

The development of egg-laying behaviour and nest-site selection in a strain of white laying hens

This thesis is also available as a publication of the Centre for Poultry Research and Extension,
Spelderholt 9, 7361 DA Beckbergen, The Netherlands

**Promotoren: dr. P. R. Wiepkema, hoogleraar in de ethologie
dr. ir. E. H. Ketelaars, hoogleraar in de pluimveeteelt**

B. Rietveld-Piepers

The development of egg-laying behaviour and nest-site selection in a strain of white laying hens

Proefschrift

ter verkrijging van de graad van
doctor in de landbouwwetenschappen,
op gezag van de rector magnificus,
dr. C. C. Oosterlee,
in het openbaar te verdedigen
op woensdag 4 februari 1987
des namiddags te vier uur in de aula
van de Landbouwuniversiteit
te Wageningen.

*Aan Willem,
onze ouders
en Nils*

Stellingen

I

Er bestaat bij leghennen geen relatie tussen sociale dominantie en nestkeuze.

(Dit proefschrift)

II

Acceptatie van een bepaald legnest door leghennen is afhankelijk van ervaring opgedaan met legnesten in de weken voor en tijdens de legperiode.

(Dit proefschrift)

III

Om desorientatie van leghennen, gehuisvest in grote stallen te voorkomen, b.v. bij het terugzoeken van een geprefereerd legnest, verdient het aanbeveling de stallen heterogeen in te richten.

IV

Individuele verschillen in fysiologische en ethologische stress reacties opgeroepen tijdens aversieve stimulus-situaties bij dieren werd aangetoond bij mensen (Miller, 1980), terug te voeren kunnen zijn op individuele verschillen in de gevolgde "coping-strategie".

S.M.Miller, 1980. In: "Coping and Health". Plenum Press, New York.

V

Aangezien de kans groot is, dat proefdieren, die speciaal voor dierproefdoeleinden onder laboratoriumomstandigheden worden gefokt, abnormaal gedrag ontwikkelen, zullen de resultaten van biologische experimenten uitgevoerd met deze dieren met de nodige terughoudendheid moeten worden geïnterpreteerd.

VI

Door leghennen te huisvesten in alternatieve grondsystemen worden omstandigheden inherent aan huisvesting in batterij-kooien, die als welzijnsbeperkend worden verondersteld weggenomen. Desondanks verdient het aanbeveling de alternatieven niet alleen op technisch-economische parameters, maar

ook op het welzijn van de hennen te evalueren.

VII

Zelfmedicatie, zoals dat wordt mogelijk gemaakt door de verkoop van homeopathische middelen, kan de verantwoordelijkheid voor de eigen gezondheid verhogen. Dit positieve effect kan echter teniet worden gedaan, door het toepassen van zelfmedicatie als alternatief voor een bezoek aan een allopathisch of homeopathisch arts.

VIII

Probleemgestuurd hoger onderwijs leidt tot een doeltreffender integratie van de aangeboden leerstof dan de meer gangbare didactische methode (doceren).

H.G. Schmidt, 1982. In: "Probleemgestuurd onderwijs". SV0-reeks no.57. 's-Gravenhage.

IX

Als de af- en uitspoeling van fosfaten vanaf landbouwgronden blijft toenemen, zal defosfatering in rioolwaterzuiveringsinstallaties nauwelijks nog op de kwaliteit van het oppervlaktewater.

X

Wat betreft de uitvoering van het beleid ten aanzien van deeltijd-arbeid geldt vaak: "...tussen droom en daad staan mensen in de weg en praktische bezwaren...".

Naar: W. Elsschot, 1910. In: "Het huwelijk".

XI

Gezien de recente ontwikkelingen rondom het gebruik van bloedzuigers in de plastische chirurgie, zou de naam van dit dier niet langer met een negatief denkbeeld geassocieerd moeten worden.

B.Rietveld-Piepers

The development of egg-laying behaviour and nest-site selection in a strain of white laying hens.

Wageningen, 4 februari 1987

VOORWOORD

Eind 1981 startte, in samenwerking met de Vakgroep Veehouderij, Sectie Ethologie van de L.U. Wageningen, op het C.O.V.P. "het Spelderholt" te Beekbergen een drie-jarig onderzoekproject getiteld "Oorzaken van buiten-nest-eieren bij op de grond gehuisveste leghennen". Deze eerste fase werd mede gefinancierd door het "Fonds Welzijn Landbouwhuisdieren". De hier op volgende schrijffase werd gesubsidieerd door het "Wageningenfonds" en het "Fonds Landbouw Export Bureau 1916-1918". De resultaten van dat onderzoek staan vermeld in dit proefschrift.

In de eerste plaats dank ik mijn promotor prof. dr. P.R. Wiepkema voor de mij geboden gelegenheid dit onderzoek uit te voeren. Zijn opbouwende kritiek en waardevolle adviezen heb ik gedurende iedere fase van het onderzoek als stimulerend ervaren. Mijn andere promotor, prof.dr. ir. E.H. Ketelaars, ben ik erkentelijk voor zijn deskundige commentaar en praktische aanwijzingen. De vele prettige discussies die we gedrieën hebben gevoerd, hebben bijgedragen tot de uiteindelijke inhoud van dit manuscript. Prof.dr. M.T. Frankenhuis wil ik bedanken voor zijn op- en aanmerkingen en zijn deskundige commentaar betreffende hoofdstuk 2.

Leden van de projectgroep "buiten-nest-eieren", ir. H.J. Blokhuis en ir. D.A. Ehlhardt, ben ik dank verschuldigd voor hun begeleiding en adviezen gedurende de praktische uitvoering van het onderzoek. Ing. C.L.M. Koolstra dank ik voor haar hulp bij diverse werkzaamheden, waar ik alleen onmogelijk uitgekomen was en ir. A. Siegerink voor zijn assistentie bij het onderzoek beschreven in hoofdstuk 5.

Voor zijn hulp bij de verwerking van de gegevens met de computer ben ik J.W.C. Pol dank verschuldigd, terwijl ik P.J.W. van Schagen en ir. P.F.G. Vereijken erkentelijk ben voor de vele statistische adviezen. J.H. Heuver en D.Tromp waren altijd "in" voor het opsporen en aandragen van literatuur; mijn hartelijke dank hiervoor. De proefopstellingen werden veelal gebouwd door de Technische Dienst, terwijl de Proevendienst altijd zorgde voor een tijdige levering van de leghennen. Beide diensten wil ik hierbij bedanken. G.Vos en P.Veldhuis wil ik bedanken voor de prima verzorging van "mijn" hennen en voor de dier-vriendelijke wijze, waarop zij met hen omgingen.

G.J. Gijsbertse-Huiberts, S. van Ojik en ing. K. de Roo verleenden hulp bij het drukbaar maken van de tekst, terwijl de grafieken getekend werden door F.F. Putirulan; hiervoor mijn hartelijke dank. De foto's werden gemaakt door F. Klinge, terwijl de tekening op de omslag van de hand van A.Grips is. Dr. K. Carlstead dank ik voor het corrigeren van de Engelse tekst van hoofdstuk 4.

Familie, vrienden, kennissen, medewerkers van "het Spelderholt" en de Sectie Ethologie van de L.U. te Wageningen dank ik voor de getoonde belangstelling in de loop der jaren, die ik altijd zeer op prijs heb gesteld.

Een niet te onderschatten rol bij de tot standkoming van dit proefschrift werd gespeeld door Willem, aangezien de uitwerking van de gegevens en het op schrift stellen van dit manuscript voor een groot gedeelte in huiselijke kring heeft plaats gevonden. Enerzijds fungeerde hij als een onontbeerlijk klankbord, anderzijds hebben de vele discussies die ik met hem heb gehad een stempel op mijn werk gedrukt. En natuurlijk wil ik ook Nils noemen. Een groot gedeelte van dit proefschrift werd geschreven gedurende zijn babytijd. Hij gaf me de nodige plezierige afleiding, waardoor ik steeds weer met nieuwe energie mijn schrijfwerkzaamheden kon hervatten.

Tenslotte wil ik iedereen bedanken die aan de totstandkoming van dit proefschrift heeft bijgedragen, maar niet met name is genoemd.



Contents

Chapter	Page:	
1.	General introduction	1
1.1.	Animal welfare research	3
1.2.	Alternative housing systems	6
1.3.	Scope of the present study	8
2.	Reproduction in poultry: literature review	11
2.1.	Introduction	11
2.2.	Structure of the ovary and oviduct	11
2.3.	The ovulatory and ovipository cycle	13
2.4.	Ovulation and its hormonal control	14
2.5.	Behaviour related to reproduction	16
3.	General method and materials	23
3.1.	Rearing period	23
3.2.	Experimental conditions	23
3.3.	Observations	25
3.3.1.	The weeks before laying	26
3.3.2.	The laying period	27
4.	Egg-laying behaviour and nest-site selection of domestic hens kept in small floor-pens	31
4.1.	Introduction	32
4.2.	Materials and methods	33
4.3.	Results	35
4.3.1.	The development of egg-laying behaviour	35
4.3.2.	Nest-site choice	36
4.3.2.1.	Social factors and nest-site choice	39
4.3.3.	Floor-eggs	43
4.4.	Discussion	44
4.5.	Conclusions	47
5.	Nest-examinations, their biological significance	49
5.1.	Introduction	50
5.2.	Experiment 1	52
5.2.1.	Materials and methods	52
5.2.2.	Results	56
5.2.2.1.	Glances and inspections in the weeks before laying	56
5.2.2.2.	Glances and inspections in the egg-laying period	60
5.2.2.3.	Early nest-examinations and later nest preference	62
5.2.3.	Discussion	64
5.3.	Experiment 2	66
5.3.1.	Materials and methods	66
5.3.2.	Results	67
5.3.3.	Discussion	70
5.4.	Conclusions	71
6.	The percentage of floor-eggs as influenced by experience with different types of nests	73

6.1.	Introduction	74
6.2.	Experiment 1	75
6.2.1.	Materials and methods	75
6.2.2.	Results	76
6.2.3.	Discussion	78
6.3.	Experiment 2	80
6.3.1.	Introduction	80
6.3.2.	Materials and methods	81
6.3.3.	Results	81
6.3.4.	Discussion	83
6.4.	Conclusions	85
7.	Egg-laying records and pre-laying behaviour of floor-and nest-layers	87
7.1.	Introduction	88
7.2.	Physiological factors	88
7.2.1.	Materials and methods	89
7.2.2.	Results	91
7.2.2.1.	Egg-production pattern	91
7.2.2.2.	Lag-duration pattern	92
7.2.2.3.	Consistency in site use	93
7.2.3.	Discussion	94
7.3.	Pre-laying behaviour of floor-and nest-layers	95
7.3.1.	Materials and methods	96
7.3.2.	Results	99
7.3.2.1.	Pacing and orientation away from the flock	99
7.3.2.2.	Eating, drinking and preening	100
7.3.2.3.	Sleeping/resting	101
7.3.2.4.	Nesting behaviour	101
7.3.3.	Discussion	103
7.4.	Conclusions	104
8.	General discussion	105
8.1.	Development of nesting behaviour and nest-site selection	105
8.2.	Factors affecting floor-laying	107
8.2.1.	Social factors	108
8.2.2.	Nest-box management	109
8.2.3.	Accessibility of the nests	113
8.2.4.	Individual differences	113
8.3.	Recommendations and their practical significance	115
	Summary	119
	Samenvatting	125
	References	133
	Curriculum Vitae	

CHAPTER 1

General Introduction

Since World War II livestock husbandry has been highly intensified. Traditional systems in which livestock was kept have been superseded by more intensive methods. A characteristic feature of this process was the move towards larger units while the total number of farms decreased. Laying hens, for example, used to be housed outdoors in free-range systems. Then they were kept indoors in large flocks in deep litter or slatted-floor houses, but nowadays these systems have almost entirely been replaced by the battery-cage, a system which was known as early as the 1920's. Fattening pigs are kept indoors without any bedding material on concrete floors and sows for breeding are mostly tethered in individual stands, while a large number of veal calves are housed individually in crates (Brambell, 1965; Commissie Veehouderij-Welzijn Dieren, 1975).

This trend was noticeable in nearly all European countries and it was most obvious in the poultry industry. In 1957 England and Wales only counted 50 poultry farms with more than 5000 laying birds; in 1964 the number of such farms was nearly 1000 (Brambell, 1965). This development was also obvious in the Netherlands. In 1960 more than 100,000 units kept an average of 171 laying hens per unit; in 1973 29,000 units kept an average of 616 hens, while the total number of hens was the same (Commissie Veehouderij-Welzijn Dieren, 1975). From 1976 until 1984 the number of small units keeping less than 400 hens decreased from about 10,000 to about 2,000, whereas the number of units with more than 10,000 hens increased from 444 to 893. Moreover, during this period the total number of hens highly increased as well (CBS, LEI, 1985).

This change in the production systems of eggs from traditional to intensive systems was largely due to a high degree of technical progress. Housing hens indoors in cages allowed and facilitated the automation of food and water dispensation and dung removal. As a result, a small number of attendants could look after a large number of birds. Disease levels were kept down by high levels of hygienic standards and by the use of vaccines. These factors brought about savings in the production costs and thus improved profitability, which is the aim of the producer. Nowadays in most

European countries and the U.S. of America about 90 % of the laying hens are kept in cages (Mason and Singer, 1981). However, in the early sixties scientists and the general public started to express much concern for the well-being of farm animals kept under intensive circumstances and for that of hens kept for egg-production in battery-cages in particular (Harrison, 1964). Since then the production of meat and eggs in intensive systems has been discussed frequently, not only from the view-point of ethics (Singer, 1975; Zimmer, 1983) but also from the view-point of animal rights and interests (Boon, 1979; Boon, 1983).

One of the earliest reactions to this concern for the welfare of farm animals was the appointment of a committee in England. Its members were asked to examine the conditions in which livestock are kept. Their final aim was to advise whether "standards ought to be set in the interest of their (=livestock) welfare, and if so what they should be" (Brambell, 1965). Several years later in the Netherlands a "Commissie Veehouderij-Welzijn Dieren" was appointed by the Nationale Raad voor Landbouwkundig Onderzoek (N.R.L.O.). Their task was a.o. to answer questions such as which factors influence states of welfare in farm animals and which problems and possible recommendations for the improvement of animal welfare need further investigation. Finally the aim of both committees was to end up with legislation, which intends to ensure an optimal standard of welfare for farm animals. However, recommendations should on the other hand be flexible enough to permit a progressive development of new systems of animal husbandry.

In the meantime one of the measures introduced by the U.K. in 1968 were the Codes of Practice which emphasized that at least basic (behavioural) needs should be met (Perry, 1983). In the Netherlands a legislative measure has been proposed and accepted implicating that each hen in a multi-bird cage must be provided with at least 400 cm² cage surface and 10 cm food-trough length (Staatsblad, 1984). Recently in Switzerland a referendum was held about keeping hens in battery-cages. More than 90% of the public voted against cages resulting in a complete ban of the cage in the future in that country (Anon., 1983). In the future comparable measures are intended to be taken, not only in the Netherlands (Persberichten Min. van L&V, 1984) but also in other European countries (Scholz, 1984), although these will have to be based on results of research.

It was well recognized by the advising committees that there is a lack of information on criteria which would enable an objective assessment of welfare in farm animals and they stressed the need for more behavioural studies to be carried out on farm animals. Moreover, investigations to improve existing systems and to develop possible alternatives were advised. A first step in this direction was made by the Commission of the European Communities (CEC) who called together an "ad hoc" expert group on animal welfare in 1979. Questions of first concern were judged by this group to be those of poultry welfare. A three-year welfare research program started in 1981. This Commission financed research that looked at better battery-cage design, social space requirements, alternative systems to battery-cages, "feelings" in poultry and at nest-site selection (CEC report, 1984).

