently, in caged hens during the pre-laying phase (Brantas, 1977). Other reports have indicated that some laying hens, while not actually seeking out the company of, or proximity to, another hen, are nevertheless undeterred by the presence of a flock-mate in their nest selection (Turpin, 1918).

Alternatively, some hens appear to devote a considerable proportion of their time while selecting or sitting on the nest, to defending it from other prospective nest users. Perry *et al.* (1971) reported an instance in which one particular hen removed all hens from an entire nest-set and patrolled the territory for 30-60 minutes before eventually sitting in one of the nests.

As previously noted, the cockerel appeared to play some role in the nesting sequence of captive feral fowl studied by McBride *et al.* (1969). While this was not recorded in the study conducted by Duncan *et al.* (1978), or for domestic strains in floor pen environments (Wood-Gush and Gilbert, 1969b), this case does serve to illustrate further that nesting behaviour may be influenced by other members of the flock.

(e) Individual variability

Most researchers who have observed and reported nesting behaviours of hens, regardless of their environment, have noted that a considerable variation exists within a group of birds in the range of activities performed and in the extent or intensity at which they are performed. For example, Turpin (1918) recorded a large range of time-spans spent on the final nest up to lay within flocks of hens of two breeds. He also noted that a large variation existed in the proportion of total time different hens spent on the nest before and after laying. These differences were unrelated to the hens' rates of production.

In many cases, particular hens have exhibited behaviours which the observer has considered to be outside the general range of variation exhibited by the flock and so worthy of special mention. Wood-Gush (1971b) reported that some hens in his studies exhibited persistent 'idiosyncrasies' such as leaping against pen walls or persistent calling. Iodiosyncrasies such as persistent calling in floor pens (Wood-Gush, 1963), unusual position and stance at oviposition in laying cages (Wood-Gush and Gilbert, 1969a) and extreme defence of the nest (Perry *et al.*, 1971) have also been noted.

It is evident from the literature that while genotype, age or degree of experience, social factors and particularly the nesting environment may all interact to determine the range of nesting behaviours that a hen is likely to exhibit, the exact form of the behaviour pattern is very much an individual characteristic.

2.1.3 Control of nesting behaviour

It has long been recognised that nesting behaviour may be elicited without an accompanying egg being laid. Turpin (1918) reported several instances in which hens would visit nests regularly and spend considerable time on the nest on some days without laying. He cited several earlier reports in which hens were observed to visit nests and sit in them on the appropriate day and hour at which they were expected to lay, without laying. In a later study, Cole and Hutt (1953) reported the occurrence of nesting in ovulating but non-laying hens. They concluded that the urge to nest was not induced by the presence of a shelled egg in the uterus.

During the course of behavioural studies, Wood-Gush (1963) observed the premature dropping of a shell-less egg which was not preceded by characteristic pre-laying behaviour. Some hours later the hen which had been noted to do this began performing her pre-laying behaviours at the time she should, indicating that the presence of an egg in the oviduct was not affecting the timing or occurrence of its nesting behaviour. This observation prompted Wood-Gush to investigate the behaviour of birds which had been rendered chronic shell-less egg layers by surgical means. He found that normal pre-laying behaviour could occur in the absence of a hard-shelled egg in the oviduct. He went on to find that hens in which the infundibulum had been stitched up, rendering them chronic internal layers, also appeared to nest normally. Hens which had the oviduct entirely removed also nested normally, indicating that the oviduct is not necessary for nesting behaviour to be elicited.

An earlier study conducted by Rothchild and Fraps (1944) had shown that removal of the ruptured ovarian follicle at the time the egg released from it was in the oviduct, invariably resulted in a delay in the time of lay of between one to seven days. These results indicated that the ruptured follicle was important in determining the timing of oviposition of the egg released from it. Wood-Gush and Gilbert (1964), following up this lead, investigated the effect of removal, ligation or manipulation of the most recently ruptured follicle, removal of the follicle nest due to rupture, or removal of several immature follicles and some ovarian wall, on the occurrence and timing of nesting behaviour and oviposition. They found that removal or ligation of the most recently ruptured follicle (the post-ovulatory follicle) affected the nesting behaviour of a large proportion of birds. These treatments also delayed oviposition in the majority of cases. Manipulation of the most recently ruptured follicle did not produce these effects, nor did the other treatments. These findings established that nesting is dependent on the integrity of the most recently ruptured follicle. The results also suggested that the initiation of nesting behaviour, the timing of oviposition and the termination of nesting behaviour may be differentially controlled, since one of these parameters could be affected by the treatments independently of the others.

The foregoing experiments had indicated that the follicle may have been exerting its influence by hormonal means. Since progesterone was known to occur, and was capable of inducing ovulation in the fowl, Gilbert and Wood-Gush (1964) conducted an experiment to determine whether progesterone could induce nesting behaviour in ovariectomized hens pre-treated with oestrogen. However, progesterone had no effect on the incidence of nest entry or the form of the behaviour pattern shown. On the other hand, Gilbert (1965) was able to show that the ovarian follicle of the hen is well innervated. This suggested that neural mechanisms may be involved in the control of nesting behaviour by the post-ovulatory follicle.

Gilbert and Wood-Gush (1965) investigated the possibility of a neural mechanism by blocking afferent impulses from the post-ovulatory follicle by means of cocaine injections into the follicle. While cocaine injection did affect nesting behaviour in a proportion of cases, it was not as effective in disturbing nesting behaviour as either removal or ligation of the post-ovulatory follicle had been in the earlier study. Saline injections into the follicle were ineffective in disturbing nesting behaviour. Although it was possible that cocaine did not exert as great an influence on nesting behaviour as a result of the relatively short time over which its blocking effect would have been felt, they concluded that a neural component was in some way involved, but hormonal mechanisms were probably also implicated.

In a further experiment (Gilbert and Wood-Gush, 1968) it was shown that when ovulation took place under anaesthesia, surgery, or after cocaine or saline injection into the pre-ovulatory follicle, the resulting nesting behaviour was little, if at all, affected. Artificial rupturing of the follicle resulted in disturbed nesting except if it was performed within about one hour of the expected ovulation time. These results indicated that a change in the physiological state of the bird occurs shortly before ovulation, and that the integrity of the follicle up to this point must be maintained if normal nesting behaviour associated with the egg resulting from that ovulation is to occur.

A later investigation of the effect on nesting behaviour of removal of the post-ovulatory follicle either 4 or 20 hours after ovulation indicated that the integrity of the post-ovulatory follicle must be maintained at least 20 hours after ovulation if normal nesting is to ensue (Gilbert and Wood-Gush, 1972). The proportion of nestings found to be abnormal, rather than completely abolished, as a result of the treatments was different for two strains of hens studied, suggesting that strains may have different thresholds to the hormone(s) produced by the post-ovulatory follicle or that the hormone(s) may be produced at different rates by the follicle in different strains.

In an attempt to clarify whether hormonal or neural mechanisms were operative in the control of nesting behaviour, Wood-Gush and Gilbert (1970b) studied post-operative nesting patterns displayed by hens which had undergone ovarian transplants. Ovarian tissue was transplanted to another site in the abdomen of these birds and all ovarian tissue removed from the original site. Normal innervation of the ovary could therefore not be re-established. Nesting behavious, as compared with that of sham-operated control hens, was largely unaffected by the transplant. They concluded that a neural mechanism was not necessary for nesting and that the previously described effect of cocaine injection must have been due to side-effects of the drug rather than to its blocking effect on sensory and motor impulses.

Encouraged by reported suggestions of fluctuating blood progesterone levels during the egg laying cycle and the probable production of that hormone by the post-ovulatory follicle, Wood-Gush and Gilbert (1973) again attempted to induce nesting behaviour in ovariectomized hens by hormonal means. However, in these experiments they used hens with nesting experience for the ovariectomies, and injected the oestrogen pre-treated hens with progesterone and oestradiol, an oestrogen known to occur naturally in the hen. In their previous study (Gilbert and Wood-Gush, 1964) hens were ovariectomized well before they had ever experienced egg laying and nesting behaviour and the birds were treated with progesterone and diethyl stilboestrol, a synthetic oestrogen.

Hens of two breeds both exhibited nest examination and nest entry behaviour following administration of both progesterone and oestrogen (oestradiol). The number of nest examinations was much higher following treatment with both hormones than following treatment with oestrogen alone. However, oestrogen itself was thought to have some role in influencing nest examination, since hens treated with oestrogen alone performed more nest examinations than did normal hens on non-laying days. Nest entry rarely occurred when oestrogen alone was administered, but was greatly increased by progesterone plus oestrogen treatment. This result suggested that nest entry and nest examination may be differentially controlled.

Other component activities of the nesting sequence may also be under the influence of other controlling factors. Wood-Gush and Gilbert (1969b) had noted the occurrence of 'pre-lay' calling in pullets some days before their first eggs were laid and before their first ovulation. These observations suggested that this behaviour could therefore not be under the control of the post-ovulatory follicle, but since the ovaries may have been capable of producing oestrogen, this hormone could be involved. Following oestradiol treatment, young, immature females were observed to elicit the pre-laying call and orient themselves away from their pen-mates in the same manner as adult nesting hens. They did not, however, display the restlessness characteristic of adult hens in this phase.

Further evidence has been produced indicating the importance of progesterone in the control of nesting behaviour. Gilbert and Wood-Gush (1976) found that administration of exogenous progesterone to intact hens led to delayed oviposition and a high frequency of abnormal nestings associated with these. Wilson and Sharp (1976) have also proposed that a pre-ovulatory surge of progesterone influences the timing of the oviposition resulting from that ovulation. Presumably the timing of nesting behaviour would be similarly affected.

Since little was known about the control of nesting behaviour by the central nervous system, an obvious progression was to investigate the co-ordinating role of the nervous system in nesting behaviour. From previous studies progesterone and oestrogen were known to in some way control, together or separately, at least some aspects of nesting behaviour. It was of interest to find where in the central nervous system these hormones were acting. Wood-Gush *et al.* (1977), using autoradiographic techniques, were able to identify cells labelled with both oestrogen and progesterone as well as testosterone in the hyperstriatum ventrale of the telencephalon of hens. The hyperstriatum dorsale and nucleus intercalatus hyperstriacticus were found to contain cells labelled with oestrogen alone. It was apparent from these studies that the hyperstriatum was likely to be in some way involved in the control of nesting behaviour.