In the Netherlands in 1979 a "Studiecommissie Grondhuisvesting Leghennen" was appointed by the "Coördinatiecommissie Huisvesting en Verzorging Landbouwhuisdieren" of the N.R.L.O. at request of the "Commissie Welzijn Landbouwhuisdieren". One of the tasks of this group was to propose a research program in order to meet problems that arise when hens are kept in floor-systems, like a.o. the higher feed-intake, the occurrence of floor-eggs and feather-pecking and the higher labour and housing costs (Studiecommissie Grondhuisvesting Leghennen, 1980).

More research on welfare may help to evaluate existing and alternative housing systems. In the following sections some literature on welfare research demonstrating what problems may arise in assessing states of welfare is reviewed (section 1.1). Second, in order to improve welfare of farm animals, their environment might be changed. Therefore section 1.2. reviews some literature concerning the development of alternative systems. Some of these systems are expected to give rise to several problems such as the occurrence of floor-laying, which leads to the scope of the present study, as described in section 1.3.

1.1. Animal welfare research

The assessment of welfare needs a multi-disciplinary approach as agreed upon by many researchers (Duncan, 1978; Dawkins, 1980; Hill, 1983b; Wood-Gush, 1983). Research fields are veterinary sciences, physiology and etho-

logy.

Trauma and the presence of diseases are obvious signs of reduced well-being. Productivity may also be taken as an index for welfare, however the use of this measure has been criticized. Hill (1983b) stated that before relating performance to stress and thus reduced well-being, the measure must be adequately defined. For instance, as a result of a change in the environment of a laying hen the number of eggs produced may be reduced, but egg-weight may be increased, thus leaving the total egg mass output the same. In this case the change could be said to reduce or unaffected the performance, depending on the parameter of productivity selected. Dawkins (1980) raised a more general critical point i.e. good growth rate or productivity may not be incompatible with suffering. Therefore interpretations of experiments using productivity measures are not easy.

An ethological approach to assess welfare is the use of preference tests. It is assumed that animals will choose in the best interest of their welfare. Dawkins (1976) and Hughes and Black (1973), for example, carried out preference tests in poultry comparing environments differing in many ways. Although a preference for one over the other environment was shown, the choice appeared to be influenced by the environment in which the hens lived prior to the test. From this and the doubts raised by Duncan (1978) that animals are not expected to make rational choices, it is concluded that such experiments are not the most suitable ones to assess states of welfare in animals.

Physiological parameters such as heart and respiration rates and body temperature have been successfully used as parameters for identifying stressed hens. Hens subjected to fear inducing stimuli showed a rapid increase in heart rate (Duncan and Filshie, 1979).

Other physiological parameters like changes in hormone concentrations (corticosteroids) have also been used as parameters of stress. However, the use of this indicator gave rise to particular problems. Firstly a large diurnal variation is found (Beuving and Vonder, 1977). Moreover, certain stressors may produce significant changes in the measures but other stressors do not. Exposure of hens to heat, thirst or hunger, all heavily stressors, failed to give a corticosterone response. In contrast, crating birds prior to blood-sampling or immobilization by hand gave a large and rapid rise (Beuving and Vonder, 1978). In another experiment by Beuving

(1983) corticosterone levels were measured in birds housed in cages without a nest-box, which is supposed to be a stressful situation and with nest-boxes. On the first day after the removal of the box an increase in the corticosterone level was detected. However, this response had disappeared after 40 days of laying without a nest-box, which may have been due to habituation. Nevertheless, the hens without a box still showed more restless behaviour than did hens with a box, even on the 40th day after the removal of the nest-box. From these results it is concluded that firstly more physiological research is necessary in order to elucidate the influence of different stressors on hormonal changes. Secondly, it is a plea for not using one or the other parameter in isolation in order to assess welfare in animals, but to link behavioural and physiological evidence.

An approach to the concept of animal welfare using ethological and physiological processes is presented by formulating the organisation of behaviour in terms of a regulatory model (Toates, 1980; Wiepkema, 1985). The model states, that each organism lives in an environment with changing "Istwerte" and the corresponding "Soll-werte". If the discrepancies between Istwerte and Sollwerte cannot be restored by a program (integrated ethological and physiological activities), conflicts will arise leading to states of stress. If the animals are forced to live under such circumstances these conflicts may develop into abnormal behaviour (Wiepkema, 1982) leading to injury of pen-mates like ear-and tail-biting in piglets (Van Putten and Dammers, 1976), tail-biting in fattening pigs (Van Putten, 1980; Ruiterkamp, 1985), feather-pecking in laying hens (Hughes and Duncan, 1982; Blokhuis and Arkes, 1984) or urine sucking in veal calves (Unshelm et al., 1982; de Wilt, 1985). Another type of disturbed behaviour is the performance of stereotypic movements like barbiting in tethered sows (Cronin and Wiepkema, 1984). Animals developing these stereotypies are unable to cope adequately with the environment they are subjected to (Wiepkema, 1982). Evidence supporting this view was provided by Cronin (1985). It was concluded from experiments with tethered sows that stereotypies might function to reduce the perception of the negative aspects of the environment. It has been proposed to use the mentioned types of disturbed behaviour as means to assess welfare in farm animals (Wiepkema et al., 1983). A combination of approaches as described above may help in assessing welfare and in evaluating existing and alternative housing systems for farm animals.

1.2. Alternative housing systems

Although stress free environments are unlikely to exist it is recognized that, among basic requirements also "adequate freedom of movement and ability to stretch wings" has to be included in achieving acceptable levels of welfare in poultry (Code of Practice, 1983). Since cages confine hens and limit their behavioural repertoire, several experts still agree that this way of housing hens is associated with a state of reduced well-being (Sainsbury, 1980b; Craig and Adams, 1984).

In order to increase the hen's well-being either the genetical constitution might be changed (Beilharz, 1982) or the environment. A genetical approach might be selection against a particular behaviour that is associated with and indicates jeopardized well-being. However selection against, for example, responsiveness to fear inducing stimuli might reduce egg-production. Thus selecting for a positive trait might result in an unforeseen selection against another desirable one. Therefore selection for behavioural changes should be accompanied by careful studies on the underlying genetic mechanism (Craig and Adams, 1984). Furthermore, changing the genetical constitution takes a lot of time.

Welfare improvements can be achieved on short term by changes in cage design. As shown by Tauson (1984) foot-health was considerably improved by providing cages with perches and low cage floor slopes. Another recent field of research has been the re-appraisal of traditional floor-systems like the perchery (Anon., 1983; Henderson, 1984). However, keeping hens on the floor is still regarded by some authors as an "unhygienic disaster" (Roepke, 1984), while other authors prefer cages to floor-housing to avoid feather-pecking and floor-eggs (Münchmeyer, 1984). Moreover, the most economic system for egg-production is the battery-cage. It is evident that production costs will increase with floor-systems (Studiecommissie Grondhuisvesting Leghennen, 1980).

One possible approach to this problem is to change the consumer's and buyer's attitude towards eggs produced in cages. If they are prepared to pay the higher price needed to support the more expensive systems, hens could be kept on the floor again. However, an investigation into this field

pointed out that only 13,4 % of the French and 43 % of the German buyers did not want to purchase eggs produced in cages (in: Masic and Pavlovski, 1985). It is obvious that these percentages are too low to cover the higher production costs.

Therefore the possibility to design competing, and thus profitable, alternative systems was investigated. Moreover, these alternatives had to promote the well-being of the hens as well. Research in this field started in England by Elson (1976) and Bareham (1976). They introduced the get-away cage: a large cage (about 80x100x65 cm) provided with perches, nests, multiple feeding and drinking positions and a sand-box. This cage type has also been tested in Germany (Wegner, 1980; Wegner et al., 1981) and in the Netherlands (Brantas, 1981). However, after several try-outs this alternative did not appear to be practically and commercially viable. There were a lot of problems; hens would use the sand-boxes for egg-laying, they scratched sand out of the boxes on the manure belt (Wegner et al., 1981) and moreover they were contaminated with manure from hens perching above (Elson, 1981).

Since then other cage types were developed. In the past it had already been theorized by McBride (1970) that "it should be possible to design houses which have many tiers of lattice floors...Naturally, corridors would be necessary for men to walk through. Technically the provision of waterers, automatic feeders and nests at a number of levels is no serious problem. The disposal of manure and provision of ventilation could pose some problems (..) but we are particularly competent to solve these technical problems." Several years later some alternatives developed by European researchers were introduced. These new systems had one characteristic in common: the available vertical space in the hen house was optimally used by the construction of wire slats, perches or extra wire floors (Hill, 1981a; Fölsch et al., 1982; Wegner, 1983; Ehlhardt et al., 1984a). As a result higher stocking densities (10-15 hens per m² and 20 hens per m² in the Dutch system) are reached as compared with traditional deep litter systems (7 hens per m²) and stocking density in cages (20 or more hens per m²) is approached. Since stocking density is, next to food-intake, one of the crucial factors in determining production costs of any floor-system (Hill, 1981b), the new systems may prove to be a promising alternative.

1.3. Scope of the present study

Most of the alternatives described above have been tested for several years. Although good results are obtained still many problems like high food intake, high levels of ammonia attributed to wet litter, feather pecking and cannibalism have to be overcome. Another problem common to all floor-systems is the reluctance of a various percentage of hens to use the laying nests provided (Hill, 1983; Rauch and Wegner, 1984; Ehlhardt et al., 1984a). This has considerable economic implications such as loss of eggs, dirty eggs and time-consuming egg-collection. Acceptation of alternatives will be promoted if problems of this kind are solved (Studiecommissie Grondhuisvesting Leghennen, 1979). Therefore it was decided to start a three-year investigation into nest-site selection in laying hens kept in floor-pens. The general aim is to trace factors that cause floor-laying.

In the past several studies related to the problem of floor-laying in laying hens have been carried out. Some studies had an orientating character, while nearly all other studies concentrated on the question which characteristics of nests or which zootechnical circumstances might affect the hen's nest-site-choice (see also chapter 8). However, the problem of floor-eggs has not yet been solved and the process of nest-site selection is not yet fully understood. Therefore more systematic ethological studies in this field are worthwhile.

Although the approach taken to the problem in the present study was an ethological one, the important role of physiological processes in egg-laying and nesting behaviour is recognized and some literature on this subject is reviewed in chapter 2 of this thesis.

Chapter 3 presents a description of the rearing and experimental housing conditions, the hens used in this study and the general method followed.

Since scant information has been reported on the behaviour in the weeks before laying, it was decided to observe the development of nesting behaviour in individual immature pullets in order to get more insight into the phenomenon of floor-laying. Furthermore, the impact of social factors on the hen's nest-site choice is investigated. Chapter 4 is devoted to these developmental and social aspects of nesting behaviour.

Moreover, such a developmental study is of interest from a biological point of view. Selecting a nest is supposed to be a gradual process, which

point of view. Selecting a nest is supposed to be a gradual process, which is expected to start several weeks before the hens come into lay. During this period they are supposed to gather information about environmental properties such as potential nesting sites. Two experiments designed to test this hypothesis are presented in chapter 5.

In chapter 6 the influence of early experience with different types of nests is studied on the number of floor-eggs.

In order to find out whether floor-laying is caused by irregularities in physiological processes underlying egg-production or by other factors, egg-production records and pre-laying behaviour of floor- and nest-layers are described and compared to each other. The results of this study are presented in chapter 7.

Chapter 8 discusses the results from the present study in relation to other studies concerning nest-site selection in domestic fowl. Finally, conclusions are formulated from which recommendations are derived in order to reduce floor-laying in domestic fowl.

Chapter 2

Reproduction in poultry

2.1. Introduction

The reluctance of domestic fowl kept on the floor to use nest-boxes provided may be caused by many various factors. Physiological processes are known to play a major role in the regulation of egg-production and nesting behaviour. Hence, irregularities therein may lead to abnormalities in egg-laying and thus to floor-eggs, as well. Knowledge of the physiology of individual hens may elucidate to what extent the occurrence of floor-eggs may be due to physiological abnormalities. Although the approach taken to the problem in the present study is an ethological one, physiological irregularities are also reflected in, for example, abnormal egg-production and abnormal nesting behaviour. Therefore differences in these parameters between hens are detectable and it may be possible to use such parameters in order to find out to what extent floor-laying is caused by abnormalities in the physiology. This method, which has been used in chapter 7, requires a description of the normal egg-laying and nesting behaviour.

Because the present study did not intend to carry out physiological research, this chapter reviews literature concerning this subject. Furthermore, literature on the normal egg-laying and nesting behaviour is reviewed in both Red Jungle Fowl and free-living and captive domestic fowl.

2.2. Structure of the ovary and oviduct

In the chicken only the left ovary and oviduct are functional. In the ovary a large number of follicles are carried on follicular stalks (Gilbert, 1971a). Most of these follicles contain white yolk and have diameters less than 3 mm. Usually four to seven follicles contain yellow yolk and have diameters of about 7 mm. These follicles are referred to as the follicular hierarchy, because they mature in a sequential manner.

Each follicle consists of a centrally placed oocyte, containing yolk material, surrounded by a wall of six layers (Gilbert and Wells, 1984). The

theca layer is involved in the production of the steroid hormone oestradiol, while cells located in the granulosa layer are known to produce another steroid hormone, progesterone. There is a gradual decrease in the concentration of oestradiol in the theca layer, while there is an increase in the concentration of progesterone in the granulosa layer during follicular maturation. Both the theca and granulosa layer produce the same amount of testosterone (Bahr et al., 1983).

The oviduct, a long tube, extends from the ovary to the cloaca. It consists of five segments: the infundibulum, magnum, isthmus, uterus and vagina (figure 2.1).

At the time of ovulation the mature follicle is ruptured and the ovum (=oocyte) is engulfed by the infundibulum. If this process fails, the ovulated ovum is deposited in the abdominal cavity and is gradually reabsorbed, a process which is referred to as "internal laying" (Wood-Gush, 1963; Wood-Gush and Gilbert, 1970). If the ovum is engulfed by the infundibulum, then it spends various amounts of time in each area of the oviduct. The magnum, the largest part of the oviduct, has a thick wall and contains glandular tissue, which secretes amounts of albumin (=the protein of the egg). By peristaltic movements of the magnum the ovum arrives in the isthmus where the two shell membranes are secreted. Then the ovum arrives in the uterus where it receives its shell and pigment (Bahr and Nalbandov, 1977). Finally, 25-26 hours after ovulation, uterine muscle contractions are initiated by a neurohypophyseal hormone, arginine vasotocin, which finally leads to

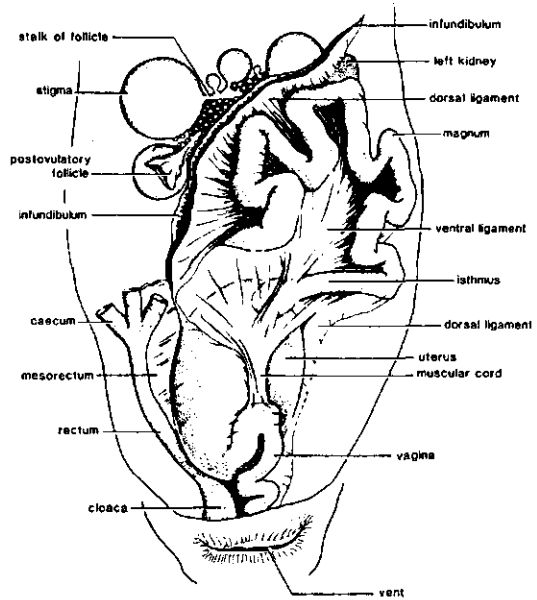


Figure 2.1. Schematic representation of the oviduct (after King and McLelland, (1984).

the expelling of the egg (Sturkie and Mueller, 1976; Tanaka et al., 1984).