In order to investigate the role of the hyperstriatum in nesting, Wood-Gush and Gentle (1978) studied the nesting behaviour of hens with lesions in this area of the brain. All hens with hyperstriatal lesions performed normal nesting behaviours such as calling, pen exploration, litter scraping and rotations and extended sitting. However, hens did not gravitate towards the trap-nest as they would do normally. This was most obvious in the case of hens with extensive ablations which also involved the hyperstriatum ventrale, as opposed to those with superficial hyperstriatal ablations. Hens with extensive ablations also failed to exhibit the usual conservatism in nest site usage and failed to orient to a corner or examine trap-nests. The area of the hyperstriatum ventrale ablated was similar to that which had been shown to bind oestrogen and progesterone (Wood-Gush *et al.*, 1977). Ablations involving the posterior telencephalon had no such effects, nor was the behaviour of sham-operated control birds affected.

Salzen and Parker (1975) had previously suggested that hyperstriatal lesions affect the continuing orientation of chicks towards a stimulus. This led Wood-Gush *et al.* (1977) to postulate that both oestrogen and progesterone act on neurones in the ventral hyperstriatum to affect the attentional mechanisms of the hen, causing the hen to respond to, and sustain the response to, the stimuli relevant to nesting. The hyperstriatum is therefore important in the visual selection of a nest site and the maintenance of orientation towards the nest, but not in the early appetitive nesting behaviour pattern.

While the timing of oviposition, and so nesting behaviour, would appear to be governed by progesterone, a temporal relationship also appears to exist between the pre-ovulatory luteinising hormone (LH) surge and the resulting oviposition (Wilson and Sharp, 1973). Wilson and Sharp (1976) have suggested that the effect of progesterone in determining the timing of oviposition may be mediated indirectly by causing an increase in plasma LH concentrations, since progesterone injections can stimulate LH secretion (Wilson and Sharp, 1975). It is therefore possible that LH, which is intimately involved in the control of ovulatory and ovipository cycles in the hen (see Gilbert, 1971; Gilbert and Wood-Gush, 1971) could also be involved in the control of some aspects of nesting behaviour. It is undoubtedly involved indirectly, if not directly, in at least temporal aspects of the nesting sequence.

One hormone that may have a role in the control of some aspects of nesting behaviour is prolactin. It is generally accepted that this hormone is involved in broody behaviour (Sturkie, 1976) to which nesting behaviour is closely tied. Many component motor patterns of incubation behaviour are also essential elements of incubation in ground nesting species (Baerends, 1959).

Evidence for a role of prolactin in incubation or broody behaviour in turkeys is quite strong. Incubation behaviour in the turkey has been found to be associated with elevated prolactin levels, which gradually begin to increase from about ten days prior to the onset of broodiness (Proudman and Opel, 1981). Burke and Dennison (1980) also reported a dramatic increase in prolactin levels at the onset of broodiness in the turkey.

Evidence of involvement of prolactin in broody behaviour of domestic fowl also exists. In White Rock hens, serum prolactin concentrations were found to be consistently higher in broody than in laying hens (Bedrak *et al.*, 1981). In the case of bantams, prolactin concentrations in the blood have been reported to be highest when birds begin to incubate eggs (Sharp *et al.*, 1979).

Contradictory evidence for the role of prolactin in maternal behaviour has, however, been produced (e.g. Shani *et al.*, 1973) and some reports of hormone levels in broody turkey hens indicate that prolactin levels in broody and non-broody laying hens may not always be measurably different (Etches *et al.*, 1979a; McNeilly *et al.*, 1978).

Prolactin may also be involved in the laying or nesting sequence of poultry. Higher prolactin levels have been found for laying as opposed to non-laying female turkeys (McNeilly *et al.*, 1978; Scanes *et al.*, 1979), and domestic fowl (Burke and Dennison, 1980). Prolactin concentrations in turkeys have also been shown to increase with the onset of laying (Etches *et al.*, 1979a), and its release may be controlled by oestrogen (McNeilly *et al.*, 1978). In laying domestic fowl, prolactin level has been shown to vary with the ovulatory cycle, being highest immediately after oviposition (Bedrak *et al.*, 1981) and being related to the pre-ovulatory surge of LH (Scanes *et al.*, 1977). Diurnal fluctuations in prolactin related to the ovulatory cycle have also been reported in turkeys (Sharp *et al.*, 1981). In Ruffed Grouse (*Bonasa umbellus*), plasma prolactin levels have been shown to increase as the number of eggs in the nest increases (Etches *et al.*, 1979b).

The preceding evidence indicates that prolactin levels may vary throughout the ovulatory cycle and may be involved in maternal behaviour, at least as it relates to incubation. It is also possible that prolactin may be involved in the control of certain nesting behaviours. Times spent in sitting, egg rolling behaviour and nest attentiveness would seem to be likely behaviours that may be influenced by this hormone, as they appear to be incubation-related activities. It is interesting, in this respect, that prolactin levels are highest immediately after laying in fowl (Bedrak *et al.*, 1981) when potentiality to sit or manipulate eggs may be high. Wood-Gush (1975a) has previously suggested a role of prolactin in egg rolling behaviour and pointed out the practical implications of this if egg rolling is equated with early incubation behaviour. However, he also indicated that this behavioural phase could be under the control of progesterone instead.

Another hormone that fluctuates in the ovulatory cycle, such that it could be involved in the control of certain behaviours related to nesting, is testosterone, the level of which drops significantly following ovulation and oviposition and which would appear to be released by the maturing follicles (Shahabi *et al.*, 1975). Testosterone concentrations in turkey hens have been found to be higher in laying than non-laying birds (Scanes *et al.*, 1979). However, concentrations of testosterone and LH prior to the last oviposition of a sequence vary little with respect to oviposition, while pre-ovulatory surges of both these hormones are evident (Etches and Cunningham, 1977). This suggests that these hormones may be involved in the ovulatory process but have little effect on the nesting and ovipository process.

Oviposition and the behaviours related to expulsion of the egg may be controlled differently from other aspects of the nesting sequence. Wood-Gush and Gilbert (1964) provided evidence to suggest that although the initiation of nesting behaviour, the timing of oviposition and the termination of nesting behaviour are temporally related in such a way that each occurs at the correct time in the nesting sequence of a normal hen, any one of them can be affected independently of the others.

Pituitary hormones, and particularly those from the posterior pituitary, have, for some time, been implicated in the control of oviposition (Riddle, 1921; Burrows and Byerly, 1940, 1942). Later research (Opel, 1966) suggested that arginine vasotocin, which was known to be a neurohypophyseal hormone in the hen (Munsick *et al.*, 1960) may have been involved. Plasma arginine vasotocin levels have been found to increase markedly during oviposition and drop quickly thereafter (Douglas and Sturkie, 1964). At the same time the content of vasotocin in the posterior pituitary has been found to decrease significantly at oviposition, suggesting a rapid discharge of arginine vasotocin from that organ into the blood at oviposition (Tanaka and Nakajo, 1962). The primary role of this hormone in oviposition was further implicated by the finding that injections of vasopressin, the mammalian analogue of vasotocin (Sawyer, 1964), could induce premature oviposition in the hen (Gilbert and Lake, 1963; Rzasa and Ewy, 1970). The activity of vasopressin in the induction of oviposition in both of these studies was found to be much greater than that of oxytocin, also a chicken neurohypophyseal hormone (Munsick *et al.*, 1960).

Vasotocin release at oviposition in the hen may not, however, necessarily be responsible for the resulting oviposition. Sturkie and Lin (1967) found that if oviposition was delayed by ephedrine sulphate injection or advanced by pitressin injection, the oviposition was not associated with an increase in vasopressin. They suggested that there was no causal relationship between the release of vasotocin and oviposition.

Intrauterine injections of prostaglandins have been shown to induce premature oviposition (Hertelendy, 1972; Hertelendy *et al.*, 1974) and prostaglandin synthetase activity has been found in the oviduct of the hen (Christ and Van Dorp, 1972). The activity of both vasotocin and prostaglandins in the control of oviposition is therefore probable, but as yet very little is known of how, if at all, these hormones may influence the behaviours related to oviposition.

While progesterone apparently has an important function in the control of nesting behaviour, the abovementioned hormones, and perhaps others involved in the control of ovulation and oviposition in the hen (see review by Gilbert, 1971), may also have some role and could be further investigated. Similarly, the mechanisms by which these hormonal effects are mediated and where they act in the central nervous system warrant further investigation.

2.2 The Choice of a Nest Site

2.2.1 Selection of a nest site in a natural habitat

(i) Nest site characteristics of wild gallinaceous birds

(a) *Junglefowl*

Reports of the types of sites used by junglefowl for nesting in the wild indicate that these birds tend to lay in sites on or near the ground in very rudimentary types of nests. Baker (1930) reported that Burmese Red Junglefowl (*Gallus gallus spadiceus*), the reputed progenitor of today's domestic fowl, lay in depressions in the ground which sometimes contain accumulations of leaves. Their close relative, the Indian or Common Red Junglefowl (*Gallus gallus murghi*) is found to nest in depressions scratched in the ground or in natural hollows. The nest may be devoid of any lining or may be well-lined with assorted vegetative rubbish. Occasionally, eggs are not even laid in a hollow and are found under bushes or in clumps of bamboo. In other cases eggs may be found in hollows formed in a heap of grass, leaves and other debris. He noted instances of nests being found between two and four feet above the ground in the middle of bamboo clumps.

Smythies (1953) reported that although Red Junglefowl eggs are generally laid on a few leaves at the base of a bamboo clump or bush, one nest was found to be situated in the fork of a tree about five feet above the ground. Most of the junglefowl use similar types of nests. Sálim Ali (1969) described the nest of a Grey Junglefowl (*Gallus sonnerati*) as a shallow scrape in dense undergrowth, lined with dry leaves. Similar Red Junglefowl nests are described by Delacour (1951) and Collias and Collias (1967). The one exception may be the Ceylon Junglefowl (*Gallus lafayettei*). Henry (1959) stated that these hens make similar scrape nests with only meagre lining on the ground under the shelter of a tree trunk, stump or rock and concealed by vegetation. However, he also indicated that many nests, possibly the majority, are made above ground level in sites such as the tops of dead stumps or heaps of rubbish caught up in the tangled jungle vegetation, or even in deserted nests of larger birds. The tendency for Ceylon Junglefowl to build up off the ground has also been reported by Baker (1930) and others.

The one characteristic noted by Baker (1930) for all junglefowl nests was that they were generally well concealed. Concealment was apparently achieved in different ways. He suggested that Red Junglefowl prefer to lay in densely tangled secondary growth often associated with deserted cultivation clearings. These areas, he pointed out, were always very matted and impenetrable near ground level. Other types of nesting areas used were dense bamboo forest, which has some undergrowth, dense bush and tree forests.

(b) *Other Gallinaceous Species*

Amongst the Phasianidae family, nests used by hens tend to be very similar. While the habitats in which the different species nest may vary, the nests themselves tend to be much the same. Pheasant nests are usually little more than a collection of dead leaves and grass lying in some natural hollow under a bush or tree, as the descriptions of the nests of various pheasant species by Baker (1930) would seem to indicate.

A number of studies of nesting in pheasant populations established in wildlife areas and at free range have provided considerable information about nest selection habits of these birds. Hamerstrom (1936) described nests of the Ring-necked Pheasant (*Phasianus colchicus*) in such a situation and found that all nests were near the ground and were mostly a scooped out or natural depression about ¼-1½ inches deep, lined with whatever materials were at hand, such as grass, twigs, leaves and sometimes a few pheasant feathers. Although most nests were scooped out, others were on slight elevations. There appeared to be no preferred direction of exposure or nest opening and little evidence of roof building.

In several studies, for example Dumke and Pils (1979), it has been noted that a wide range of plant species tends to offer suitable concealment for pheasant nests in any particular study area. No preferences for plant species were detected in nest placement by Trautman (1960). Dumke and Pils (1979) found that a diverse plant community was preferred for nesting purposes. Areas where a variety of plant species was found to provide a matrix of vegetative clumps and open areas were popular nesting sites. However, they also found that pure stands of certain species were also favoured at particular times of the year when they provided a good canopy under which hens nested. Types of cover favoured for nesting changed through the nesting season. In particular, those plant species which tended to become rank declined in importance for nesting purposes, presumably because their value as concealment was reduced.

Hamerstrom (1936) reported that pheasant nests were often found in sites affording complete or partial cover from above, although many were without overhead cover of any sort. The possibility that pheasant hens may select nest sites on the basis of the microclimatic conditions in the site, particularly temperature and humidity, has been suggested by Francis (1968).

Pheasant hens tend to nest within the territory or home range of their flock (Seubert, 1952), but towards its periphery (Dumke and Pils, 1979). These researchers also found that nest sites tended not to be located near areas of heavy use by the hens or by other hens or cocks in harem associations, despite the fact that apparently comparable nesting cover existed in these areas.

Tendencies for hens to lay at peripheries in other situations have also been noted. Hamerstrom (1936) found that pheasant hens exhibited a preference for the edge zone in the case of nests in large blocks of homogeneous cover. Higher densities of nests were found to be associated with fencerows and roadsides rather than in large blocks of cover by Trautman (1960), Baskett (1947) and also by Linder *et al.* (1960) who point out that this occurred despite the fact that such areas tend to be subject to high levels of predation, particularly by mammals.

No other indications of factors which may influence nest siting in pheasants have been found. Hamerstrom (1936) was not able to find any relationship between the siting of nests and the distance to trees or water, nor in the drainage of sites.

Nests of Japanese Quail (*Coturnix coturnix japonica*) are said to resemble those of the Ring-necked Pheasant (Kovach, 1974). Many of the conditions under which pheasant have been found to nest also apply to Bobwhite Quail (*Colinus virginianus*). Klimstra and Roseberry (1975) found that nearness to an edge was apparently desirable for nesting, since almost 60% of the nests found by them were within five metres of a noticeable break in the cover pattern. Fencerows and roadsides were again popular. The impression gained was that maximal nesting utilisation only eventuated when the preferred vegetational conditions occurred in association with habitats which exhibited a generally open aspect. Cover which was too uniformly thick to allow some access to bare or nearby bare ground was usually avoided.

In the closely related Tetraonidae family (Peters, 1934) nest siting is in many ways similar to that of the Phasianidae. Some information on nest siting of grouse is available. Like the pheasants, Red Grouse (*Lagopus lagopus scoticus*) nest within the cock's territory (Watson and Jenkins, 1964). Bump *et al.* (1947) surveyed a large number of Ruffed Grouse (*Bonasa umbellus*) nests and found that one of the most significant relationships was one with proximity to openings in the forest. They concluded that the desirability of a nesting site varied inversely with its distance from an opening, irrespective of the type of cover.

In fact, nests were sometimes located in openings. This tendency was not necessarily related to plentiful food sources, since there was no greater attraction to recent slashings, which provided the best sources of food, than to other openings. These workers reported that the nest itself is lined and the edges built up of materials within the reach of the hen sitting on the nest, and sometimes contained a few feathers. Most frequently, the nest would be located at the base of a tree or stump.

Keppie and Herzog (1978) also found that most nests of Spruce Grouse (*Canachites canadensis*) in their study area were close to the base of a single tree. The sites selected did not offer much protection from inclement weather. However, hens tended to occupy better sheltered sites, as assessed subjectively by the amount of concealment at nest sites, as they progressed from yearling to adult age. It was interesting to note that success of the nests as determined by numbers of clutches for which incubation was completed, was greatest for well hidden nests or nests with about 50% lateral and overhead confinement ratings than for very exposed nests. Wood-Gush (1975a, citing Jenkins *et al.*, 1963) cited information indicating that Red Grouse nests are generally sheltered and overhung by foliage, although a proportion are open above. Most nests were on well drained ground and most on flat rather than sloping ground.

Several reports of nesting types of ptarmigan appear in the literature. Parker (1981) indicated that Norwegian Willow Ptarmigan (*Lagopus lagopus lagopus*) apparently nest within the cock's territorial boundary. Similarly, Watson (1972) found ptarmigan hens to nest within 50 m of the cock's main lookout. He also reported that nests were found in a natural hollow or one scraped in the ground and that they usually occurred in the open, partly sheltered by a large stone. No preference was detected for direction faced.

Giesen *et al.* (1980) also stated the importance of rocks in the siting of nests of White-tailed Ptarmigan (*Lagopus leucurus*). Forty per cent of nests were found in rock or boulder fields and a large proportion of nests in turf areas were sited near rocks or boulders. Most nests were protected from the wind and occurred in natural depressions. Materials used in nest construction reflected the vegetation at the site. An interesting parallel with the pheasant reports exists in their finding that most of the nests in krummholz were at the edge of a shrub clump or near an opening.

One point to emerge from these reports of nest siting by gallinaceous birds in the wild, is that each species has tended to develop a particular mechanism to achieve concealment of the nest. Whether this is a species specific adaptation to the type of nesting habitat available in the respective environments is difficult to say. The pheasants, for example, seem to achieve concealment through siting their nests in heavy overhead cover, grouse, next to a tree or stump. Sharma (1972) reported that the peahen (*Pavo cristatus*) prefers a thorny site for nest building, which he attributed to the protection that the thorns afford. Giesen *et al.* (1980) suggested that although rock in particular, but also vegetative cover, seems to be important in the siting of ptarmigan nests, it is probably more important for protection from inclement weather than for concealment. Most incubating females are exposed and apparently rely on their cryptic plumage for camouflage.

(ii) Site attachment and experience of the nesting bird

Hens of all gallinaceous species tend to use the one nest site for any one clutch, except in cases of promiscuous egg dropping and dump nesting which, as previously mentioned, occasionally occur. However, if nests of wild hens are destroyed or unsuccessful, re-nesting in the one season may occur. Re-nesting occurrence in Ring-necked Pheasant is well documented (Seubert, 1952; Linder *et al.*, 1960; Gates, 1966; Dumke and Pils, 1979) and also occurs in other gallinaceous species. The breeding season of Red Junglefowl in Thailand is reported to be of sufficient length that individual hens may make several attempts to nest (Johnson, 1963). Grouse are known to re-nest (Edminster, 1947; Bump *et al.*, 1947; Zwickel and Lance, 1965; Zwickel, 1975; Maxson, 1977) and recent evidence has suggested that ptarmigan may re-nest (Giesen and Braun, 1979b). Hungarian partridges (*Perdix perdix*) are also known to frequently attempt second nestings if initial nests are destroyed (Knott *et al.*, 1943).

Information obtained on the siting of re-nesting attempts suggests that hens do not use the same area or type of cover in re-nesting attempts. Dumke and Pils (1979) reported that 65% of Ring-necked Pheasant re-nests were in different cover types and a considerable distance away from the original nest. Re-nests were never found in the same block of cover. Kuck *et al.* (1970) also reported that pheasants in their study did not re-nest in the same area. Gates (1966) determined that most re-nesting pheasant hens remained in the general vicinity of their original site, but found striking differences in the cover type used for re-nesting.

Most gallinaceous hens tend to avoid using one site for more than one clutch. Bump *et al.* (1947) recorded no cases in which the same specific site was used more than once in a long term study of Ruffed Grouse nesting habits. They found that nests of different hens tend to occur a considerable distance apart, although some instances of two hens contributing to the one nest were recorded. The tendency for grouse to change their preferences for level of nest concealment with age, or experience, has already been noted (Keppie and Herzog, 1978).

(iii) Nest selection by feral fowl

The feral fowl population established on an island off the coast of Scotland (see Wood-Gush and Duncan, 1976) was studied in later seasons and the nesting habits and habitats were observed and recorded by Duncan *et al.* (1978). They reported that most nests were found in a shallow depression, were sometimes scantily lined with a few pieces of dead vegetation and an odd feather, or were bare.

The sites chosen by these feral fowl showed great variety, but a feature common to them all was that they were well concealed, at least from the human eye. Concealment was achieved in a number of ways. Some nests were discovered in holes with solid overhead cover, others were in more open sites with vegetative cover. Some nests were in darkness, others in daylight.

Nests discovered for individual hens showed that a number of hens chose markedly different sites for successive clutches, while others chose very similar types of nest. This did not seem to relate to the success or otherwise of the previous site. Successive nests were usually found in the same general area.