2.3. The ovulatory and ovipository cycle

In domestic fowl eggs are laid in sequences or "clutches": a series of eggs separated from each other by one or more pause days (Gilbert and Wood-Gush, 1971). The occurrence of ovulation is restricted to an 8 to 10 hour period of the 24 hour day. In hens maintained on a schedule of 16 h light and 8 h darkness, the first ovulation of the sequence occurs about 7-8 hours after the onset of darkness (Fraps, 1965) and therefore the first egg of a sequence is usually laid in the morning. Subsequent follicles do not ovulate until after the first oviposition (Morris, 1973, in: Wilson and Cunningham, 1984). Therefore subsequent eggs are laid progressively later each day resulting in an interval between ovipositions, which is usually greater than 24 hours. This interval minus 24 hours is called the "lag". Within a sequence the lag is greatest between the first and second egg, then decreases during the middle of the cycle and increases again towards the end of a sequence (Gilbert and Wood-Gush, 1971). The last follicle in a sequence ovulates about 15-16 hours after the onset of darkness and thus the last egg in the clutch is usually laid during the afternoon. Then one or more pause days follow. The number of eggs in the sequence and the number of pause days can be regular or irregular. In hens with long sequences ovulation occurs shortly after oviposition, while shorter sequences are caused by a longer interval between oviposition and ovulation (Gilbert and Wood-Gush, 1971; Sturkie and Mueller, 1976).

The rate of ovulation in hens maintained on short day photoperiods is significantly less than in hens maintained on long day photoperiods (Morris, 1967). Recently it was shown that this effect of long photoperiods can also be achieved by the substitution of one complete long period by short pulses of light at the appropriate time of the day (=photosensitive period). For example, if 18 week old hens are kept on a schedule of 8L:16D and are then transferred to one of 4L : 16 D with a further period of 4L given at different times during the hours of darkness, the 4 hour light period is most effective in stimulating ovulation when given between 5 and 9 hours after the end of the main photoperiod. This phenomenon is explained

by the existence of a circadian rhythm of sensitivity to light. The two 4 hour periods of light proved to be nearly as effective in stimulating ovulation as a complete 16L : 8D schedule if provided in a schedule of 4L : 5D : 4L : 11D. Thus, the occurrence of ovulation does not depend on how much light the bird receives in 24 h, but on whether light falls during the photosensitive period (Wilson, 1982, in: Wilson and Cunningham, 1984).

2.4. Ovulation and its hormonal control

The hormonal control of ovulation involves a hypothalamic hormone (luteinising hormone-releasing hormone (=LHRH)), two anterior pituitary gonadotrophins, (luteinising hormone (LH) and follicle stimulating hormone (FSH)) and finally steroid hormones, produced by the ovary (progesterone testosterone and oestrogens (Scanes, 1984)). A third anterior pituitary gonadotrophin is prolactin. This hormone, however, has been reported to decrease ovarian steroidogenesis and to depress LH secretion during broodiness (Scanes, 1984).

A feed-back loop exists between the hypothalamus-pituitary system and the gonads (figure 2.2). As a result, during the ovulatory cycle a low level of tonic LH secretion is maintained by the negative feed-back action of progesterone. However, during a particular part of the ovulatory cycle, a pre-ovulatory surge in the LH and progesterone concentration occurs, which is followed by ovulation (Johnson, 1984; Wilson and Cunningham, 1984).

To find out whether the plasma concentration of progesterone rises prior to that of LH or vice versa, hens were treated with an inhibitor of progesterone synthesis, aminoglutethimide (AGT). No preovulatory surge of LH was initiated after the administration of AGT. It was concluded that the pre-ovulatory LH release is initiated by progesterone (Johnson and van Tienhoven, 1981). Progesterone release itself is known to be initiated by maturing follicles (Gilbert and Wells, 1984). Subsequently this initial release of progesterone is supposed to stimulate the secretion of small amounts of LH (Scanes, 1984). It is suggested that this initial LH release, and possibly progesterone, exerts a priming effect on the largest preovulatory follicle, which in its turn responds with the production of more progesterone (Johnson et al., 1984) and possibly testosterone (Wilson and

Cunningham, 1984). This positive feedback loop is maintained until the preovulatory peak of LH is reached after which the ovary no longer responds to further release of LH with progesterone secretion and ovulation will follow (Johnson, 1984).

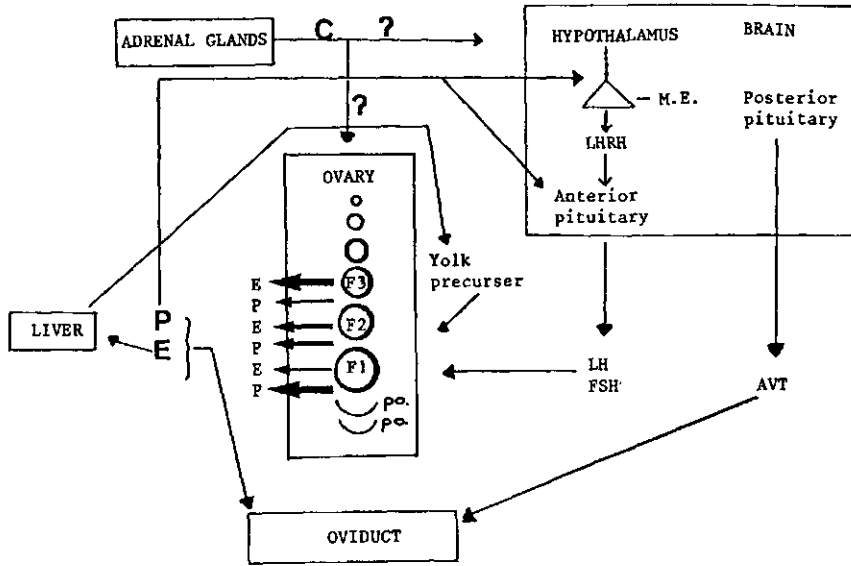


Figure 2.2. Schematic representation of the hormonal control of the ovulatory cycle (after Scanes, 1984).

AVT= arginine vasotocin; C= corticosterone; E= oestradiol; F1-3= pre-ovulatory follicles; FSH= follicle stimulating hormone; LH= luteinising hormone; LHRH= luteinising hormone-releasing hormone; M.E.= median eminence; P= progesterone; po= post-ovulatory follicle.

No ovulation will occur in the absence of a mature follicle (Johnson and Bahr, 1985). The process of follicular maturation is mainly controlled by the pituitary hormone FSH. As mentioned before, there is a graduation in maturation of ovarian follicles, the so-called follicular hierarchy. About six days before ovulation the ovum begins growing at a rapid rate (rapid growth phase) and yolk is laid down in concentric layers. Oestrogens promote the synthesis of yolk precursors in the liver (Scanes, 1984; figure 2.2).

The control of the follicular hierarchy itself is not yet fully under-

stood. Perhaps FSH and LH play an important role because administration of both hormones prevent the hierarchy and multiple maturations and ovulations may occur (Sturkie and Mueller, 1976). It has also been suggested that the maturation of each follicle in the hierarchy is initiated by the previous ovulation (Etches and Schoch, 1984) or consequently by a fall in the plasma concentration of LH (Wilson and Cunningham, 1984).

Under a certain lighting regime the pre-ovulatory surges in LH and progesterone are always restricted to a particular period of the day. If a follicle does not mature within this period, no ovulation will occur, which explains why sequences of egg-laying are separated by intervals of one or more pause days. Recently a mechanism has been suggested responsible for the timing of ovulation in the hen. The possibility was raised that the adrenal gland played a role because administration of corticosterone could induce premature ovulation (Etches and Cunningham, 1976, in: Wilson and Cunningham, 1984). Since corticosterone secretion follows a diurnal rhythm, (Beuving and Vonder, 1977) and since the position of the period during which the LH surge occurs, is regulated by changes in light (onset of darkness), it is possible that adrenocortical hormones contribute to the mechanism, which determines the timing of ovulation (figure 2.2).

To test this hypothesis, Wilson and Cunningham (1980) treated hens with a drug, metyrapone, which reduces the secretion of corticosterone. The pre-ovulatory surge of LH was now released at intervals of 26-27 hours at times throughout the day, instead of being restricted to an 8-10 hour period. Eggs were laid then at any time of the day and it was concluded that corticosterone was involved in the timing of ovulation.

In conclusion, the ovulatory-ovipository cycle of the hen is controlled by the interaction of two independent systems: follicular maturation on the one hand and the pre-ovulatory release of LH on the other. The latter may be under the control of the production of corticosterone, which, under certain lighting regimes, follows a diurnal rhythm.

2.5. Behaviour related to reproduction

Pre-laying behaviour

Each time the laying of an egg is preceded by particular behavioural

elements. This will be referred to as pre-laying or nesting behaviour, which has been extensively described in domestic fowl housed under different circumstances. Hens kept in a floor-pen provided with trap-nests about to lay become restless and give a characteristic call, which has been referred to as pre-laying (Wood-Gush and Gilbert, 1969b) or laying call (Konishi, 1963). However, the occurrence of this call is not restricted to the laying situation (Schenk et al., 1984) and therefore these authors use a more general term i.e. "Gakeln". Sometimes the hen turns away from pen-mates by making escape movements. Then the head is put into several nest-boxes (Wood-Gush, 1963), which has been referred to as "nest-examinations"; however, it was suggested that this type of behaviour could be considered as intention movements to enter a nest (Wood-Gush, 1963; Gilbert and Wood-Gush, 1971; Wood-Gush and Gentle, 1978). After a while one particular nest is entered and the hen sits down. Time spent on the nest varies between one and two hours. Wood-Gush (1963) provided some evidence that the total time spent in nesting behaviour varied with the duration of the lag; a positive lag resulted in an increase and a negative lag in a decrease. At the time of oviposition a characteristic posture is adopted. Then the hen may leave the nest and cackle but sometimes sitting is resumed for a while (Wood-Gush, 1963).

Wood-Gush (1975) more closely observed nesting behaviour in a floor-pen covered with wood-shavings and some feathers. Nest-boxes were not provided. After the hen had chosen a site for oviposition, usually a corner, she sat down and started rotating while pushing her feet sideways, which resulted in a hollow surrounded by a rim of nesting material. Sometimes wood-shavings were picked up and thrown on her back which would fall off on the rim. This primitive form of nest-construction always occurred in the hours, rather than days before oviposition even in the case of the first egg of a sequence. Similar results were reported by McBride et al. (1969) who described pre-laying behaviour of domestic fowl kept in a pen of 30 m square and provided with boxes with earth floors.

Feral domestic fowl also performed most of the elements as described for fowl kept in pens. However, they seemed to occur at a reduced intensity or frequency. The pre-laying call for example was given, but it was never very loud or persistent. Hens that were seen to enter a nest did so without obviously examining other sites as hens in pens do. The hens were never

heard to cackle immediately after leaving the nest (Duncan et al., 1978).

Fölsch (1981a) studied the impact of domestication on the reproductive behaviour. Nesting behaviour of Red Jungle Fowl (Gallus Gallus Spadiceus), which have never been exploited for egg-laying and were kept under free-range conditions, was compared to that of a highly domesticated laying hybrid kept in floor-pens but with the possibility to move outdoors. During nesting four phases were distinguished: 1) isolation from the flock and nest-examination, 2) entering the final chosen nest, 3) oviposition and its characteristic posture and 4) sitting on the nest until the moment it is left. The behaviour of both strains was highly comparable and resembled that described for domestic penned and feral hens.

In the same study Fölsch (1981a) compared the behaviour of hens kept in cages without nests with that in pens with a wire or litter floor with nests. In caged hens the duration of phase 2 to 4, as distinguished by the author, was highly reduced as compared to that of hens kept in the floor systems provided with nests, while the total amount of time spent in nesting behaviour was nearly equal. The first mentioned hens appeared to spend most of the time in restless movements like pacing up and down the cage. Similar results were obtained by Wood-Gush and Gilbert (1969a) in a group of caged White Leghorns. In contrast, caged hybrids of Rhode Island Reds and White Sussex tended to sit, "nest" and preen more and were less engaged in escape behaviour than were the White Leghorn hybrids (Wood-Gush, 1969). In a later study Wood-Gush (1972) provided evidence that these differences in nesting behaviour might be due to strain differences in response to sub-optimal stimuli.

Nest-site selection

In wild gallinaceous birds nesting behaviour and nest-site selection is not easy to observe because of the segregative nature of the hens (Green, 1982). In their study on the reproductive behaviour of free-living domestic hens Duncan et al. (1978) reported, that a hen's absence from the flock usually indicated that she had come into lay. Moreover, since the behaviour preceding the egg-laying period itself has never been a subject of study, it is unknown how long a hen takes to select a nesting-site or how the final choice is established.

In contrast to many other species of bird feral and domestic fowl do not build elaborated nests. In feral Red Jungle Fowl a nest only consisted of a slight depression lined with just a few leaves and some small feathers (Collias and Collias, 1967). The nests of domestic fowl released on an island were also no more than shallow depressions in the ground, which were either natural or had been formed by scraping. However, they were all very well hidden and covered with vegetation indicating, that concealment is an important element in nest-site selection (Wood-Gush and Duncan, 1976; Duncan et al., 1978). Red Jungle Fowl and a white commercial layer (Fölsch, 1981b) accepted nest-boxes provided but they would also use a natural hollow in the ground, which was lined with some feathers, straw or leaves.

In captive domestic fowl, belonging to a feral population, the cock was observed to escort a hen to potential nests. When approaching a suitable site he would tidbit and give a series of clucks. Then he started making scrapes in the ground and as a result of this a shallow hollow was scratched in the earth, a behavioural display that has already been described by Kruijt (1964) as "cornering". This habit was also carried out in nest-boxes (McBride et al., 1969). Similar results were reported in White Leghorn hybrids (Wennrich, 1978; Fölsch, 1981b) and Red Jungle Fowl (Fölsch, 1981b); however, in a study on feral domestic fowl the cock was never seen to escort a hen to a nesting site (Duncan et al., 1978). Since nest-sites are usually located at several hundred yards from the flock in free-ranging conditions, escorting behaviour of the cock might serve the protection of the hen against predators. None of these studies elucidate, whether the final selection of a site was determined by either the hen or the cock or by both of them. Nevertheless, the cock might play an important role in nest-site selection, as well.

Usually captive (McBride et al., 1969) and feral domestic fowl (Duncan et al., 1978) showed conservatism in nest-site use, at least within clutches. They would use one nest for several days but then changed nests to lay a second clutch in another nest-site. Sometimes nests were left in the middle of a sequence because they appeared to be unsuitable for some reason (Duncan et al., 1978), or because a hen was disturbed by another female while laying (McBride et al., 1969). Pinned domestic fowl consistently used the same site, not only within, but also between clutches (Wood-Gush, 1954). Wood-Gush (1975) provided evidence that it is the site

in the pen that governs the use of the same nest on subsequent days, and not the nest itself. Even hens kept in cages without nest-boxes showed a tendency to use the same site for subsequent ovipositions (Wood-Gush and Gilbert, 1969a).