They also found that no nest site was used twice, even by different hens. The authors noted that hens showed extreme conservatism within clutches but extreme changeability between clutches and seasons in their nest selection. They suggest that this may be an anti-predator, ant-parasite or general hygienic device.

One observation reported was a case in which two hens hatched from the same clutch chose very different nesting sites to those that they had been hatched and brooded in. This prompted the researchers to suggest that early experience may have little effect on later nest selection habits.

Unfortunately, the study conducted by McBride *et al.* (1969) on a well-established population of feral fowl on an uninhabited island off the coast of Queensland, Australia, gave few details of the types of sites chosen by these birds for nesting.

2.2.2 Factors influencing nest selection by domestic hens

(i) *Presence of Eggs*

One of the earliest documented investigations of the selection of different types of provided nests by domestic hens was reported by Turpin (1918). He allowed hens in floor pens the choice of nests which contained four, three, two, one or no eggs at the beginning of each day and recorded the number of eggs that were laid in each of the alternatives daily. More eggs were laid in nests with one or two eggs than in nests initially containing three or four, and even fewer in those with no eggs. He then compared the numbers of eggs that would be laid in nests which were provided with real, china or no nest-eggs. The results suggested that nests containing real nest-eggs and china nest-eggs were both used to a much greater extent than nests containing no nest-egg but that the real egg was more effective in this respect. Further investigations revealed that nests containing white nest-eggs were no more popular than nests with brown nest-eggs for Rhode Island Red hens and that nests containing wooden and plaster of paris eggs were all equally attractive and as a group more attractive than an empty nest to Rhode Island Red and White Leghorn hens for nesting purposes. He was also able to show that more hens would lay in nest-sets in which the back 'door' of the nests was closed, so as to provide more secluded nests, and in which nest-eggs were provided, than in open nest-sets in which nest-eggs were not provided. He was, however, unable to determine the relative importance of the factors 'seclusion' and 'presence of an egg' in this experiment.

These studies conducted by Turpin (1918) can be criticised in several respects. He failed to recognise the possible influences of experiential and social factors, but did point out that since eggs were only gathered once daily, the numbers of eggs collected would not represent the actual relative attractiveness of nests for as soon as one egg was laid in any of the nests provided, its attractiveness to following hens could be altered. His studies only measured gross differences in response to certain factors, but they do serve to illustrate that selection of nests can be influenced by the presentation of an egg or egg model to mature laying hens, and possibly also by other factors.

Bressler (1961) noted that hens in his studies tended to respond to plastic egg decoys and also tended to remain longer on nests when these nest-eggs were in use.

(ii) *Floor Type or Nesting Material*

A possible role of the type of nesting material in selection of nests by domestic hens has been suggested in a number of studies. Hansen *et al.* (1948) reported apparent 'preferences' of White Leghorn and New Hampshire pullets for various nesting materials. They found that straw, excelsior and wood fibre were preferred to wood shavings, which in turn were preferred to rice hulls, almond shells, diatomaceous silica pellets and cork bark particles. However, no description of how these preferences were established was given. Similarly, Siegel and Howes (1959) report differences in preference of White Rock pullets for nests containing either wood shavings, fine calcined clay, coarse calcined clay, hay and sugar cane, but do not give details of how preferences were detected or which material types were preferred.

Daly *et al.* (1964) reported differences in the numbers of floor eggs laid in pens in which one of seven different nesting materials was provided. Most floor eggs were laid in pens with ground corn cobs as the nesting material and least in pens with a mixture of shavings and grit. The other treatments, including wood shavings alone, grit alone and shredded newsprint, resulted in intermediate levels of floor-laying. On the other hand, Baker (1962) failed to find significant differences in levels of floor-laying in pens in which four different nesting materials, namely, a fine perlite ore, a find calcined clay product, soft wood shavings and peanut shucks, were used. He did, however, note that hens did not remain long in nests containing perlite ore and calcined clay, unlike hens using nests containing shavings and peanut shucks, and suggested that the finer particled materials may have been more comfortable to hens.

Murphy (1969) was unable to show that the presence or absence of nesting material in wooden trap-nests had any effect on selection of nests by mature Brown Leghorn hens. However, the hens used had previous experience of nests containing varying amounts of litter and had possibly never experienced bare nests and so may have been unable to identify nests without litter as unfavourable until they had entered the trap-nest on the occasion of testing.

Wood-Gush (1975b) measured the number of paces and time spent in sitting in the pre-laying half hour and the corresponding time on non-laying days for individual hens in cages with conventional wire floors with slopes of 1 in 5 and in cages in which the floor was replaced with a metal tray containing litter. He found that hens paced less and sat more in the cages with the litter floors than in cages with sloped wire floors. Although the experiment was unable to differentiate between flatness and the presence of litter (or solid, as opposed to wire floor), an earlier experiment had indicated that, at least when options of 1 in 6 and 1 in 3 were offered, only a weak tendency to sit more on less steep floors during the pre-laying half hour was detected. Whether a tendency to sit in certain nesting environments can be equated with preferences for such environments in nesting may be open to speculation. Certainly, behavioural studies have indicated that pacing in the pre-laying period may be indicative of frustration resulting from inability to find or use suitable nests (Duncan, 1970; Wood-Gush, 1972; Brantas, 1980) and sitting would seem to be the opposite response.

There is therefore some indication that hens may respond to the presence of a nesting material and perhaps differentially to different nesting materials, in the selection of a nest. Bressler (1961) was able to obtain levels of nest usage in deep litter floor pens with nests containing a moulded, fibrous roll-away nest cushion, similar to those obtained with litter nests. While this could be seen to indicate the importance of the capacity of nesting material to provide a nest-shape for the nesting hen, it should be noted that floor-laying rates, as measured in this study, may not necessarily be indicative of preferences for or against certain nest types. The results of this study should also be viewed with some caution since the reported findings were not analysed statistically.

(iii) *Light Intensity*

Darkness is a factor often stated to be important to nest seeking hens (e.g. Smith, 1963; Anon., 1972). However, little experimental evidence has as yet been produced to verify that this is the case. Murphy (1969) found that Brown Leghorn hens with previous experience of laying in dark trap-nests placed on the floor, chose dark, low nests more often than they chose any other combination of low/elevated nest level with dark/illuminated (light) nest type. A further experiment indicated that one group of hens showed a significant preference for nests of familiar height rather than familiar brightness, while another group chose the two factors with equal frequency.

Additional experiments have indicated that more hens chose dark nests than light nests when the two options were both provided in ground level nests (Wood-Gush and Murphy, 1970). However, when pullets about to lay their first egg were tested with dark or light nests, seven of the ten pullets observed laid in light nests, the remaining three birds laying on the floor. They concluded that the hens did not prefer dark nests unless they had some experience of them. However, it should be noted that these inexperienced pullets had no experience in the use of trap-nests or in the process of selecting a nest and laying. Since nervousness in the nesting situation may have been a factor, these pullets may have first made exploratory entries into the better lit nests because they were initially reluctant to enter a dark, unfamiliar area. It is also possible that examination of nests in the early stages of nesting behaviour may not be directed towards the nest types that eventually release sitting and remaining behaviour. Hens with experience in the use of trap-nests may learn to avoid nest entry in this nest examination phase and so only enter the preferred nest options later in the nesting sequence.

Wood-Gush (1972) compared times spent sitting and the number of paces taken in the pre-laying hour, and the corresponding hour on a non-laying day, by hens of two strains in ordinary battery cages and in cages with solid metal walls on two sides and back. One strain, a Rhode Island Red x Light Sussex hybrid, sat significantly longer and paced significantly less in the 'enclosed' cages. The other, a White Leghorn strain, was unaffected in this respect. When observed in cages in two pens which differed in light intensity, the Brown strain hens paced significantly more during the pre-laying hour n the light than in the dark environment. White hens, on the other hand, tended to be more active during the pre-laying hour in the dark than the light environment. The results suggested that 'enclosure' and darkness may both act as releasers for sitting behaviour in the nesting phase, at least for one strain of hen. Wood-Gush suggested that the differences observed between the two strains may be due to differences in responsiveness to these two releasers.

(iv) *Sense of 'Enclosure' or Confinement*

The sense of 'enclosure' or confinement may, in fact, be more important than darkness *per se* in determining selection of nest site, as pointed out by Murphy (1969). Certainly, it would seem that the most popular floor-laying sites selected by hens in large, deep litter floor sheds are neither the darkest nor the least draughty (Perry *et al.*, 1971). Most situations in which the sense of 'enclosure' is enhanced, except under controlled conditions, are also likely to be situations of reduced light intensity. Therefore results such as those presented by Turpin (1918) in which most eggs in a pen were laid in nest-sets in which the back of the nests was closed and nest-eggs provided, as opposed to the nests being open and without nest-eggs, may indicate responsiveness to a sense of 'enclosure' or light intensity or both factors. Similarly, the tendency for hens to lay under 'shelters' in colony cages (Hurnik and Walker, 1974) could reflect responsiveness to either of these factors. From the foregoing review it would appear that the role of light intensity in nest selection is at present unclear.

The size of the nest, or at least the opportunity it affords for a number of hens to use the site at once, may also be of importance when considering nest usage by hens. In this respect it is interesting to note that floor egg levels, in Leghorn pens with community nests, have been reported by Parnell and Quinsenberry (1951) to be higher than in pens with conventional nests. Of course, many factors may be involved in such an effect. Mutual disturbance of birds, reduced nesting space per bird, lack of visual isolation from other hens and differential light patterns are possibly some such factors.

(v) *Colour of the Nest*

One interesting series of reports has indicated that colour preferences may influence selection of nest. Hurnik *et al.* (1973a) found that when presented with nests which differed in colour, individual hens tended to display preferences for particular colours, although preference for specific colours in the nest choice varied greatly amongst individuals. Hens which had been 'selected' for colour responsiveness as chicks (Hurnik *et al.*, 1970) were also found to exhibit a higher responsiveness to colour and other stimuli from the nest, for example nest level and order, than hens from an 'unselected' population. A correlation was found between colour preference at an early age and colour preference in nesting. They did, however, detect a change in colour choice at nesting in these birds, particularly in the case of hens which had preferred yellow and green when tested as chicks. Colours with a lower reflectance seemed to play a more important role in nesting activity.