Hormonal control of nesting behaviour

From the observation that a hen dropped a soft-shelled egg without performing any nesting behaviour, it was concluded that a hard-shelled egg in the uterus initiated nesting behaviour (Wood-Gush, 1963). To test this hypothesis hens were made into chronic shell-less layers by surgical means. Most hens lost the shell-less egg somewhere during the dark period. A number of other hens was made into chronic internal layers by stitching up the infundibulum. As a result ovulated ova did not enter the oviduct but were dropped in the body cavity. Moreover in a number of hens the oviduct was entirely removed. In all these hens normal egg-laying behaviour did occur at the time an egg had to be laid (Wood-Gush, 1963). The same results were obtained if the egg was expelled prematurely by the injection of vasopressin (Beuving and Vonder, 1981). Obviously the presence of a hard shelled egg is not necessary for nesting behaviour to occur, nor is the presence of the oviduct provided ovulation has occurred.

As was demonstrated by earlier studies, the duration of the lag between eggs is increased by damaging the post-ovulatory follicle, in other words oviposition of subsequent eggs was delayed (Conner and Fraps, 1954, in: Gilbert and Wood-Gush, 1971). Since lag-duration and nesting behaviour seemed to be related (see above), it was suggested that the post-ovulatory follicle might be implicated in the process that controls nesting behaviour. Wood-Gush and Gilbert (1964) investigated this possibility further by removing immature or penultimate follicles or the latest post-ovulatory follicle in hens whose nesting behaviour was well known. The first two treatments only affected nesting behaviour of a very small number of hens. However, in 75 % of the hens nesting behaviour was abolished after removal of the latest post-ovulatory follicle. Apparently the post-ovulatory follicle plays an important role in the control of the nesting behaviour.

Subsequent experiments revealed that this role was not performed by neural pathways (Gilbert and Wood-Gush, 1965), but more probably by hor-

mones. To investigate this further a naturally occurring oestrogen, rather than a synthetic one, and progesterone were injected into 9-month-old ovariectomised hens (Wood-Gush and Gilbert, 1973). Progesterone was chosen, since it was assumed to be produced by the post-ovulatory follicle (Gilbert, 1971b). Oestrogen alone could induce nest-examinations in these non-ovulating hens, while nest-entries only occurred when progesterone was injected as well. Administration of progesterone was most effective in this respect when preceded by a period of at least 6 weeks in which the hens had been treated with oestrogen. From these experiments it was concluded that the post-ovulatory follicle and ovarian hormones play a major role in the occurrence of nesting behaviour.

Summarizing, the literature reviewed in the previous paragraphs demonstrates that the hormonal regulation of the ovarian-ovipository cycle and of the nesting behaviour is rather well understood. Irregularities may occur during ovulation or during the expelling of the egg and may lead to abnormalities in egg-production and nesting behaviour and thus to floor-eggs, as well.

Furthermore, the review shows that nesting behaviour has been extensively described in domestic laying hens kept under several housing conditions. Although pre-laying behaviour is modified to some extent by keeping hens under different circumstances, all behavioural elements are present. Even the nesting behaviour of a commercial light hybrid strain was highly comparable to a strain that has not been exploited for the egg-producing industry. This indicates that the pre-laying behaviour is conservative under several conditions and that domestication and selection in favour of egg-production did only exert minor influence on this type of behaviour. However, it is unknown how long a hen takes to select a nesting site or how the final choice is established.

Domestic hens are, like most gallinaceous birds with precocial young, ground nesters and do not build elaborate nests, although nests were all very well concealed. Captive domestic hens use nest-boxes provided but they also use shallow hollows in the ground. From this point of view floor-laying in domestic fowl kept in pens for commercial purposes is not considered to be an aberrant type of behaviour. However, in poultry industry it is a highly unappreciated trait for reasons mentioned before.

It may be possible to find out to what extent floor-laying in domestic

hens is caused by physiological irregularities by comparing egg-production records and nesting behaviour of floor-and nest-layers. In chapter 7 this is investigated further.

Chapter 3

General method and materials

3.1. Rearing period

In all experiments cage-reared White Leghorn hens were used. One of the groups under study was derived from an experimental line of the Centre for Poultry Research and Extension "Spelderholt", while the other groups were all derived from commercial strains (Shaver Starcross 288 and Hisex), reared at units specialized in rearing laying hens. Hens were subjected to several routines like beak-trimming and vaccination. The lighting regime was 23 hr light-1 hr darkness during the first two days, which was followed by a regime of 8 hr dimmed light (5 lux) - 16 hrs darkness until an age of 16 weeks.

3.2. Experimental conditions

Fifteen to 20 hens were housed at an age of 16 weeks in small floor-pens, 4 m square. Half of the pen was provided with litter, a mixture of wood-shavings and chopped straw. In the remaining area wire was placed over a droppings pit about 50 cm above the floor. A food-trough was placed on the wire. An automatic drinker and a perch were fixed above the wire. The hens were fed ad lib on dry mash and water.

Each pen contained 6 individual nest-boxes (30x30x30 cm). In one of the pens three nest-boxes were placed on the litter on each side of the pen (figure 3.1a), while in the other pens the nest-boxes were all placed along one side opposite the droppings pit (figure 3.1b). Nest-floors were covered with wood-shavings or buckwheat husks (litter-nests) or with synthetic grass (=astroturf) or a wire basket, which allowed eggs to roll out of the nest into a collection channel (roll-away-nests). The pen's walls had wired sides to a height of about two meter and its top was covered with a net.

The pens were placed in a window-less, well-insulated hen-house with a concrete floor. Fluorescent lighting tubes with dimmers were used to light the house. Forced-draft ventilation controlled the climate. In winter the



Figure 3.1a. Floor-pen provided with 3 nest-boxes on each side of the pen.



Figure 3.1b. Floor-pen provided with 6 nest-boxes opposite the droppings pit.

house was heated by means of 6 gas heaters fixed on the wall of the hen-house, 3 on each side.

On the day of arrival at the Centre a lighting schedule was maintained of 10 hours light and 14 hours darkness. The light period was lengthened with one hour each week until a lighting regime of 14L-10D was reached. Lighting tubes were suspended in three rows along the hen-house. In contrast to commercial laying conditions (Sainsbury, 1980a), light intensity was kept high (about 75 lux) to enable the recording of behaviour by means of a video-camera (see below).

Since the hens had been reared in cages, they had to learn to jump onto the wire. In order to facilitate this process a step-up was placed in front of the droppings-pit. In the evening, after the lights had gone out, two low intensity lights were kept on for about one hour in order to give the hens the opportunity to find the perch on the wire. Sometimes the attendant had to chase them onto the wire to prevent them from using the nests as a resting place. After about one week the hens got accustomed to the situation and started roosting some time before the onset of darkness.

In summer the temperature varied between 18 and 24°C while in winter values between 18 and 20°C were reached. Sometimes, in particular after cold nights temperature could be lower than 18°C but at daytime, during the laying period, it never fell beyond 14°C.

The experiments started with a thickness of about 70 mm of litter placed on each pen's floor. After a few weeks some litter was added in order to keep it in a friable state. If, due to splashing of water or defect drinkers the litter started caking, it was always replaced entirely.

3.3. Observations

Observations were made by means of a video-recorder (in colour). A camera with a wide-angle lens was placed above a pen. For identification purposes hens were marked with a felt-pen on their backs and necks. The frequency and duration of the behavioural elements were recorded in a sequential order by using an event recorder (More, Observational Systems Inc., Seattle, Washington). The data were then dumped into the host-computer of the Centre for further processing.

The total observation period was divided into two parts: the weeks preceding the actual laying period (from an age of 16 weeks) and the laying period itself. In the next paragraphs behaviour recorded during these two stages is described separately.

3.3.1. Weeks before laying

To registrate the development of nesting behaviour observations were made daily during 1 or 1.5 hr, from an age of 16 weeks until the first egg was laid. For each flock sample sessions were recorded at different times between 8.30 h and 16.30 h according to a schedule that prevented biasing to a particular period of the day. Since each hen in the group was discernable all the time, the focal-animal-sampling method (Altmann, 1974) was used. For a number of hens, chosen at random from the flocks under study, the frequency and/or duration of the behaviours of interest were recorded. Elements recorded were defined as follows:

NESTING-BEHAVIOUR

(as defined by Wood-Gush, 1963,1971,1975; Wood-Gush and Gentle, 1978; Wood-Gush and Gilbert, 1969b).

*Nest-examinations: initially only "nest-box inspections" were distinguished defined as putting the head into a nest-box which could be followed by pecking against the wall or by pecking up some nesting material. In subsequent experiments also "glancing at the nest-box" was distinguished: peering into the nest-boxes from a distance while the neck is held straight out in a horizontal position. The head is turned sideways, while the right and left eye are used alternately.

The other elements belonging to nesting behaviour, as described under 3.3.2., were never observed in the weeks before laying.

SOCIAL BEHAVIOUR:

Rank-order in a group was based on dyadic agonistic encounters observed during each sample session. Ranking of the hens was achieved by using a social rank index defined according to a combination of the number of

dominant and subordinate birds. This method is described in more detail in chapter 4. Most of the elements distinguished have measurable durations (seconds). However, since the frequency of occurrence is of most interest in determining the rank order, they were all considered to be point events. The behavioural elements were defined as follows (Kruijt, 1964):

AGGRESSION:

- *Frontal threatening: stretching out the neck in the direction of a pen-mate, the neck feathers are erected.
- *Leaping: bumping the breasts against each other while the legs are thrown forward
- *Pecking: vigorous movements made with the beak directed to the head or the neck of a pen-mate.
- *Chasing: following at a high speed; the body posture is erected.

SUBMISSION in reaction to aggressive acts:

- *Freezing: standing motionless while the head is lowered to the ground; the feathers of the tail are kept closed and downwards.
- *Avoidance: moving away from the aggressor.
- *Escape: moving away at a high speed, while the body posture is hunched.

3.3.2. The laying period

The laying period was considered to start on the day the first hens in a flock came into lay. In order to determine rank order in the weeks before and after that day, recording of social behaviour was continued until each hen in the flock had come into lay.

A common method to find out if a hen is prepared to lay is palpation (Sykes, 1955; Draper and Lake, 1967). However, in this study most hens were very restless and showed escape behaviour in the hours before they had to lay their first egg. Because of the conspicuousness of this behaviour only video-pictures were used to determine the day of first oviposition.

To identify eggs laid by individual hens video-pictures were used mainly. However, after the 7 week lasting filming period for some, usually subordinate hens, nest-site choice had still to be determined. Therefore another method (Riddle, 1908; Hughes, 1977) was used. Individual hens were fed gelatine capsules filled with a dye (Sudan Black B and Sudan IV (=red)),

which is attached to the yolk-lipid of the follicles. A single dose i.e. one capsule, colours all rapid growing follicles (see section 2.4) present in the ovary at that moment. The dye is present for the first time in the yolk of an egg about 2 or 3 days after its administration. The coloured ring is then situated on the outside of the yolk. Rings in subsequent eggs are nearer to the centre of the yolk each day. Finally, the last and smallest ring appears in the centre of the yolk. The number of days a coloured ring will be visible depends upon the number of rapid growing follicles that were present at the moment of administration, but usually 7-10 eggs were coloured.

A schedule of capsule feeding was maintained for a number of hens belonging to the same flock. For example on day 1 hen A was given a Sudan Black capsule, hen B a Sudan IV, hen C a mixture of both and hen D was given a Sudan IV capsule on day 2, which was followed by a Sudan Black on day 3. As a result each of the 4 hens produced its own and specific colour pattern in the yolk. In order to detect a dye, eggs were hard-boiled for about 12 minutes and then cooled off quickly. Finally the yolks were cut across with a sharp knife and the coloured rings were visible.

Since we were interested in the influence of the cock's presence on the hen's nest-site selection cornering-sequences performed by the cock were registered. When doing this the cock assumed a half crouched posture while lowering the breast to the ground. The legs are lifted alternately while stamping or the legs are making scratching movements. Sometimes ground-scratching movements are made with the head. This display is usually accompanied by "corner-calls", soft repeated rhythmically sounds or by "tidbitting calls", a higher more clucking-like noise. These vocalisations have an attracting influence on the hens (Kruijt, 1964). The cock's behaviour was only described in qualitative terms.

In order to compare the pre-laying behaviour between hens belonging to different groups the frequency and duration of each behavioural element were recorded. During these sessions the duration of a particular act was defined to be the amount of time elapsed between its onset and end without being interrupted by another element. The following behavioural elements were registered:

*Laying call or "gakel": calling with the beak well open while the abdomen

is rhythmically moved up and down; one call consists of a long introducing element followed by one or more short elements divided by short intervals (Wood-Gush and Gilbert, 1969b; Schenk et al., 1984).

*Nest-box-examinations: nest-box inspections and glancing at the nest-box (see above).

*Nest-box entry: a nest-box is entered fully, while the hen stays in a standing position.

*Nest-construction: sitting in a nest-box, in the litter or on the wire, while manipulating the litter with the beak, rotating the body and scraping with the legs.

*Nest-sitting: sitting quietly on the nest, in the litter or on the wire, only occasionally changing position.

In the same study also other behavioural elements were recorded. Some of them may be indicative of frustration or conflict:

*Stereotyped pacing: walking up and down the pen in a restless way, with steps higher than normal.

*Orientation away from the flock: jumping or flying up in attempting to escape from the pen.

*Preening: the feathers and skin are stroked and pecked at by the beak.

*Eating: pecking at food particles from the food-trough.

*Drinking: taking up water from the drinker.

Finally for a number of hens the time and site of oviposition were recorded.

CHAPTER 4

EGG-LAYING BEHAVIOUR AND NEST-SITE SELECTION OF DOMESTIC HENS
KEPT IN SMALL FLOOR-PENS

B.Rietveld-Piepers, H.J. Blokhuis and P.R.Wiepkema

Published in *Appl.Anim.Behav.Sci.*,14: 75-88

4.1. Introduction

One of the problems arising when hens are kept in floor-pens is the failure to lay in nest-boxes provided. This has considerable economic implications, such as loss of eggs, dirty eggs and time-consuming egg-collection. A knowledge of the factors which cause this floor-laying is important from both practical and theoretical viewpoints. Most research carried out on this subject has concentrated on which characteristics of nests may affect the hen's choice of a nest (Wood-Gush and Murphy, 1970; Hurnik et al., 1973 a,b; Dorminey, 1974; Kite et al., 1980; Appleby et al., 1983b). However, the aim of this study is to describe the development of the egg-laying behaviour of individuals kept in small flocks in order to obtain more insight into the behavioural aspects of floor-laying. Relevant questions are, for instance, do hens examine the nest-boxes before they come into lay? Also, once a hen has chosen a nest-site for oviposition, will she use the same site on subsequent oviposition days or, as has been mentioned by Duncan et al. (1978) in feral living hens, will she choose different sites for successive clutches?

Another question this paper is concerned with is which characteristics of hens are associated with laying in nest-boxes or using the floor as a nesting site. Because rank is associated with priorities in the use of facilities for which hens compete (McBride, 1970; Banks et al., 1979), social dominance might be one of the factors affecting the hen's choice of a nest. Moreover, Lee et al. (1982) reported an association between social rank and age at first oviposition in small flocks of hens; high-ranking birds came into lay before low-ranking birds. Thus subordinates searching for a suitable nesting site might find preferred nest-boxes occupied and, as already mentioned in broiler parents by Perry (1977), dominant birds will defend nest-sites against subordinates. From this a relationship might be expected between rank and floor-laying.

A final social factor studied here is the presence of the cock. Similar to their wild ancestors, penned domestic cocks perform a behavioural display called cornering, which tends to entice the hens towards the cock. The cock assumes a half-crouched posture while stamping with its feet and giving tidbitting calls (Kruijt, 1964; McBride et al., 1969; Wood-Gush, 1971).

The present paper describes the development of the egg-laying behaviour of individual hens and their nest-site choice. Special interest is put on the question of whether social dominance and the presence of a cock affect the hen's nest-site choice.

4.2. Materials and methods

This study was carried out from December 1981 until March 1983. Seven flocks (15 - 21 hens per flock) of White Leghorn hens, reared in cages, were housed in small floor-pens (2x2 m²; figure 3.1.). Two types of nest-boxes were used; 1) individual nests provided with wood-shavings (=litter nests) and 2) individual nests provided with a wire floor where eggs roll out of the box into a collection channel (=roll-away nests; figure 3.2).

One of the flocks was made up of an experimental line from the Centre and was placed at an age of 18 weeks in a pen with 6 litter-boxes, 3 on each side of the pen (about 5 cm above the floor; Flock 1). The other 6 were all derived from commercial strains (Hisex or Shaver 288) and were housed in floor-pens at an age of 16 weeks. Two of them were provided with 6 litter-boxes along one side of the pen (Flocks 2 and 3). In each of the remaining four pens 6 roll-away boxes were placed (Flocks 4, 5, 6 and 7). In 4 of the 7 flocks nest-boxes were opened permanently on the day the birds were placed in the pen, while in the other 3 flocks boxes were opened on the day the first egg in the flock appeared (see also table 4.1). Further housing and management conditions have been described in chapter 3.

Observations

Behavioural observations started in December 1981 for flock 1, in June 1982 for flock 4, in September 1982 for flocks 2, 3, 5 and 6 and in March 1983 for flock 7. Flock 1 was observed for 10 weeks, whereas observations in flocks 2-7 stopped on the day all hens had come into lay i.e. after about 7 weeks.

Thirty-seven hens, randomly chosen from the seven flocks, were observed regularly. In the weeks before these hens came into lay their behaviour was filmed according to a sampling schedule (i.e. 1 h daily, except for week-

Table 4.1. Flock composition and pen-arrangements of the 7 groups under study.

Flock	Strain	Number of hens	Males	Age at arrival (weeks)	Age at opening nests(weeks)	Properties of nests
1	Exp. line	15	1	18	18	Litter
2	Shaver 288	19	-	16	20	Litter
3	Shaver 288	21	-	16	16	Litter
4	Hisex	18	1	16	20	Roll-away
5	Shaver 288	20	-	16	16	Roll-away
6	Shaver 288	19	-	16	20	Roll-away
7	Shaver 288	15	-	16	16	Roll-away

ends) somewhere between 8.30 and 16.30. The frequency and duration of nest-examinations and entries, which have been defined before were recorded. Nest-examinations (or entries) were scored as successive if they were separated by an, arbitrary chosen, interval of more than 30 seconds. For the same 37 hens a global description was made of the behaviour preceding the first oviposition. Age at first egg (days) was determined for each hen in all flocks.

For each hen in flock 1 nest-box choice was recorded on subsequent oviposition days during the first two months of the laying period in order to study perseverance in nest-choice. These data were also used to find out if hens were consistent in laying on the floor or in a nest-box. Individual nest-choices were also recorded from hens belonging to the other 6 flocks by using video-pictures. After the seven week long observation period recording of nest-choice was continued by administration of fat dyes which coloured the yolk. This method is described in more detail in chapter 3.

The relationship between dominance and nest-choice was investigated in all flocks. Social rank was based on dyadic agonistic encounters recorded from the same video-pictures as those used for the description of the development of the egg-laying behaviour. During this hour the following behavioural elements which have been defined before were recorded:

*Aggression: pecking;threatening;leaping ; chasing;

*Submission: freezing; avoidance; escape .

Moreover, the identity of the initiator and recipient were registered. The cock's behaviour in flocks 1 and 4 was described in qualitative terms.

In flock 1 eggs were removed shortly after they had been laid. In the other flocks eggs were collected once a day. During the first 10 (flock 1) or 6 weeks (flocks 2-7) of the laying period the total number of floor-and nest-eggs (and the number of the nest-boxes) was recorded. This could provide some information about which factors might influence the number of floor-eggs.

Statistics

To study the relationship between social status and nest-site selection a Spearman's rank correlation test was applied (Siegel, 1956).

4.3. Results

4.3.1. The development of egg-laying behaviour

To describe the development of egg-laying behaviour the following procedure was used. For all 37 observed hens the day the first egg was laid was referred to as day 0 (figure 4.1). On that day and on the days prior to day 0 the mean frequency of nest-examinations and entries per hour per hen was calculated. The number of hens contributing to the mean of a particular day varied between 9 and 37, firstly because not every hen was observed on each day (week-ends), secondly because in 3 out of the 7 pens the nests had been closed during the weeks before the first egg in the flocks appeared and thirdly because not all hens came into lay simultaneously. Figure 4.1 presents the mean frequency of nest-examinations per day (day -13 to day 0) and per week (week -5, -4 and -3). Nest-boxes were frequently examined, but they were almost never entered until the day the first egg was laid. During the whole period no nesting behaviour e.g. rotating or scraping in a box or in the litter was seen.

Sometimes nest-boxes were entered to rest or to preen. However, using boxes for this purpose was very uncommon and restricted to a few

individuals.

In the hours just before the first egg was laid, most hens were restless while showing stereotyped escape behaviour such as pacing and orientation away from the flock, expressed as attempts to escape out of the pen. Because of the conspicuousness of this behaviour, the assessment of the day a hen was to come into lay was easy.

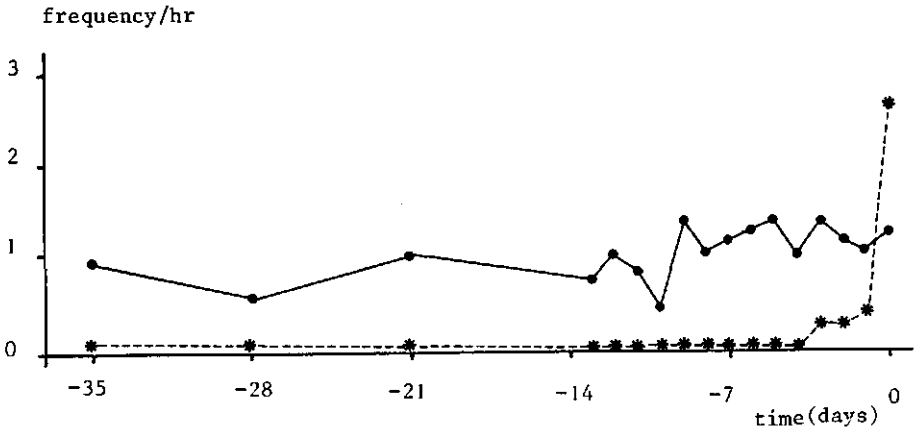


Figure 4.1. The mean frequency of nest-box examinations (●—●) and nest-box entries (*---*) in the weeks before laying. For all hens the day of first oviposition is referred to as day 0. For further explanation see text.

4.3.2. Nest-site choice

To measure the perseverance with which the hens from flock 1 chose the same nest-box on subsequent days, the following parameter (perseverance index $p(i)$) was used:

$$p(i) = \frac{\text{The number of the same choices on subsequent oviposition days}}{\text{Total number of subsequent choices}}$$

Subsequent choices were judged as equal when a hen had chosen the same nest-box for subsequent ovipositions. Because perseverance in nest-choice

is expected to be most obvious within clutches, transitions between clutches and from Friday to Monday were not taken into account. A hen might use the same nest but not necessarily on subsequent days. Therefore another measure, a frequency index $f(i)$, was used to describe consistency in nest-box choice:

$$f(i) = \frac{\text{Highest number eggs laid in the same nest}}{\text{Total number of nest-choices}}$$

Then each hen was characterised according to the two parameters $p(i)$ and $f(i)$. Hens whose nest-site choice had been recorded in less than 10 days were excluded from analysis.

If both measures were equal to or larger than 0.7 a hen was judged to persevere in nest-choice. Figure 4.2 shows that only one of the 13 hens (number 10) was consistent in her choice within clutches: she nearly always chose the same box on subsequent days but started another egg-laying

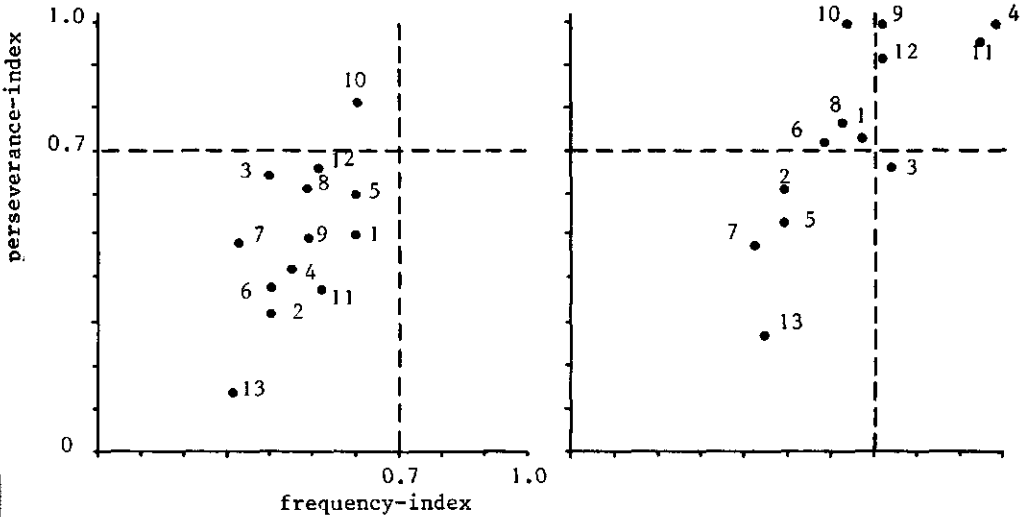


Figure 4.2. Description of the hens according to the parameters used to represent consistency in nest-box choice. Choices were judged as equal if a hen had chosen the same nest-box (left) or if a hen had chosen a box on the same side of the pen (right).

sequence in another nest-box.

The other hens frequently changed nest-boxes (figure 4.2), which is a rather unexpected result. It could be that nest-boxes along one side of the pen were too close to each other. Therefore it was decided to study consistency in nest-use on each side of the pen (boxes on one side of the pen were separated from those on the other side by 1.70 m). Each hen was once more characterised according to the two parameters, but the three nest-boxes along one side of the pen were regarded as one nest. This analysis revealed that 4 of the 13 hens nearly always used the same side of the pen ($p(i) > 0.7$; $f(i) > 0.7$). Four birds did choose the same side of the pen on subsequent days and started another egg-laying sequence on the other side of the pen ($p(i) > 0.7$; $f(i) < 0.7$). One hen used nest-boxes on one side of the pen more frequently although not always on subsequent oviposition days ($p(i) < 0.7$; $f(i) > 0.7$). The remaining four hens did not show any consistency in their nest-choice behaviour (figure 4.2).

Consistency in using the floor or a nest-box as a nesting site was examined by using the following parameter:

$$f(i)_{\text{nest}} = \frac{\text{Total number of eggs laid in a nest-box}}{\text{Total number of eggs laid}}$$

and

$$f(i)_{\text{floor}} = 1 - f(i)_{\text{nest}}.$$

For 67 hens $f(i)_{\text{nest}}$ and $f(i)_{\text{floor}}$ were calculated. Hens scoring higher than 0.7 on one of the two measures were taken together and from these values the mean (\pm S.D.) was calculated. This analysis revealed that 52 hens were consistent in using a nest-box as a nesting site, 13 hens always laid on the floor, whereas only 2 sometimes laid on the floor as well as in a nest-box (table 4.2).

Table 4.2. Consistency in nest-use represented by a frequency-index for laying on the floor or in a nest. See text for further explanation.

Number of hens	f(i)nest	f(i)floor
52	0.98 \pm 0.03	0.02 \pm 0.03
13	0.00	1.00
2	0.54 \pm 0.16	0.46 \pm 0.16

4.3.2.1. Social factors and nest-site choice

Dominance

In order to study stability in rank-order, ranks were determined in flocks 1-7 during the period before (about 4 weeks) and after (about 3 weeks) the first egg in a flock was laid. Because one hen in flock 1 had already come into lay, dominance ranks in this flock were determined during the period before the second hen came into lay (about 10 days) and the four weeks thereafter. Within a pair of hens the one who won a fight was considered to be the dominant hen. If aggressive acts occurred equally in both directions, no dominant or subordinate hen was distinguished. However, if one hen exceeded the other in aggressive acts she was considered dominant.

The social status of each hen was represented by a social rank index $S(i) = 0.5(D - S + N + 1)$ (Lee et al., 1982), where D is the number of hens dominated by a hen, S is the number of hens dominating a hen and N is the total number of hens in the flock. Social rank indices estimated for each hen during the 2 periods showed a strong correlation (Spearman's $r(s) > 0.7$; $p < 1\%$) in all flocks. These results correspond with those reported by Lee et al. (1982) and Rushen (1982); they also found a strong correlation between rank-order before and after sexual development.

In a flock with N individuals and a linear hierarchy social rank indices will have a mean of $(N+1)/2$ and a variance of $(N+1)(N-1)/12$ (Lee et al., 1982). Because of triads and undetermined relationships, social rank indices will show reduced variances and will aggregate near the mean, i.e.

a large number of hens will have the same index. In that case this measure will not have the descriptive value necessary to study the relationship between social status and nest-site choice. Therefore in each flock the theoretical variance of the social rank-indices in the case of a linear hierarchy and the observed variances were calculated. If the equation $\text{variance observed}/\text{variance theoretical}=1$, then a linear hierarchy is reached. The results of this procedure are presented in table 4.3. Social rank based on data of the second period (after coming into lay) appeared to approach linearity more than rank based on the first period (before laying). Therefore social rank indices estimated during the second period were used. Because flocks 2, 4 and 6 showed reduced variances as compared with the other flocks ($O/T < 0.35$) they were excluded from analysis.

In three of the remaining 4 flocks, i.e. in flock 1, 5 and 7, a significant relationship was found between age at first egg and social status;

Table 4.3. Observed and theoretical variances of social rank indices before and after the first egg in a flock appeared. The extent to which the hierarchy in a flock reaches linearity is expressed by O/T.

Flock	Theor.var.	Obs. var.	O/T	Obs. var.	O/T
		Period 1		Period 2	
1	18.6	10.9	0.58	12.3	0.66
2	30.0	7.8	0.26	9.0	0.30
3	36.6	5.3	0.14	13.7	0.37
4	26.9	5.3	0.19	9.6	0.35
5	33.2	8.4	0.25	12.3	0.37
6	30.0	8.4	0.28	6.3	0.21
7	18.6	7.8	0.42	12.3	0.66

high-ranking hens came into lay before low-ranking ones (Spearman's $r(s) > 0.71$; $p < 0.01$), so dominant hens had first nest-choice and could occupy one or two adjacent preferred nest-boxes. In flock 3 no relationship was found between age at first egg and social status.

Data from flock 1 were used to investigate the relationship between

consistency in nest-box choice and dominance. Sometimes agonistic encounters took place near the nest-boxes and now and then hens were seen to peck at other birds while sitting on the nest. However, this did not express itself in a relationship between dominance and nest-use ($r(s)$ between $p(i)$ and $s(i) = 0.18$, N.S.; $r(s)$ between $f(i)$ and $s(i) = 0.10$, N.S.).