It is difficult to imagine that these findings regarding colour preferences have any biological significance. Perhaps colour could be of assistance in location and recognition of the individual's nest in the wild, but the stimulus value of colour *per se* in releasing nest examination and entry may be minimal. In this respect, it is interesting to note that in the study conducted by Hurnik *et al.* (1973a), a grey, or non-coloured, nest type was more often selected than any other. Taken alongside the observation that preferences tended to change towards those colours of a lower reflectance in nesting, this may be indicative of an indirect effect of colour on preference for some other factor such as light intensity.

Irrespective of how or why such responses to colour in nesting are elicited, it is possible that individual differences could be used to influence nest usage patterns of hens housed in conditions with limited nest variety. Hurnik *et al.* (1973b) were able to increase the frequency of nest eggs in pens by provision of a nest-set containing individual nests of five colour alternatives as compared with that in pens with 'plain' common galvanised iron nests. Hurnik and Walker (1974) were also able to produce results suggesting that use of shelters for nesting in colony cages could be manipulated by the use of colour on the inside walls of the shelter. The further finding that colour could be used on feeders and feed as a stimulus for feed consumption (Hurnik *et al.*, 1971) would tend to lend further credence to the suggestion that the preferential use of certain colours in nesting is merely an artifact.

(vi) *Position of the Nest*

Another factor for which hens have been noted to demonstrate a preference for or against in nesting is that of nest level or height. Woods and Laurent (1958) recorded higher numbers of eggs laid in top nests as compared with bottom nests by an unspecified strain of laying hen, but give no indication of what elevation the nest-set was hung at or of the facilities provided for gaining access to the nests. As previously reported, Murphy (1969) found that mature hens experienced in the use of floor level, unilluminated trap-nests exhibited a marked preference for this nest type when allowed to choose between combinations of high or low and dark or light nests. Hurnik *et al.* (1973a) found that the use of two nest levels by Columbian breed hens differed markecly. A greater number of hens laid in the lower nests which were 48 cm from the floor than in the upper nests, which were 78 cm from the floor. The body weights of those hens which consistently selected upper level nests were no different from those that repeatedly selected lower level nests. This observation prompted the suggestion that individual motivational states and social factors may have been responsible for such a distinct segregation. However, these authors did not indicate what the previous experience of these hens had been in terms of nesting facilities, so the possible influence of prior experience in determining their nest level preferences cannot be ruled out.

A possible effect of position in the nest-set has been noted by several researchers. Murphy (1969) found that hens tested in her studies were not choosing nest-boxes at random with respect to their position in the row. Woods and Laurent (1958) reported that hens had a tendency to shun the nests at the end of one row in their study, but there was no pattern with respect to individual nests insofar as the number of eggs that were laid was concerned. Clumping of eggs in different nests each day was observed, possibly resulting from the tendency for different hens to select the first nests of the day and for hens laying later in the day to select these nests because they contained eggs. No explanation for the differential use of nests in different positions in a set has as yet been suggested.

A further factor that should be considered in the interpretation of studies revealing differences in nest level usage is the ability of hens to get to, or into, certain nest levels. As an example, Karunajeewa and Bagot (1978) reported a marked tendency for White Leghorn x Australorp hens fed on a whole grain diet to lay in lower nests whereas hens of the same breeding and history, but fed on a diet of mash, preferred to lay in upper nests. Lower and upper nests were 61 and 96 cm from the floor respectively. They suggested that these differences may be due to the distended crops of whole grain fed hens causing some discomfort when hens were attempting to reach the nests in the upper tier. This difficulty in using upper nests was apparently aggravated in the case of hens which were also fitted with plastic polypeepers which restricted their forward vision.

(vii) *Prior Experience of the Hen and Effects of the Individual*

As has already been indicated on several occasions, previous experience seems to considerably influence the selection of nests by domestic hens. This has already been noted for nest level (height) and illumination in the studies conducted by Murphy (1969). The tendency for hens to lay in the same nest for consecutive nestings has been recorded by Wood-Gush (1954). Wood-Gush (1975a) also showed that six out of ten hens, placed alone in small pens with litter floors during the nesting phase, laid in the same nest for both ovipositions in a sequence for six pairs of observations. Hens were apparently attracted to the site rather than the nest, for five of six hens elected to nest in the site that they had previously laid in. Only one hen laid in the nest she had previously constructed but which had been displaced 50 cm from its original site. Wood-Gush and Gilbert (1969a) also report tendencies for individual hens to lay in particular quadrants of a battery cage over a number of ovipositions.

Perry *et al.* (1971) studied the laying patterns of 11 randomly selected broiler hens in a large, controlled environment shed and found that the choice of nest site was highly repeatable for floor-layers. These hens always sat within 30 cm of their previous sites. Hens nesting in a nest-tube showed more variation, but did show a marked tendency to sit in the nest they had last laid in. An average variation of three nest-boxes from the original nest selected was found for these hens, which were often thwarted when their nest was already occupied and so entered the first empty nest that was available.

In addition to the tendency for hens to display preferences for particular nests, there also seems to be a tendency for individual hens to respond differently to certain stimuli. Murphy (1969) suggested that her results may indicate variations between individual hens regarding the relative importance of height and light intensity. Hurnik *et al.* (1973a) also report differential responses to colour and nest level alternatives in the choice of laying site. The existence of individual variation in responsiveness to certain stimuli from potential nest sites would enhance adaptability to habitat in the wild progenitors of domestic fowl and allow for distribution of nests throughout the habitat. Conservatism with regard to nests selected for successive eggs in a sequence would allow addition to, and completion of, clutches which would normally, in these wild birds, result in incubation.

2.3 Nest Usage and Floor-Laying Tendencies

A number of factors have already been mentioned to be useful in the manipulation of nest usage habits in housed flocks of domestic hens. However, most aspects of nest design and the means of reducing floor-laying have been determined empirically by people involved in the poultry industry and the principles thereafter accepted and practised in poultry production (Turpin, 1918; Smith, 1963; Anon., 1972). However, the actual value of these measures has generally not been assessed experimentally. Factors believed to be of importance include nest to bird ratio, partitioning of the nests, the provision of seclusion or darkness, size of the nest, and provision of nest-eggs (Turpin, 1918).

Smith (1963) also suggests that a nest must be comfortable, private, dark (or at least not exposed to direct sunlight), cool and accessible if it is to be acceptable to nesting hens. He also stressed the importance of 'educating' pullets early, by housing the birds in the laying shed about a fortnight prior to commencement of production with some nests open for investigation, of leaving the first few eggs laid in the nests to attract nest-seeking hens and of preventing 'dark spots', such as dark corners or areas under low nests, which may encourage floor-laying.

Others (e.g. Anon., 1972) have also suggested that floor-laying may be reduced by allowing hens sufficient time, prior to the onset of production, to become accustomed to the housing and nesting environment by placing nests "where birds want them" and not too high above the floor. Additional factors reported to be important in the reduction of floor-laying included the provision of privacy and nesting material in nests which should be big enough to allow birds to enter and turn around in, early collection of floor eggs, gradual movement of nest-sets into elevated positions only after the hens have had early experience of them at ground level, pen layout which ensures nests are easily reached from the areas of greatest activity in the shed and confinement of floor-layers in nests as a training procedure (Anon., 1972).

Several factors have been shown experimentally to influence floor-laying tendencies. Daly *et al.* (1964) found that floor eggs percentages from pens with differing nesting materials were considerably different. As mentioned previously, floor egg percentages were highest in pens with ground corn cobs as the nesting material and lowest in pens which had a mixture of wood shavings and grit in the nests. Baker (1962) was unable to show a significant effect of different nesting materials on levels of floor-laying in his studies. Siegel and Howes (1959) found differences in preferences for certain nesting materials, but expressed doubt that these would influence nest usage levels if all nests within a pen contained the same nesting material.

Bressler (1961) reported that floor-laying levels in pens with moulded fibrous roll-away nest cushions were no worse than those in pens with litter nests. However, floor eggs were slightly more numerous in pens with nest cushions during the first few months of production. His results must be viewed with some caution since they were not statistically analysed. He also reported that the provision of decoy eggs in nests initially reduced floor-laying levels in another study, but the value of these decreased as flocks reached peak production since they encouraged hens to remain on the nest for extended periods of time, necessitating the introduction of more nest-sets in these situations.

The numbers of floor eggs laid by hens in deep litter laying houses with wire-floored or Danish-type roll-away nests have been found to be worse than those recorded in similar houses provided with either darkened community nests or open-front single nests, both containing a nesting material (Anon., 1964). Increased floor-laying levels have also been reported for pens of Leghorns with community nests when compared to pens with conventional single open nests (Parnell and Quisenberry, 1951).

Hurnik *et al.* (1973b)were able to increase the frequency of nest eggs laid by two breeds of laying hen by provision of nest-sets in which the individual nests were painted different colours, as compared to nest-sets in which the nests were non-coloured (galvanised iron nests).

Dorminey (1974) reported that White Leghorn pullets housed in fan-ventilated pens without open windows produced a higher incidence of floor eggs than did pullets housed in open pens with open windows and natural ventilation, but were unable to say which of the factors, lighting or ventilation system, may have been important in this respect. In darkened pens illuminated by artificial light, dwarf White Leghorn hens demonstrated a preference to lay in the nests on the wall under the bulb rather than those on the wall opposite the bulb.

The use of a 100 watt rather than a 25 watt bulb in the pen resulted in a lower percentage of floor eggs for similar nest locations. Also, moving of pullets to their laying pens with nests installed at 23, as opposed to 18, weeks of age resulted in a significantly higher incidence of floor-laying.

The importance of familiarity with the nesting set-up to subsequent floor-laying patterns is further borne out by a study conducted by Craig (1980). He compared the subsequent use of nests by laying White Leghorn hens transferred directly from colony cages to floor mating pens, placed directly in the nests and confined for 12 hours, or placed in nests and confined for four hours on each of the first three days in the floor pen. Nests used were three tiered, the bottom level being elevated 50 cm above the pen floor. The percentages of floor eggs found in pens in which hens had been transferred directly to the floor dropped over the six week test period. However, floor egg percentages from both pens in which the hens had been placed directly in nests and confined for 12 hours, or had been confined in the nests for four hours on each of the first three days, were low, and decreased to 1% at the final week of recording.