Data collected from flocks 1, 3, 5 and 7 were used to find out if floor-laying is associated with social status. In each of these flocks, 3 dominance classes were distinguished; low-, middle- and high-ranking hens. Sixty-one hens from these flocks had been identified as nest- or floor-layers. Each of these hens was classified according to social status and nest-site choice. Table 4.4 shows that no association was found between rank and floor-laying; floor-layers were about equally represented among the 3 dominance classes ($\chi^2 = 1.4$; $df=2$; N.S.).

Table 4.4. The number of low-, middle- and high-ranking hens that always used a nest or laid on the floor.

Nest-choice	Social rank			Total
	Low	Middle	High	
Nest	10	21	16	47
Floor	3	4	7	14
Total	13	25	23	61

The cock

Both cocks in flocks 1 and 4 were frequently seen enticing hens. They performed a complete cornering sequence in front of the nest-boxes, while lowering their breast on the floor, scratching with their feet in the litter and giving tidbitting calls. As a result of this display a number of hens always approached.

The cock appeared to have an important role in nest-site choice, as was demonstrated by some short experiments. These were carried out in order to find out if the hens could be induced laying on the floor. All 6 nest-boxes

were closed at 17.00 p.m. Because 3 (corner) nests were mostly favoured in this flock, the next morning at 8.30 a.m. only the 3 boxes that were used less frequently were opened. A few minutes later the cock started cornering and he also entered the nest-boxes. That day all eggs were laid in the 3 boxes left open.

Closing of nest-boxes was continued for several days. Once 4 of the 6 boxes were closed, but no floor-eggs were laid. If boxes were opened too late in the morning, the cock started enticing hens into the corner of the pen. The cock always interfered if hens were fighting for food and he was also observed to threaten quarreling birds near the boxes.

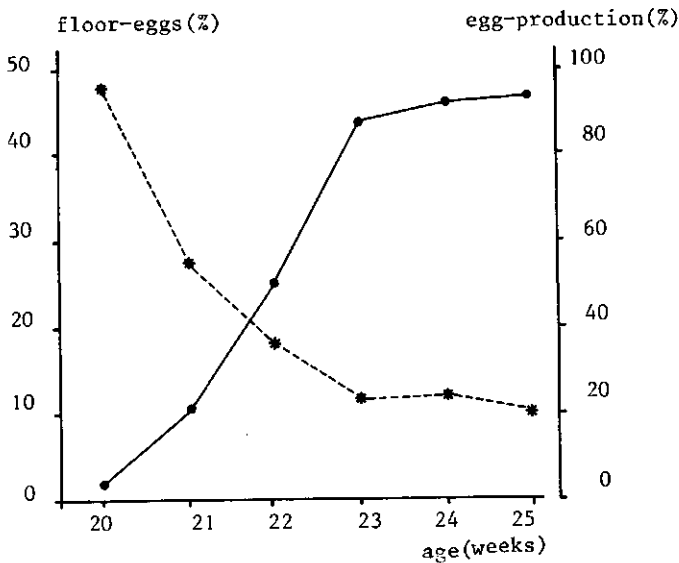


Figure 4.3. Mean percentage of floor-eggs (*---*) and the total egg-production (●—●) during the first six weeks of the laying period in all 7 flocks.

4.3.3. Floor-eggs

For all flocks the total number of floor-and nest-eggs were taken together. Because most nest-users would only lay their first egg on the floor, most floor-eggs were found at the start of the egg-laying period. In the course of the laying period the percentage of floor-eggs decreased while the total egg-production increased (figure 4.3). Floor-eggs were laid on the wire as well as on the litter. Some floor-layers would pace about the pen while now and then peering into the nest-boxes. They almost never entered them or sat in them. These hens appeared to loose their egg. Other floor-layers, however, apparently preferred a particular site in the pen; some of them always laid near the feeder, while other hens always used the same corner of the pen.

Once a nest-user was seen to lay a floor-egg. She left the nest-box after she had spent some time in it and joined in with dustbathing pen-mates, while laying the egg on the floor. Obviously two behavioural systems were simultaneously activated; the egg-laying and the dust-bathing behaviour.

To get some information about which factors might influence the number of floor-eggs, the flocks were divided into four groups according to the properties of the nest-boxes and the presence of a cock. Table 4.5 shows

Table 4.5. Association of the presence of a cock and the properties of the nest-boxes with floor-eggs as a percentage of the total production.

Properties of the nests	Cock present		Cock absent	
	Flock number	%	Flock number	%
Litter	1	4.4	2	4.1
			3	8.1
Roll-away	4	8.4	5	57.0
			6	20.3
			7	36.2

the percentage of floor-eggs recorded for each flock during the first 6 weeks of the laying period. These data indicate that more floor-eggs were found in flocks with roll-away nests than in flocks with litter nests. There is also some indication that the presence of a cock reduced the number of floor-eggs in the flock provided with roll-away boxes.

4.4. Discussion

The present results revealed that laying hens frequently examined nest-boxes in the weeks before they came into lay; however, these boxes were almost never entered. A few days before or in the hours preceding the first oviposition, nest-entries suddenly occurred at a much higher rate. Because nesting in feral fowl is characterised by secrecy and concealment (McBride et al., 1969), it may be that our circumstances inhibited early nest-entries. Such an explanation is supported by the fact that almost all hens tried to escape out of the pen on the day they laid their first egg. Maybe entries would occur more frequently if nests were placed in an adjacent compartment where no food and water is supplied and where human activity is kept to a minimum.

However, the sudden increase in nest-entries can also be explained from physiological knowledge about nesting behaviour in hens. Perhaps nest-examinations started at an age of 16 weeks under the influence of the developing ovaria. The increase in the frequency of entries might have been induced by the hormone progesterone shortly after the first ovulation by the post-ovulatory follicle (Wood-Gush and Gilbert, 1973, 1975).

Only one of the 13 hens in flock 1 was consistent in nest-box use within clutches. However, 8 of them always used the same side of the pen within clutches, and 4 of these always used the same side of the pen. These results suggest that the hens did not discriminate between the 3 nest-boxes along one side, but they chose to nest either on the left or on the right side of the pen. Probably the 3 nest-boxes were placed too close to each other and they may have been regarded as one nest. This behaviour is well understood if the nest-site selection of feral fowl is taken into consideration; here nests are well separated (McBride, 1970). Conservatism in nest-box choice between and within clutches was much greater in domestic

fowl (Brown Leghorns) kept in floor-pens provided with trapnests (Wood-Gush, 1954).

Using different sides of the pen for successive egg-laying sequences resembles the results reported by Duncan et al. (1978) for feral living hens. The authors stated that choosing different sites for successive clutches might function as an anti-predator device.

The remaining 4 hens did not appear to prefer any nest-site in particular, which may have been due to the fact that the eggs were removed shortly after they had been laid. Comparable results were reported by Duncan et al. (1978) in feral fowl; hens abandoned nest-sites because they were in some way unsuitable (e.g. too wet).

The choice to use a nest-box was only made once, which enabled us to distinguish "nest-layers" and "floor-layers". No relationship was detected between nest-box use and social status nor between using the floor or a nest-box as a nesting site and social status. Although agonistic interactions sometimes took place in front of the nest-boxes, they seldom occurred in a box. Most of the time nest-boxes were used simultaneously by more than one hen without overt aggression being displayed. Sitting in a box with other hens may have precluded eye-contact necessary to elicit an aggressive response by the dominant animal (McBride et al., 1963). Banks et al. (1979) noted that only resources such as food have been in short supply during the evolution of chickens; nest-sites have never been an object of competition. Therefore floor-laying caused by competition would not be expected. Perry (1977) stated that in a flock of broiler parents dominant birds removed subordinates from the nest-boxes. These results and ours are contradictory. However, if these broilers were kept in large flocks, unlike the hens in our study (maximum 21 hens), individual recognition between all flock members is very unlikely. The possibility that the two fighting birds were strangers to each other is not excluded. Perhaps the "resident" bird may have chased away the intruder.

More floor-eggs (floor-layers) were found in flocks provided with roll-away boxes than in flocks with litter boxes. Probably one or more of the properties inherent to a litter nest are preferred to those of a roll-away nest (see also chapter 6: discussion).

Another factor apparently determining which site a hen selected was the presence of a cock. If a cock was placed in a pen with roll-away boxes,

fewer floor-eggs were laid than in a pen with the same boxes without a cock. Apparently his behavioural display could elicit nest-entry and sitting in hens that possessed the innate motivation to nest despite the fact that the external stimuli are not optimal. In the pens provided with litter boxes no differences were found with respect to the number of floor-eggs between flocks with or without a cock. This might indicate that the effect of the display of the cock overrules the effect of the negative properties of the environment on the nesting behaviour of these hens. However, the difference in nest-use between flock 4 (with a cock) and flocks 5, 6 and 7 may also be due to a difference in stock.

In conclusion, nest-examinations in the weeks before the hens came into lay may be homologous to nest-searching and nest-building behaviour behaviour as described in other species of birds (Emlen, 1955; Watson and Jenkins, 1964; Watson, 1972). Therefore it is postulated that nest-examinations may serve the selection of a suitable nesting site.

Individual hens showed a different nest-box choice pattern; they probably involved different factors in their choice. Therefore nest-site selection in penned hens seems to be a rather complicated process and more research on this subject might be worthwhile.

It is also not clear which factors are involved in the process of nest-site selection that leads to either floor-or nest-layers. McGibbon (1976) provided evidence for the expression of a genetic basis for differences between floor-laying and non-floor-laying hens (Cornell Controls and Regional Reds). Perhaps the difference between hens in this study may also be genetically determined.

4.5. Conclusions

- * In the weeks before laying nest-boxes were frequently examined, however, entries or nest-building activities did not occur until the day of first oviposition.
- * Hens are consistent in using either the floor or a nest-box for oviposition.
- * Individual hens appear to involve different factors in their nest-site choice.
- * There is no relation between nest-box use and social status nor between using the floor or a nest-box and social status.
- * The cock seems to play an important role in nest-site selection.

CHAPTER 5

NEST-EXAMINATIONS, THEIR BIOLOGICAL SIGNIFICANCE

5.1. Introduction

Most small species of bird build elaborated nests (Collias, 1964; Lack, 1968), whereas larger gallinaceous birds only use a shallow pit in the ground, which is lined with some feathers ((Watson and Jenkins, 1964; Wood and Brotherson, 1981). As mentioned before (chapter 2) the nests of feral domestic fowl also consist of a shallow scrape in the ground. Nest-sites chosen showed great variety. However, they were all very well hidden (Hanson, 1970; Duncan et al., 1978; Dumke and Pils, 1979; Wood and Brotherson, 1981), which suggests that the selection of the site itself is an important element in the nesting behaviour.

In most species of bird the days of completing the nest and of first oviposition are separated by an interval of several days (Davis, 1955). In gallinaceous birds, like the red grouse and the ptarmigan, nesting behaviour and a primitive form of nest-construction occurs up to a fortnight before the oviposition of the first egg of the clutch (Watson and Jenkins 1969; Watson, 1972). However, in pullets kept in floor-pens provided with nest-boxes nest-entries and nest-construction (cf. Wood-Gush, 1975) did not occur until the day of the first oviposition (chapter 4). Nevertheless, the final choice of a site may have been made before the start of the laying period. In that case the process of nest-site selection itself is expected to start several weeks before the hens come into lay. During this period the environment may be explored and the information gathered in this way may be finally used for the selection of a suitable site.

Generally spoken animals, particularly those living in a natural habitat, benefit of exploring their environment. They may thereby locate new resource sites (food, water, nest-sites) and can act upon this knowledge later on in life. For example, a free-living hen that has familiarized itself with its environment, will have an advantage over one that has recently migrated into that area. The first mentioned will generally obtain a better nest-site and be better able to exploit available food-sources or places to hide. Thus by exploring the animal gathers information about the environment enabling it to build up an internal model of its world (= a cognitive map; Birke, 1983; Toates, 1983; Walker, 1983). Against this background we may expect naive domestic hens, that have not yet come into lay, to start exploring immediately after they enter their new environment, not only in

order to locate food and water, but also to locate potential nesting-sites.

Scant information has been reported on the process of nest-site selection in the weeks before laying in both red jungle fowl or in feral or penned domestic fowl. Our previous results (chapter 4), however, revealed that 4-6 weeks before the start of the laying period nest-boxes were frequently examined. In the past this type of behaviour has been supposed to represent an intention movement to enter a nest (see section 2.5.). In the present study, however, it is suggested that nest-examinations are homologous to nest-searching and nest-building behaviour, as described in other species of bird. In other words, examining nests may be regarded as a form of exploration and may have an information supplying function. This information might be used for the selection of a nest. Therefore each change in the environment, like altering the position of different nests, is expected to elicit an increase in the exploration response i.e. in the duration of examinations as compared to a control group.

In the previous chapter only one type of nest-examination (= putting the head into a nest-box) was distinguished. However, as has been mentioned by Wood-Gush and Gentle (1978), hens do not only perform this type of examination, which will be referred to as nest-inspection, but they also glance at the nests (= peering into a nest-box from a distance). Perhaps both behavioural elements share the same function and may show the same developmental pattern. Furthermore, every change in the environment is supposed to increase the glance duration as compared to a control group in the weeks before laying.

A similar reasoning might hold for nest-examinations performed in the hours preceding oviposition and therefore changing the nest-box order is also expected to increase the examination rate during the egg-laying period.

Moreover, if the final nest-choice is made before the day of the first oviposition, a relation might be expected between the examination pattern in the weeks before laying and later nest-preference. In other words, the distribution of the total amount of attention over the four nests in the weeks before laying may be correlated to nest-preference during the laying period.

This chapter presents the results of an experiment designed to investigate the impact of rearranging the sites of four different nests on the

nest-inspection and glance duration in the weeks before and during the egg-laying period. Moreover, it describes and compares the development of glances and inspections in the weeks before laying. Thirdly, in the first and in a second experiment the examination pattern in the weeks before laying and its relationship with later nest-preference is studied.

5.2. Experiment 1

5.2.1. Materials and methods

Experiment 1 consisted of two trials. During each trial eight 16 week-old white laying hens (Shaver 288) were housed in 4 round floor-pens. Due to genetical and environmental factors (e.g. light, social factors) not all individuals in flocks of hens are in the same developmental stage. Mutual influences attributed to differences in developmental stages can be excluded by housing one hen per pen. However, to prevent the effect of isolation, it was decided to place two hens with similar body weight and comb-measures in one pen.

The floor of the pen (1.5 m ϕ ; figure 5.1) was covered with wood-shavings; its walls had solid, untransparent sides to a height of about 1 meter. Each pen was provided with one food-and water-tray and with four different nest-boxes; nest-floors were covered with astroturf (nest 1), wood-shavings (nest 2), buckwheat husks (nest 3) or a wire basket (nest 4). Eggs laid in nest 1 and 4 rolled out of the box into a collection channel. Front entrances of the nests could be closed.

The experiment started with a one-day habituation period during which nest-boxes were kept closed. In the five weeks following this day the hens were exposed to an exploration test in the home pen from monday to friday. For this purpose nest-boxes were opened for 1.5 hour per day somewhere between 9.00 am and 15.00 pm (see also under Observations). During the first two weeks the positions of the nests never changed. Subsequently nests in two of the four pens were changed 3-4 times a week according to a random schedule (=experimental group). In the other two pens the nests were always in the same position (=control group).



Figure 5.1. Round floor-pen. For further explanation see text.

Exposing the hens to an exploration test in the home pen was continued during the egg-laying period. In this phase nest-boxes in both groups were not opened until a hen commenced performing nesting behaviour like giving the pre-laying call, orientating away from her pen-mate and pacing up and down the pen. The four nests were closed again after the hen had left the nest. In the experimental group the nests changed place each day according to a random schedule.

Previous studies on nest-site selection suggested that hens tend to avoid nests located near the door (Woods and Laurent, 1958; Hurnik et al., 1973a), while they prefer nest-boxes in corners of the pen (chapter 4). In order to prevent such place preferences:

-the hens were placed in a round pen with untransparent sides, as described

above.

- the food-and watertray displaced regularly along the wall of the pen.
- the hens were taken care of from above and from all "sides" of the pen.

However, since the top of the pen was only covered with a wire netting, the hens could use spatial cues to orientate themselves visually, a phenomenon that has also been described in the rat (Morris, 1981; Olton, 1982).

The four pens were placed in a separate area of the same hen-house as described in chapter 3. Since that particular area of the hen-house was only provided with 5 lighting tubes, lightintensity in each pen was not the same. Therefore two blocks were distinguished, a left and a right one (figure 5.2). The two treatments were allotted to both blocks as shown in figure 5.2a (trial 1) and 5.2b (trial 2). Nest-boxes in each of the four control pens were placed in a different order.

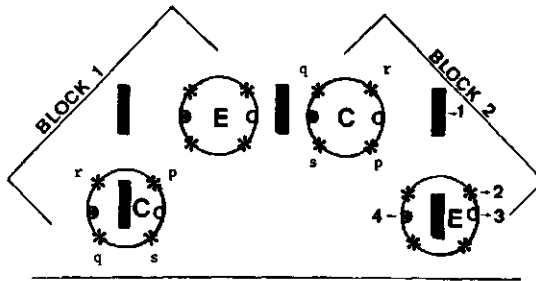


figure 5.2a

C= control pen
E= experimental pen

- 1= lighting tube
- 2= nest-boxes
- 3= water-tray
- 4= food-tray

nest-box p= astroturf
nest-box q= wood-shavings
nest-box r= buckwheat husks
nest-box s= wire basket

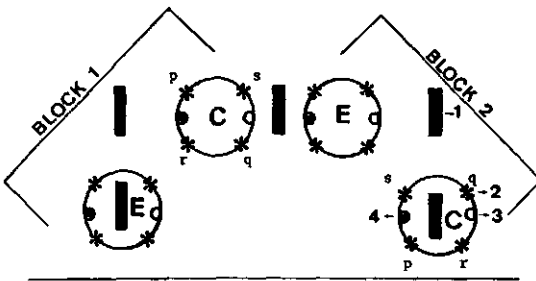


figure 5.2b

Figure 5.2. Arrangement of nest-boxes in the floor-pens and of floor-pens in the hen-house during trial 1 (figure 5.2a) and trial 2 (figure 5.2b).

Observations

Weeks before laying

For identification purposes each hen was marked with a felt-pen on her back on the day of arrival. Behavioural observations started after a one-day habituation period. Each pen was observed daily during 1.5 hr between 9.00 am. and 15.00 pm. according to a sampling schedule that prevented biasing to particular periods of the day. For each hen the following elements were registered:

- *the duration of
 - glances
 - inspections
- *the type of nest the behaviour was directed to.

The laying period

It was attempted to record each hen's pre-laying behaviour preceding about 8 ovipositions during the first 3 weeks of laying. Therefore we were forced to stop the observations as described above as soon as the first hens had come into lay. No observations were made if two hens from the same pen were laying simultaneously or if their pre-laying behaviour was overlapping to exclude the effect of mutual influences. In that case the nests were opened if the hens were prepared to lay and closed again shortly after they had left the nest.

If one of the hens in the experimental group laid several hours later than her pen-mate, the four nests once more changed place. Therefore the nest-box order in the experimental groups was sometimes altered twice a day.

During each egg-laying session the following elements were scored:

- *the duration of:
 - glances
 - inspections
 - entries
 - nest-construction / rotation
 - nest-sitting

*)the type of nest the behaviour was directed to.

For each hen the time of nest-opening, of oviposition and the final chosen nest were recorded.

Statistics

Differences in the median glance and inspection duration between the experimental and control group were tested by means of a Mann-Whitney-U-test. To test linear trends over time and to determine the association between nest-preference before and during the egg-laying period a Spearman rank correlation coefficient was computed. To find out whether individual hens showed a consistent nest-examination pattern over time a Kendall coefficient of concordance was used (Siegel, 1956).

5.2.2. Results

5.2.2.1. Glances and inspections in the weeks before laying

To find out whether behavioural data of the two hens housed in the same pen could be regarded as independent, for separate observation sessions (=1.5 hour) the total time spent in nest-examinations (=glances plus inspections) was calculated per hen. A Kendall rank correlation coefficient was computed between sets of data of two hens from the same pen.

Within 7 of the eight pairs a significant correlation coefficient was present ($N > 10$; $z > 3.0$; $p < 0.01$). Data of hens from the remaining pen tended to correlate with each other ($N > 10$; $z=1,4$; $p=0.08$). Thus, with respect to the time spent in nest-examinations two hens from the same pen did not behave independently from each other. To illustrate this, for two hens from one pen the total time spent in examining the nests is plotted per hen per observation session in figure 5.3. Therefore each pen was considered to be one experimental unit and data of two hens from one pen were averaged.

Since the results of trial 1 and 2 did not show systematic differences, they were combined. Therefore the control and experimental group were both represented by 4 pens.

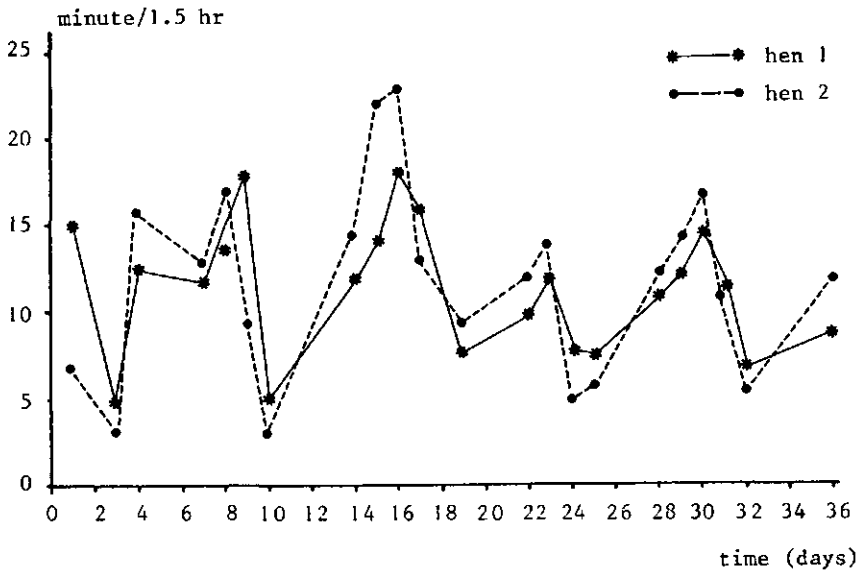


Figure 5.3. The total time spent in nest-box examinations per observation session (1.5 hr). Data stem from two hens housed in the same pen.

The mean durations of glances and inspections were calculated per 1.5 hour per pen by averaging the data of observation sessions in the period before and after the start of the nest rearrangement. The median total time spent in glances and inspections is presented in figure 5.4 for the control and experimental group. No differences were present in the median inspection duration between control and experimental hens during the period before the rearrangement of the nests. However, as a result of changing the position of the nests, experimental hens spent more time in inspecting the nests than control hens ($n_1=n_2=4$; $U=2$; $p=0.05$).

In the weeks before the nest change control hens spent significantly more time in glancing at the nests than did experimental hens ($n_1=n_2=4$; $U=2$; $p=0.05$), whereas no differences were detected between both groups with respect to this measure during the weeks after the change (figure 5.4).

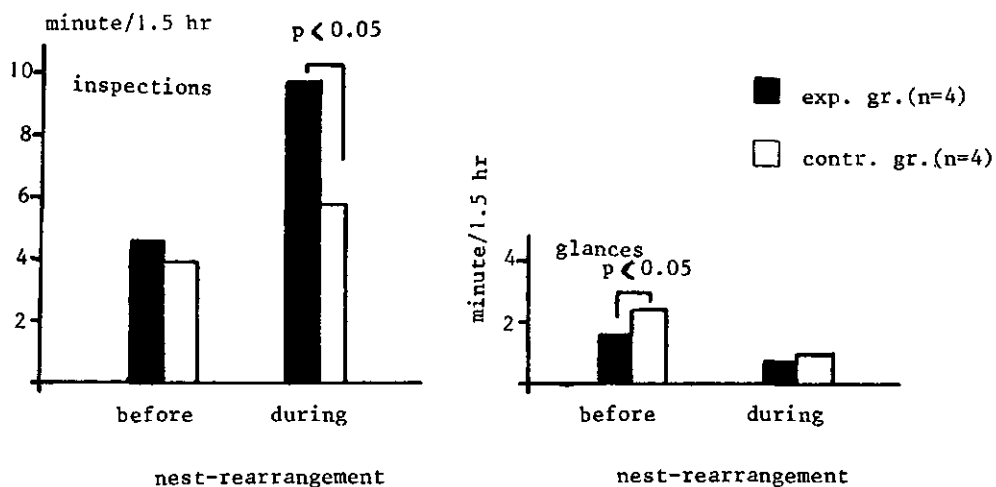


Figure 5.4. The median total duration of inspections (left) and glances (right) for control and experimental hens in the period before and during the rearrangement of nest-boxes.

Since in the experimental group the nest-box order had not been altered every day, there are successive observation sessions (1.5 hour) with a change in nest position (= A-session) and sessions without such a change (=C-session). The nest-examination rate is expected to decline if an A-session is followed by a C-session (=A-C pair) or to increase if a C-session is followed by an A-session (=C-A pair), whereas this measure is expected to be unaffected if two consecutive A-sessions (=A-A pair) or two consecutive C-sessions (=C-C pair) are compared with each other.

The median glance and inspection durations of 6 A-C, 10 C-A and 8 A-A pairs were calculated. There were no C-C pairs. To detect differences between sessions a Sign-test was applied (Siegel, 1956).

Figure 5.5 shows that the median glance duration was not affected by the treatment. However, the median inspection duration showed a significant increase if a C-session was followed by an A-session ($p=0.05$). This measure tended to decrease ($p=0.10$) if an A-session was followed by a C-session. No significant differences in the inspection duration are found if two conse-

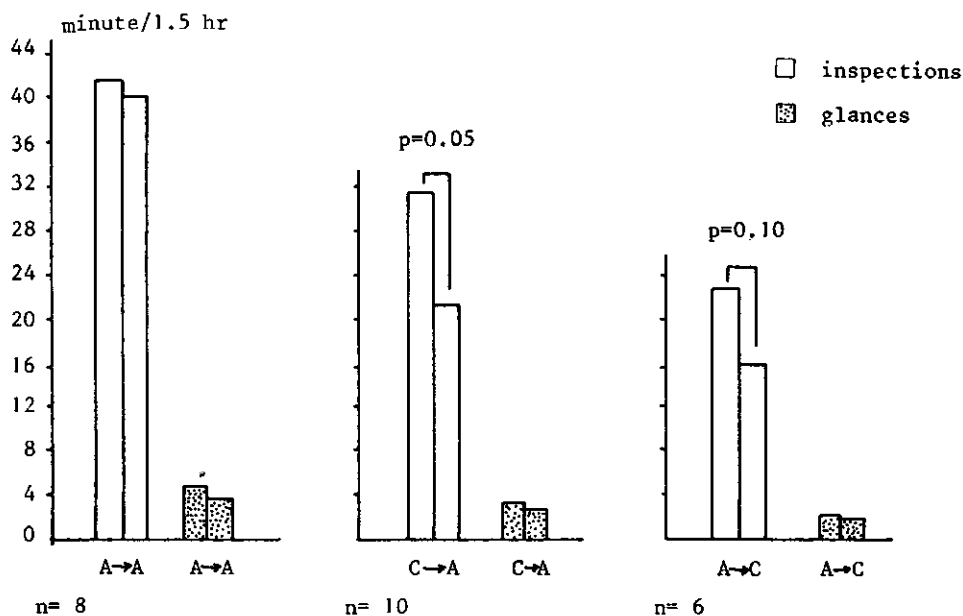


Figure 5.5. The median total duration of glances and inspections for A- A, C- A and A- C sessions. n= number of observation sessions. For further explanation see text.

cutive A-sessions are compared with each other.

From these results it is concluded that rearranging the position of the four nests resulted in an increase in the inspection duration, whereas the glance duration remained unaffected.

To describe and compare the pattern of glances and inspections over time, data were used of the control group. The whole observation period was divided into 6 phases. Each phase contained 3 to 5 observation sessions. Phase 1 to 4 were represented by data of 4 pens. At the end of phase 6 three control hens had started laying and as mentioned above observations in the weeks before laying stopped. Therefore during phase 5 and 6 data are available of 3 pens and 1 pen, resp. Phase 6 was excluded from further analysis.

For each pen the total time spent in glances and inspections was

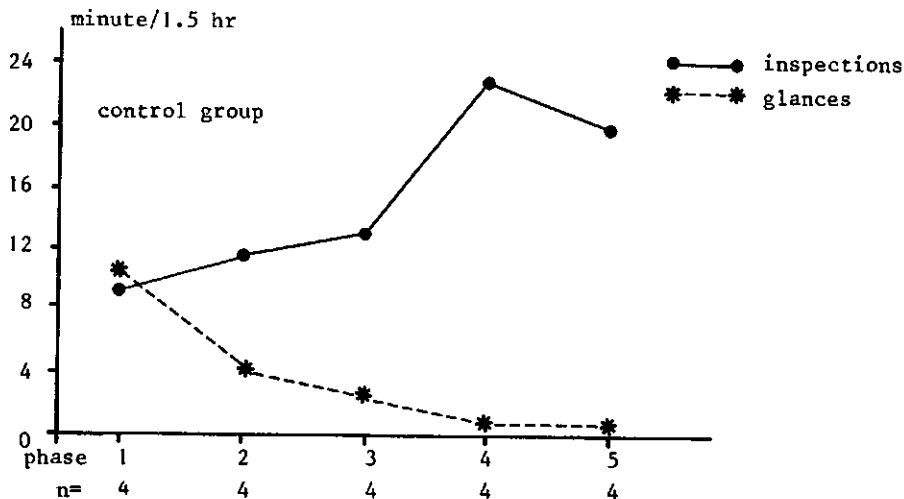


Figure 5.6. The median total duration of glances and inspections for the control in the weeks before laying. n=number of pens.

calculated per phase. Figure 5.6 presents the median duration of glances and inspections per phase. At the start of the experiment, i.e. during phase 1 and 2, both elements were performed for the same amount of time. During phase 3 to 5 nest-inspections were performed significantly more than glances ($n_1=n_2=4$; $U=0$; $p=0.01$; $U=0$; $p=0.01$; $n_1=n_2=3$; $U=0$; $p=0.05$).

With time, the median inspection duration increased (Spearman: $n=5$; $R_s = +0.90$; $p=0.10$), whereas the median glance duration showed a decrease (Spearman, $n=5$; $R_s = -0.90$; $p=0.10$).

5.2.2.2. Glances and inspections in the egg-laying period

Data are available of 8 hens, 4 control and 4 experimental hens. During the first month of the laying period each hen's pre-laying behaviour preceding 7-8 ovipositions (=pre-laying sessions) had been registered. To study the effect of changing the position of the nests over time three phases, each consisting of two or three ovipositions per hen, were distinguished. For a number of hens behaviour preceding the first few ovipositions had not

been filmed. Therefore the first phase contains records scored preceding oviposition number 4 to 9, the second one preceding oviposition number 10 to 14 and the third one preceding number 15 or more.