The possibility that nest usage may be influenced by familiarity with the nesting area is also suggested by a report claiming superior usage of automatic nest-tubes in sheds in which the nests were accessible via sloping wire ramps to the nests and in which drinkers were positioned near the nest-tubes in such a way that hens would have to mount the nest approach to use them (Anon., 1982). Although figures are not given, it is possible that nest usage may have been enhanced by either improved accessibility to the nests as a result of the sloping approaches, or increased familiarity with the nesting area engendered by proximity to drinking facilities.

Lighting regime has been shown to influence floor-laying tendencies (Walther and Newell, 1962). However, detrimental effects of short daylengths were only recorded when the lighting schedule provided hens with low hours of lighting (six hours per day increasing by 18 minutes per week), at which point production was also inhibited. It seems unlikely, therefore, that the lighting regime used under commercial conditions would have much influence on floor-laying tendencies.

Hearn (1981) found that distribution of nest-boxes in large, deep litter floor pens had no apparent effect on the percentages of floor eggs laid in them by broiler breeder hens. The time of first feeding of these birds had no consistent effect on the incidence of floor eggs either. However, the provision of plastic backs to the nests seemed to have reduced the level of floor-laying, at least in one pen in which the nest-backs were put on the nests when the birds were 26 weeks of age. Pens in which nest-backs were put on all nests a week later than this had higher floor egg percentages.

A genetic basis of floor-laying has been suggested by McGibbon (1976). Breeding tests revealed that the progeny of crosses of hens identified as floor-layers with random bred males were twice as likely to be floor-layers than the progeny of crosses of unselected hens with random bred males. The incidences of floor-laying progeny of ten inbred lines, mostly Leghorn, were markedly different also. However, laying house location and rearing experience were also found to influence floor-laying tendencies. Rearing in confinement resulted in higher floor-layer incidence than did rearing at free range. Breed differences were also noted, the two heavier strains studied, these being White Plymouth Rocks and New Hampshires, having a higher proportion of floor-laying individuals than the lighter Leghorn strain.

It is widely accepted that the proportion of floor eggs laid by a flock of birds is highest at the onset of production and declines during the first six or eight weeks of production. Such trends in floor-laying level have been demonstrated in a number of studies (e.g. Hurnik *et al.*, 1973b; Hearn, 1981). The fact that floor-laying tendencies are established in the early days or weeks of a pullet's laying history is acknowledged by most people involved in the production of fertile eggs (Smith, 1963; Anon., 1972). Perry *et al.* (1971) suggested that floor-laying habits established in hens during this phase may be difficult to change because of the high repeatability of nest site choice.

Wood-Gush (1954) observed Brown Leghorn pullets in floor pens with trap-nests provided and found that although some pullets laid their first few eggs in trap-nests, others laid their first few eggs on the floor before beginning to use the trap-nests. He put these differences down to nervousness in the early stages of lay. He also noted the existence of a third group of pullets which continually laid in floor sites and claimed that such birds did not appear to be attracted to the nests. He suggested that some factor(s) about the nest which attracted the other birds did not affect these individuals.

It is apparent that floor-laying is determined both genetically and by the housing and nesting environment provided during rearing and laying phases. Unfortunately, few studies have attempted to determine what environmental factors, or features of nest design, may influence this trait. Further studies of the nature and behaviour of floor-laying hens and of the influence of factors believed to determine nesting preferences on floor-laying tendencies are warranted. Such studies could be invaluable in the design of shed and nesting facilities for the commerical production of eggs from environments other than the highly confined and automated laying cage environment.

CHAPTER 3

STUDIES ON NESTING BEHAVIOUR

A number of factors have been found to influence the form of the behaviour pattern associated with nest selection and oviposition (see Chapter 2). Such factors which may be implicated include breed, environment, age or level of nesting experience, stage in the laying cycle as well as social factors. The object of the series of studies conducted and reported in this chapter was to expand upon the current level of knowledge of the activities comprising the nesting sequence and how their expression can be affected by these factors. It was envisaged that such studies may provide clues as to the possible stimuli important in determining nest site selection which may be useful in the design of facilities to optimise nest usage in commercial situations. The objectives and approach adopted are summarised overleaf.

Study 3.1

Nesting Behaviour in a Maturing Flock

3.1.1 Introduction

The nesting behaviour and types of nests selected by hens which are in the early stages of production may be different from those of mature laying hens. Most studies of nesting behaviour which have been conducted in the past have looked only at the behaviour patterns exhibited by mature hens. The present study was conducted in an attempt to investigate the behaviour of broiler hens related to nest-selection and oviposition, from their initial nestings and for several weeks thereafter. Relationships between the occurrences of component activities and maturity and social status of individual hens were also investigated, and the sites of eventual nesting recorded with a view to interpreting the significance of the behaviours displayed and the possible factors influencing selection of nest site.

3.1.2 Materials and Methods

(a) *Birds and Their Housing*

Thirty-seven pullets of a Hyline* commerical broiler strain were studied in these experiments. This particular type of hen was selected for the study as it was hoped that heavier meat-type birds would be most likely to provide reasonable numbers of both nest and floor laying individuals to study. They had been on a restricted feeding program in deep litter floor pens on another

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* Hyline Pty. Ltd., R149 Bringelly Road, Luddenham, NSW, 2750

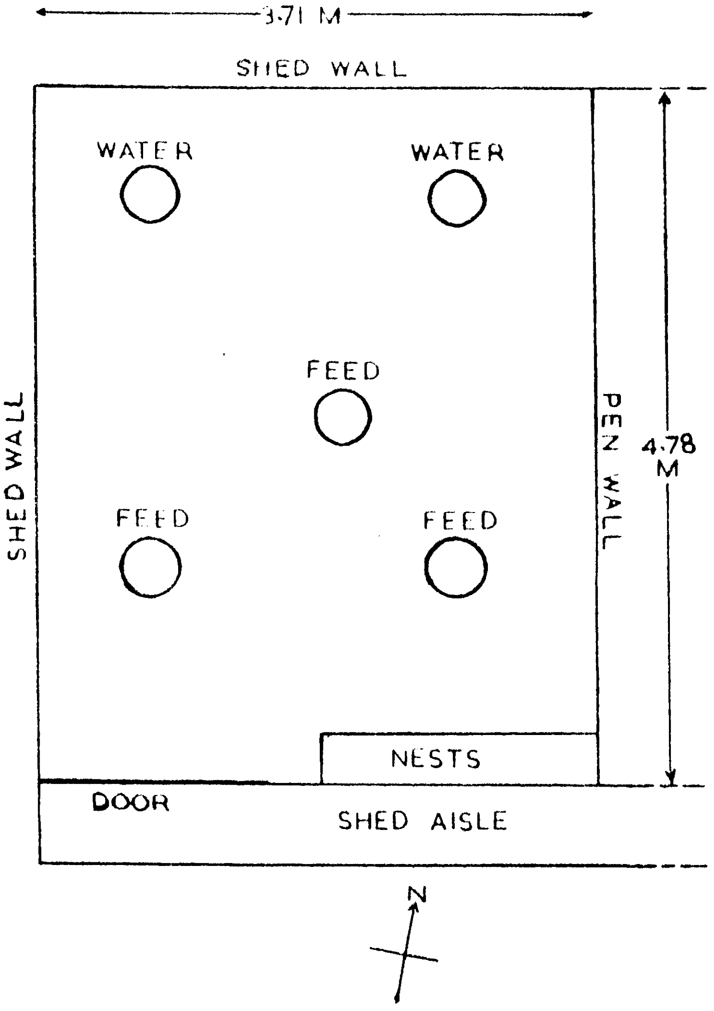


Figure 3.1.1 The size and arrangement of the broiler pen used in these studies

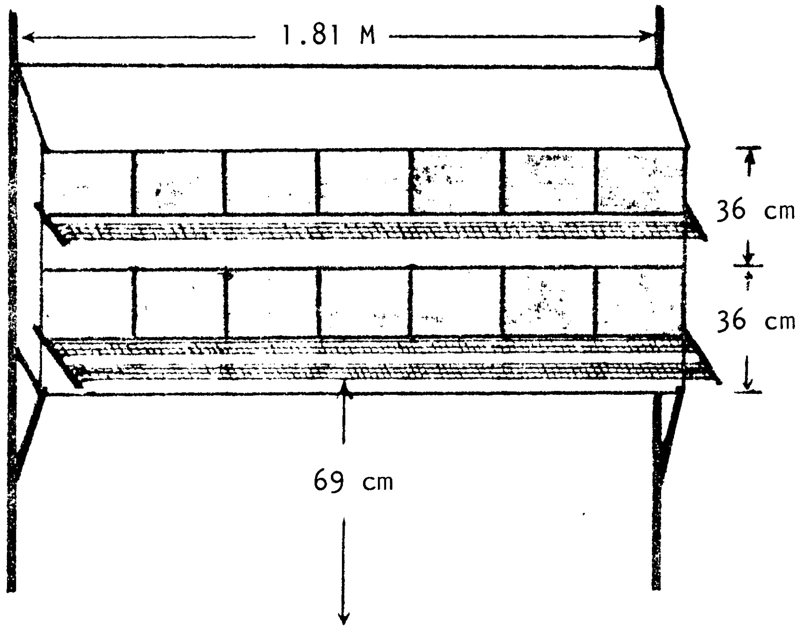


Figure 3.1.2 The nest-set originally provided in the broiler pen

University of New England (UNE) property prior to being transferred to a deep litter pen within a three-pen isolation shed on university grounds at 10 weeks of age in November, 1978. The dimensions and arrangement of this pen are given in Figure 3.1.1.

The two end walls of the shed and the roof were constructed of corrugated iron. Natural light and ventilation were admitted through slatted and wire covered windows running the length of the shed along both side walls from 73 cm above the floor to the ceiling. Below these, the shed walls were constructed of corrugated asbestos. One such wall thus became one of the shed walls, the northern wall, while the other faced onto the shed aisle. One corrugated iron shed wall also formed the western wall of the pen. The other two pen walls were constructed of sheet metal to a height of 45 cm and 2.5 cm square wire mesh above this, thus allowing hens to see into the adjacent pen and the shed aisle on these sides.

The nest-set originally provided in this pen was a double-tiered set of sheet metal nest-boxes elevated above the floor (Figure 3.1.2). Each individual nest was 36 cm x 25.9 cm x 30 cm in size, with a 15.5 cm deep nest front. The landing boards (henceforth called approaches) to lower and upper nest levels were 69 cm and 105 cm above the floor respectively and were constructed of coarse wire mesh. These were positioned so that they were 10 cm out from the nest front and could be swung up so that they closed off the entrances to the nest-boxes. Wood shavings were used as the nesting material in these nests.

On 6th March, 1979, at which stage the hens were about 28 weeks of age and 10 hens were already in production, a set of eight floor nests was placed beneath the elevated nests. These, again, were constructed of sheet metal and their dimensions are given in Figure 3.1.3. These floor nests were

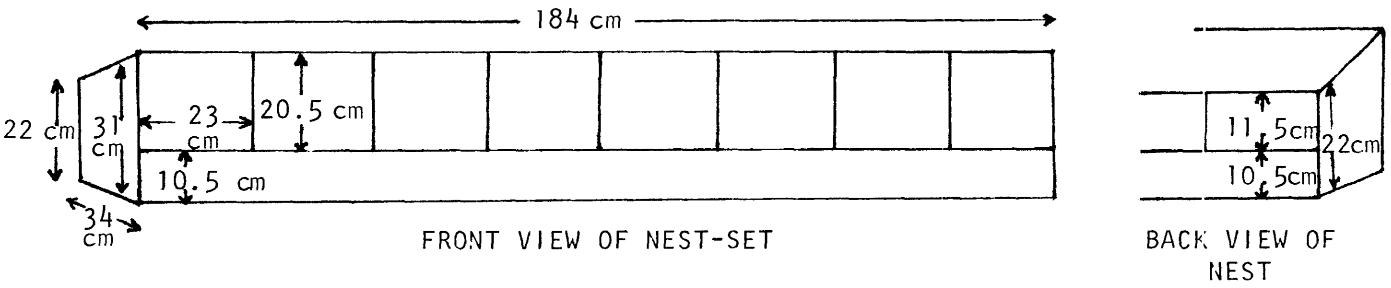


Figure 3.1.3 Size and design of the set of ground nests provided for the broiler hens

introduced into the pen because it was considered that, since the majority of hens which had laid previously were not using the elevated nests, then most of the flock would become floor layers if an alternative set of nests was not available. At the same time, the adjacent pen in the shed became occupied by a flock of 25 adult White Leghorn hens and three cockerels.

Hens were given constant access to drinking water throughout the experiments and had been restricted fed to maintain a weight 35% lighter than their full-fed controls up until the first hen began to lay, at which point they were fed daily a weighed quantity of feed equivalent to 85% of their daily *ad libitum* intake. Prior to the first hen commencing lay the pullets were fed on a commercial grower crumble ration and afterwards were on a commercial pelleted layer ration. Feed was put out once daily between 3.30 pm and 4.00 pm.

The pullets had been reared on natural daylengths through the Australian spring and summer and at 20 weeks of age began receiving additional artificial lighting increasing at a rate of 20 minutes per day per week up until they received a total of 16 hours light per day. From then on, the hens were kept under a constant 16 hour lighting regime. Artificial light was provided by fluorescent lights running along the shed roof and the additional hours were given at the end of natural daylight each day.

(b) *Observations*

All the pullets were leg banded on 20th February, 1979, at which stage the hens were about 26 weeks of age. Observation of the flock commenced on 21st February, at which stage one hen had already laid several eggs. However, the rest of the flock began to lay four or more days after observations began. This delay between the commencement of observation of the flock and the onset of laying in most of the hens allowed for familiarity of the hens with the presence of the observer and also permitted the observer to become familiar with hens' non-nesting daily behavioural patterns.

Observation of nesting behaviours and social interactions within the flock in this section of the study were completed on 11th April, 1979. The flock had therefore been under observation for 50 consecutive days.

Hens were observed between approximately 7.30 am and 4.00 pm each day by the one observer with as few observational interruptions as possible. Observations were taken from the adjacent pen from a position roughly mid-way along the shared pen wall.

Records were taken of any changes in a hen's daily behavioural pattern during the observation period. Such changes were often indicative of the onset of pre-laying behaviour and the observer quickly became familiar with even minor changes in hens' orientation, attention or position in the pen which signalled a redirection of activity towards nesting activity. When such changes were noted more attention was devoted to the observation of the particular birds which had displayed them. In this way, an inventory of behaviours displayed by individual hens both before and after laying was compiled over a number of days. Inevitably, some information was missed because of the impossibility of one observer watching all nesting birds at any one time and also because many birds would commence or continue nesting activities outside observation hours.

Particular note was made of the occurrence of several activities associated with laying. The intensity of locomotory activity was subjectively scored according to the following definitions:

*	slow, deliberate pacing of the pen (or some part of it) with occasional changes in direction only (less than 10 paces or steps, and/or changes in direction made in a 10 second interval)
**	more rapid pacing of the pen (or some part of it) with more frequent changes in direction (between 10 and 20 paces or steps, and/or changes in direction made in a 10 second interval)
***	rapid pacing of the pen (or some part of it) with frequent changes in direction and 'jumping up' pen walls (more than 20 paces or steps, and/or changes in direction made in a 10 second interval).
****	'running' pen walls, with dashes at a run across the pen and/or flight up pen walls.

Only the maximum score attained by an individual on any one day was retained. For example, a hen may have performed locomotory activity at an intensity ranked as score ** early in the nesting sequence on one particular day and then increased activity to a level equivalent to a score *** later as she approached lay, thus receiving a score *** on that day.

The occurrence of nesting calls (terminology and description as per Wood-Gush and Gilbert (1969b)) and of pre- and post-lay cackles and any other peculiar vocalisations were also noted for each hen, as were the birds' orientations and positions in the pen when these were given.

Nest building or other manipulative activities conducted on the nest were recorded and were classified as follows:

1. Rotations and foot scraping-involved revolving the body about in the nest with breast in contact with the nest floor and feet scraping outward and back from the body, so moving litter from underneath to beside the body,
2. Litter raking-jerking movements of the head and neck in the litter which resulted in litter being flicked or raked to the breast using the underneath of the beak,
3. Material gathering to the chest - in which the hen would reach out to the rim of the nest or beyond while in a sitting position, pick up pieces of litter in the beak and deposit them at the chest or on the rim of the nest,
4. Material gathering to the back - in which pieces of material, usually pieces of litter or feathers, were picked up in the beak and in the same movement, placed on the back or wing of the bird or dropped beside her body.

This latter movement either occurred while the hen was sitting within the site while she stood at the nest or walked about the pen before laying, or while she walked about the pen after laying. Material gathering in these three situations were referred to as material gathering (M.G.) 'to the back' if the activity occurred as the hen sat on the nest before laying, 'in the shed' if it occurred as the hen moved about the shed before laying, or 'after lay' if it occurred after the hen had laid.

A 'nesting' was the term which was used to describe one day on which a complete sequence of pre- and post-laying behaviour, appropriate to each particular hen, was observed to occur, usually accompanied by an oviposition. A 'laying day' was a term used to describe days on which nesting and oviposition occurred. The first occasion on which a hen ever laid an egg was therefore its first laying day and subsequent occasions were therefore referred to as its second, third, fourth and so on, laying days, regardless of whether these occurred every day in sequence, or whether there were days between them when the hen did not lay. In other words, the 10th laying day corresponded to the 10th egg ever laid, not necessarily to the 10th day after the hen had begun to lay.

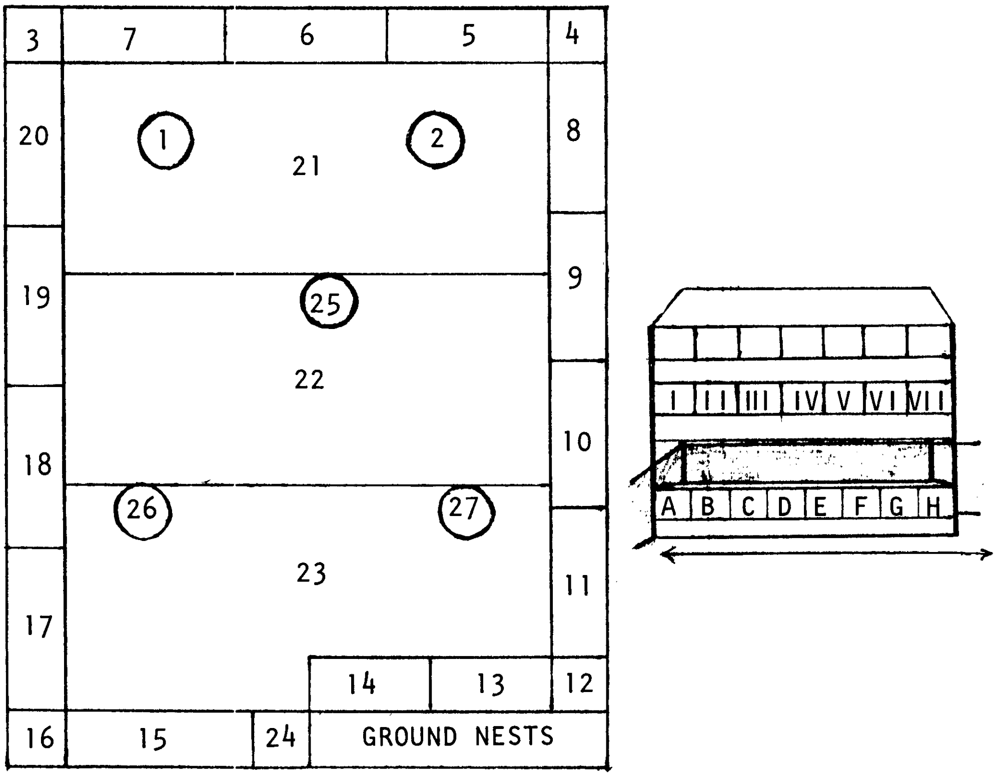
Prior to the hens coming into lay, it was decided that, in the case of poor acceptance of the nests provided for the hens, 'training' of a number of hens in the use of the elevated nests would be attempted. The training procedure involved taking those hens allocated for training and placing them on the wire perch in front of the set of nest-boxes when they were judged to be very close to laying. Ten hens were allocated for such treatment before any of them had come into lay. Hens were 'trained' in this manner on the first occasion on which they demonstrated obvious and intense pre-laying behavioural displays. This was done in an attempt to ensure that the hens were very close to laying and so highly motivated to examine and enter nests when placed in front of them. Thus, the laying day on which training was attempted varied from the first to the fifth day on which the hen laid on egg. This training procedure was only carried out on one occasion for any one hen.

An oviposition which occurred in a nest-box was referred to as a 'nest laying' and one occurring in a floor site a 'floor-laying'. The nest on which any oviposition occurred was recorded when observed, as was the position in the pen for floor-layings.

Positions of these floor and nest layings were classified as illustrated in Figure 3.1.4.

The position of each hen in the social hierarchy was established via the determination of pairwise dominance/subordinance relationships between each hen and every other hen in the flock. These relationships were only determined when each hen of a pair was sexually mature, that is, had begun to lay. This measure was taken to minimise the possibility of peck order reversals occurring at some stage in the period for which the hens were under observation.

Encounters were recorded by the observer at the same time and from the same observation point as were the details of behaviours associated with nesting. Initially, encounters were recorded as hens roamed freely about the pen, approaching and sometimes interacting with any number of other hens as they went. Encounters were only reported where both members of an interacting pair were either not laying on that particular day, had already laid that day, or were not actively engaged in any nest-related activity, such as nest calling, pacing, nest examination, sitting on the nest or nest building. This measure was taken as it was suspected that, at least in the case of several hens, peck order violations may have been occurring at a greater frequency as their search for a nest site became increasingly active. Partly as a result of this, and also because the observer had little time for additional observations during the morning, most recordings of interactions were taken in the afternoon when most of the nesting activity was over for the day.



Scale: 1 cm = 33.33 cm

Figure 3.1.4 Division of the nest-sets and floor areas for recording of position of oviposition

In this study, one hen was considered to be dominant to the other if, in three encounters between the two hens, the first pecked at aggressively or threatened the other which, in response, avoided her. The definitions of peck, threat and avoidance provided by Holabird (1955) were used. A 'peck' is defined as "a blow with the beak by one bird upon another, or a blow which fell short or which was dodged. Pecks where one bird was picking food from the beak of another are not entered". A 'threat' is defined as "one bird's raising its neck feathers while facing another, or thrusting its head forward as if to deliver a peck but then withholding it, or raising itself to its full height and standing over another bird". An 'avoid' is defined as "the movement of one bird away from another. It may not involve a movement of the whole bird but only of the head, which is often held away from the dominant bird, or down".

Feather pecking was not recorded and was distinguished from aggressive pecking by its characteristic of being less vigorous and not usually directed at the head of the other bird.

Bidirectional relationships occurred where both hens were observec to dominate the other in some of the initial three encounters. Subsequent recordings were then taken for such pairs. A decision was considered to be reached where the difference between the number of encounters which were dominated by each hen was at least two. The hen which dominated the other in the greatest number of encounters under these circumstances was considered the dominant of the pair.

Within one week of the anticipated completion date of the experiment, undetermined relationships, i.e. those for which three interactions had not yet been recorded; and bidirectional relationships, were sorted out in the following way. Undetermined pairs, both members of which had already laid or were not going to lay that day, were placed in wire crates in the pen, one pair per crate, in view of the feeder up to two hours before feeding time. When the required three interactions had taken place the pair of hens was released and replaced by another undetermined pair. Some pairs needed to remain in the crate for up to an hour after feed had been put out, or had to be retested on one or two subsequent afternoons before sufficient encounters were observed. Two crates were observed at a time.

This method was employed for finalising collection of data on relative social status for two reasons. Firstly, it increased the chance of the two members of a pair coming into contact, simply by confining them within a small area of the pen. Secondly, Duncan and Wood-Gush (1971) have shown that hens frustrated in a feeding situation show large increases in aggressive displays towards inferior hens, and that this increases with food deprivation time preceding frustration. While this may not in some circumstances be a particularly good means of determining actual dominance relationships (e.g. see Beilharz and Zeeb, 1981), hens in this study were already familiar and had previously established a peck order but were simply not reinforcing it very often.

(c) *Analysis of the Data*

(i) Nesting Behaviour

The numbers of observed ovipositions which were accompanied by pacing, calling, pre- and post-lay cackles and nest building activities were recorded for each hen. These data were then used to determine the frequency of occurrence of such activities throughout the flock. The probability of each activity determined in this way and the number of ovipositions observed for each hen were then used to calculate expected values and standard deviations of each activity for each hen. Observations which were more than two standard deviations from the expected value calculated for that particular parameter for each hen were identified.

Pairwise correlation coefficients were calculated for each parameter obtained for each hen and were also calculated for each parameter with the number of observed nestings.

The first day on which a hen was observed to nest and lay was designated L1 (representing 'laying day one'). Each subsequent observed nesting was named accordingly in sequence, i.e. L2, L3, L4 ... and so on up to Ln (n = the total number of observed nestings). The number of occasions on which nesting calls, pacing and nest building activities were recorded on each laying day in the sequence, totalled over all hens, was calculated.

The effect of experience or familiarity with the egg laying process or the effect of reproductive maturity, on the occurrence of these parameters in the hens' pre-laying behavioural repertoire was then investigated. Regression analyses were performed to test for any trend in these parameters over 'time' (or more correctly, as the number of observed layings increased). The data were transformed by arc sine $\sqrt{\text{percentage}}$ prior to analysis to stabilise the variance.

This approach, of course, ignores the probability that Lx may not represent the xth occasion on which a hen actually went about selecting a nest site. This situation arises because of the likelihood that not all nestings and subsequent ovipositions will actually be observed and also because of the possibility of nestings associated with internal layings occurring. However, exponential and third degree polynomial models were fitted to the transformed data for the activities calling, pacing - all intensities and each intensity, rotations, litter raking and material gathering to the chest. Since the recorded frequencies of material gathering 'to the back', 'in the shed' or 'after lay' were generally low, only linear models were fitted to these data. Significance tests were carried out on the regression analyses associated with the transformed data. Curves of best fit of the same order as those determined for the transformed data were also calculated for the original data. Because of heterogeneity in the variances, no meaningful tests could be carried out on these untransformed data.

Correlation coefficients, regression coefficients, multiple correlations and analyses of variance required for the analyses in the foregoing paragraphs were computed on the DEC20 computer system at the University of New England. The BAR3 program for regression analysis and two-way plotting (Burr, 1975) was used for these analyses.

The numbers of observed nestings accompanied by post-lay cackles were tabulated for elevated nest, ground nest and floor site nestings.

The numbers of hens that were observed to post-lay cackle on at least one nesting occasion and the numbers that were not observed to post-lay cackle were also determined fornestings in these three situations. To determine the effect, if any, of where the oviposition took place on the occurrence of post-lay cackles, the numbers of hens which were observed to cackle after a at least one nesting were compared for elevated nest, ground nest and floor site nestings. Chi-square analyses were performed on the data for hens nesting in these three nest situations.

From the results of all pairwise dominance/subordinance relationships a social rank index was calculated for each hen to represent its social status in the flock. The index used was one defined by Lee *et al.* (1982) as $\chi = \frac{1}{2}(D - S + N + 1)$, where D = number dominated, S = number dominating and N = group size. Hens of higher social status would therefore have larger numerical values of social rank index than would hens lower down in the social hierarchy. Pairwise correlation coefficients were then calculated between social rank index, the number of nestings observed, and percentages of total nestings which were accompanied by the recorded activities, pacing, calling, pre-lay cackling, post-lay cackling, rotations, litter raking, material gathering to the chest, to the back of the nest, off the nest before lay and off the nest.

(ii) Nest Sites Selected

The number of eggs laid in each elevated or floor nest was recorded as were the numbers laid in the different defined floor sites. The most 'preferred' nest-box or floor site was also tabulated for each hen (the 'typical' or 'predominant' selection), being defined as that nest or site in which that hen laid more eggs than in any other. The effect of position in the nest-set was analysed by comparing the number of hens preferring each nest with the expected number, assuming the null hypothesis of equal frequency of usage of each nest-box. In analysing the results, the number of hens preferring each defined floor site was compared with the expected number according to the proportion of the total floor area occupied by each site. Table 3.1.1 gives the floor areas, and the proportions of the total floor area, occupied by each floor site. Since other nest selections made by hens may be of considerable importance, particularly those made in the first week of lay when many hens had not formed attachments to certain nests, it was decided to analyse total numbers of eggs laid in each floor area. It was hoped that this would provide further information on the usage of the floor for nesting purposes.

Because of the large number of floor sites involved, many of which were infrequently used, and because several of these were very similar in nature, similar floor sites were grouped together for comparison with others. Eleven floor site areas were thus compared:

Under feeders/waterers (sites 1, 2, 25, 26, 27) - a
Corner 3
Corner 4
Corner 12
Corner 16
Corner 24
Along northern wall (sites 5, 6, 7) - b
Along eastern wall (sites 8, 9, 10, 11) - c
Along western wall (sites 17, 18, 19, 20) - d
Along front of nests (sites 13, 14) - e
Unconfined/mid-pen (sites 21, 22, 23 and 15) - f.

Table 3.1.1 Calculation of the proportion of the total floor area which was occupied by each of the 11 floor site areas

Floor Site/s	Area Occupied*	Proportion of Total Area
a. 1, 2, 25, 26, 27	4797.14	0.02804
3	1221.53	0.00714
4	1221.53	0.00714
12	1221.53	0.00714
16	1221.53	0.00714
24	1221.53	0.00714
b. 5, 6, 7	10297.43	0.06019
c. 8, 9, 10, 11	12827.73	0.07498
d. 17, 18, 19, 20	13962.00	0.08161
e. 13, 14	5060.61	0.02958
f. 15, 21, 22, 23	118029.47	0.68990
TOTAL FLOOR AREA	171082	

* measured in square centimetres (cm^2)

In each case, the null hypothesis of uniformity of preference for nestor nest site was tested using separate Chi-square analyses for elevated nest layings,ground nest layings and floor site layings.

Chi-square analyses were also performed on the partitioned data to test for preferential selection of certain floor laying areas over others.

The distribution of eggs between nests or between floor sites for individual hens was also analysed. For each hen, the null hypothesis of uniformity of distribution of ovipositions between nests in either elevated or ground nest-sets or between floor sites was tested.