In contrast to the weeks before laying the hens almost never glanced at the nests. They tended to approach and inspect the nests immediately after they were opened. Therefore the effect of the treatment is only studied on the inspection duration. Since the amount of time spent in pre-laying behaviour did not only vary between but also within individuals, for each hen the durations of inspections scored during the two or three pre-laying sessions per phase were summed. This value was transformed into the duration per 45 minutes of pre-laying behaviour.

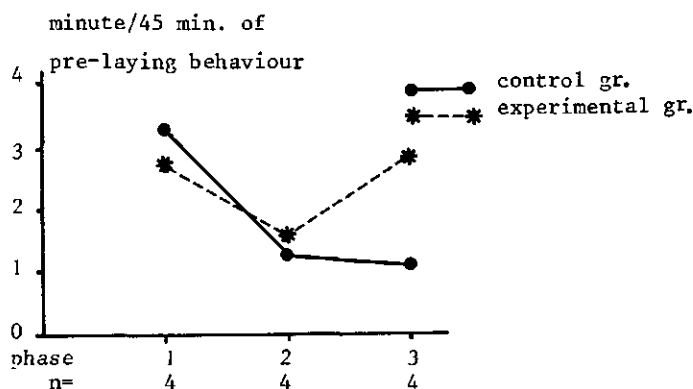


Figure 5.7. The median total duration of inspections for control and experimental hens in the egg-laying period. n= number of hens.

Figure 5.7 shows the median duration of inspections per phase presented for control and experimental hens. Hens from both the control and experimental group spent the same amount of time in inspecting the nests during each of the three phases. It is concluded that, in contrast to the weeks before laying, rearranging the position of the four nests did not affect the total time spent in nest-inspections during the laying period.

5.2.2.3. Early nest-examinations and later nest-preference

In order to study the relation between the nest-examination pattern in the weeks before laying and later nest preference, the observation period in the weeks before laying was divided into six phases as has already been described for the control group (see p.60). Data are available of 8 control hens. Because two of the experimental hens died two weeks before the start of the egg-laying period, this group is represented by 6 hens.

For each hen the examination (=glances plus inspections) duration per nest scored during the 3-5 observation sessions per phase was summed. Subsequently a Kendall coefficient of concordance was calculated per hen. The results are presented in table 5.1.

Table 5.1. The degree of coherence in the duration of examinations per nest among the five phases in the weeks before laying presented for control (c11-c42) and experimental hens (e21-e42) as expressed by the Kendall coefficient of concordance (W). *:p<0.05; **:p<0.01

Hen	Kendall's W	Hen	Kendalls' W
c11	0.36	e21	0.55 *
c12	0.23	e22	0.84 **
c21	0.61 *	e31	0.52 *
c22	0.53 *	e32	0.64 **
c31	0.67 **	e41	0.93 **
c32	0.75 **	e42	0.79 **
c41	0.84 **		
c42	0.74 **		

In six of the 8 control hens and in all experimental hens Kendall's W reached a significant value. In other words, the distribution of the examination duration over the four nests and per hen showed a consistent pattern over time. For each of these hens the relation between early nest-examinations and later nest-preference was studied. For this purpose the mean

duration per 1.5 hour spent in examining each of the four nests was computed by averaging the data scored during all observation sessions in the weeks before laying. These scores were ranked from 1 to 4 i.e. the lowest rank was assigned to the smallest score.

During the first month of the laying period each hen's nest-box-choice had been registered. Sometimes only the first egg was laid on the floor

Table 5.2. Ranknumbers assigned to each of the four nests in the weeks before laying and during the laying period presented for control (c) and experimental (e) hens. The degree of association between both ranks is represented by Spearman's Rs. For further explanation see text.

Weeks before laying					Laying period					Rs
Nest	1	2	3	4	Nest	1	2	3	4	
c21	1	3	4	2	2	4	3	1		+0.60 n.s.
c22	1	3	4	2	2	4	3	1		+0.60 n.s.
c31	2	1	4	3	1	3	4	2		+0.40 n.s.
c32	2	1	4	3	2	4	3	1		-0.40 n.s.
c41	2	1	4	3	1	2	3	4		+0.60 n.s.
c42	3	1	4	2	1	4	3	2		-0.40 n.s.
e21	1	2	4	3	2	4	3	1		0.00 n.s.
e22	1	2	4	3	2	4	3	1		0.00 n.s.
e31	3	1	4	2	1	3	4	2		+0.20 n.s.
e32	3	1	4	2	3	4	2	1		-0.40 n.s.
e41	1	2	4	3	3	4	2	1		-0.60 n.s.
e42	1	2	4	3	1	4	2	3		+0.20 n.s.

nest1= astroturf; nest 2= wood-shavings; nest 3= buckwheat husks; nest 4= wire; ranknumber 4= high, ranknumber 1= low

(see also chapter 4). Therefore the site of the first egg was not taken into account in determining the hen's nest-preference. Most hens appeared to use only one or two nests for oviposition during the whole egg-laying

period. The highest rank number i.e. number 4 was assigned to the nest that had been used for the first series of eggs or clutch, regardless whether all subsequent clutches had been laid in another nest. In that case rank number 3 was assigned to that particular nest. The remaining two or three nests were ranked according to the total amount of attention paid to each nest i.e. by summing the duration of inspections, entries, rotating and sitting scored during the 7-8 pre-laying observation sessions per hen.

The results and those of the ranking procedure in the weeks before laying are presented in table 5.2. Between these two sets of scores a Spearman rank correlation coefficient was computed. In none of the 12 hens a significant correlation coefficient was found (if tested two-tailed against a level of $p=0.10$).

In conclusion, these results do not support the view that the amount of attention paid to each of the four nests during the period considered could predict the final nest-choice.

5.2.3. Discussion

The results revealed that in the weeks before laying the duration of inspections highly increased as a result of altering the position of the four nests as compared with the control group. Likewise, the inspection duration in the experimental group increased if days without such a change were followed by days with a change and, vice versa, decreased if days with a change were followed by days without a change; no differences were found if two consecutive sessions both with a change in the nest-box order were compared with each other. These results support the hypothesis that inspections during the weeks before laying serve the acquisition of information. Obviously the previous position of the different nests in the pen is remembered, which indicates the use of a cognitive spatial map (Tolman, 1948; Toates, 1983; Walker, 1983). An animal appears to be able to code external events and the relationship between these events in its nervous system (Toates, 1983). In other words, it represents its environment in terms of places and their position relative to each other. The mismatch between the stored representation and the current stimulus situation is perceived and elicits an increase in the exploration response. O'Keefe and Nadel (1978)

claimed that the hippocampus is closely associated with this process of "cognitive mapping". The same phenomenon has also been reported in other species of bird and in rats. Marsh tits, for example, appeared to use memory for the location of stored food (Sherry et al., 1981), while rats navigated to specific points in space by learning the spatial relationship between environmental cues (Morris, 1981).

The glance duration remained unaffected by the treatment. Moreover, it was shown that glances and inspections followed a different temporal pattern in the weeks before laying. At the start of the experiment both elements were performed for the same amount of time. Over the five phase observation period the glance duration tended to decrease, whereas the inspection duration showed an increase. These results suggest that both elements do not represent the same type of exploration. Glancing may be regarded as an initial orienting response towards a new stimulus, which has been referred to as a passive form of exploration (Berlyne, 1960). Perhaps glances at the nests were initially elicited by the change in the hen's environment (= presenting the four nests by removing the front-entrances). The decrease over time may be due to habituation. Inspecting the nests may be regarded as the active form of exploration, which is characterised by approaching the stimulus and making contact (Berlyne, 1960). Control hens continued in inspecting the nests in the course of time, perhaps to ensure that nothing had changed. The interest for the nests increased when the hens approached maturity (c.f. chapter 4, figure 4.1).

During the first phase of the experiment control hens spent more time in glancing at the nests than did experimental hens. In the course of time this difference between both groups disappeared. Perhaps these control hens were initially more "careful" in exploring the new stimuli than were experimental hens.

In contrast to the results in the weeks before laying, moving the nests to new places in the laying period did not result in an increase of the inspection duration. Obviously inspections during the laying period do not serve the same function as those in the weeks before laying. Perhaps now they represent intention movements to enter the nests as has already been mentioned before (chapter 2).

In the weeks before laying most hens showed a consistent examination pattern over time. However, in none of the hens under study a significant

degree of association between nest-preference before and during the egg-laying period was found. In this experiment only three of the 14 hens under study had been observed until the day of the first oviposition, while the remaining 11 hens came into lay two to three weeks later. Therefore for most hens a two to three week observation period preceding the day of first oviposition is missing. Perhaps a possible relationship is present during that particular period. This is investigated further in experiment 2.

5.3. Experiment 2

In experiment 1 no relationship was detected between nest-preference in the weeks before and during the laying period. However, only 3 of the 14 hens had been observed until the day of the first oviposition; for the remaining 11 hens a two to three week period preceding the day of first oviposition was missing. It is possible that a relationship is present during that particular period. Therefore in this experiment the nest-examination pattern in the weeks before laying and its relation with later nest-preference is studied in hens that have been observed until the day of the first oviposition.

5.3.1. Materials and methods

Eight 16 week-old hens were housed in the same floor-pens as described in experiment 1: two hens per pen. The pen's floors were covered with a mixture of sand and hemp fibre (3:1). Housing conditions were the same as described in experiment 1. The positions of the four nests were never altered.

Observations

In the weeks before laying the same observational procedures were followed as described in experiment 1. Observations were continued until in each pen one hen had come into lay.

During the egg-laying period eggs were collected daily and each hen's

nest-site choice was registered during a fortnight.

5.3.2. Results

In three of the four pens one hen had been observed until the day she laid the first egg. In one pen two hens came into lay simultaneously and had both been observed until then. Therefore behavioural records are available of 5 hens from four pens up to the day of the first oviposition. For each hen that day was referred to as day 0.

To study the examination pattern over time the observation period preceding day 0 was divided into five phases (five days per phase). Each phase contained 4-5 observation sessions. At the end of phase 5 all hens laid the first egg.

For each hen the mean duration of examinations was calculated per nest by averaging the data of the 4-5 observation sessions per phase. Therefore each phase is represented by one score per hen.

To study the consistency in the examination pattern over time a Kendall coefficient of concordance was computed per hen. The results are presented in table 5.3.

Table 5.3. The degree of coherence in the duration of examinations per nest among the five phases in the weeks before laying presented for five hens of experiment 2 as expressed by the Kendall coefficient of concordance (W). ** :p < 0.01

Hen	Kendall's W
11	0.712 **
21	0.712 **
22	0.744 **
32	1.00 **
41	0.808 **

All hens scored a significant coefficient. Thus the distribution of the time spent in examinations over the four nests showed a consistent pattern per hen over the whole observation period.

In each of these five hens the relation between early nest-preference and later nest-choice was studied. During the weeks before laying the same ranking procedure was followed as described in a previous section.

In the laying period no behavioural observations had been carried out. In order to score each hen's nest-preference ranks were assigned to the four nests according to the number of eggs laid in a particular nest. The nest that had been used for the first series of eggs received the highest rank number.

A Spearman rank correlation coefficient was calculated per hen between the ranks assigned to each of the four nests during the weeks before laying and during the laying period. The results are presented in table 5.4.

In none of the 5 hens a significant correlation coefficient was found. It is concluded that the final nest-choice can not be predicted by the amount of attention paid to the nests in the weeks before laying.

Perhaps no relation was detected because the data were analysed too roughly i.e. per phase. Therefore a more detailed analysis was carried out.

Table 5.4. The relation between nest-examinations in the weeks before laying and later nest-use as expressed in a correlation coefficient presented for 5 hens of experiment 2. For further explanation see text.

Weeks before laying					Laying period					Rs
Nest	1	2	3	4	Nest	1	2	3	4	
hen 11	3	2	4	1	2	4	2	2		0.00 n.s.
21	1	3	4	2	2	4	2	2		+0.40 n.s.
22	2	3	4	1	2	4	2	2		+0.40 n.s.
32	2	3	4	1	4	1.5	3	1.5		+0.35 n.s.
41	1	2	4	3	2	4	2	2		0.00 n.s.

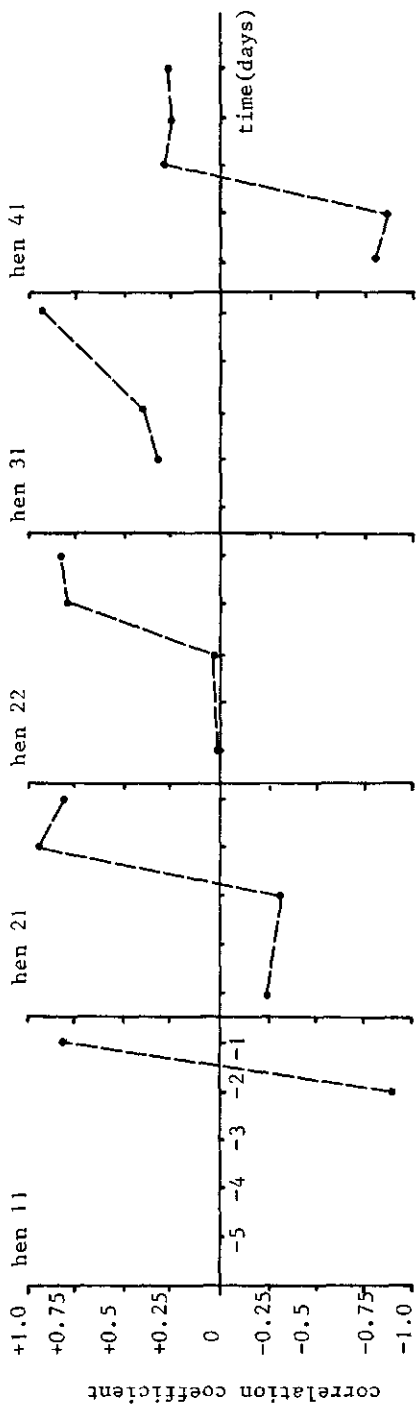


Figure 5.8. The relation between the amount of attention paid to the nests and the final nest-choice as expressed in a rank-correlation coefficient during the 5 days preceding the day of first oviposition (for further explanation see text).

In the 4 weeks preceding the day of first oviposition for 4 of the five hens 20 daily observation sessions (1.5 hour per session) were available. The fifth hen had started laying earlier and therefore for this one only 10 of such observation sessions were scored. For each observation session the total time spent in examining each of the four nests was calculated. Subsequently a Spearman rank correlation coefficient was computed between the nest-examination pattern on that observation day and later nest-choice. This procedure was carried out for each observation day in all five hens.

Until the end of phase 4 the value of the coefficient changed from day to day. However, with the approach of oviposition the value of the correlation coefficient showed an increase. One day before the day of first oviposition all hens scored a positive correlation coefficient (figure 5.8.), although the degree of association was not significant (tested two-tailed against a level of $p=0.10$). Nevertheless, it is concluded that one day before the day of the first oviposition all hens showed the tendency to spent most time in inspecting the nest they preferred for the oviposition of the first series of eggs.

5.3.3. Discussion

The results revealed that no relation was present between the examination pattern in the weeks before laying and the final nest-choice. However, one day before the first oviposition a positive correlation was found in each of the five hens under study, indicating that the hens had selected a nest-box by then.

Summarizing, it is concluded from experiment 1 and 2 that the hens gather information by inspecting the nests and that the final selection of a nest appears to be established one day before the day of first oviposition. These results might be explained by a threshold model of choice behaviour (Dawkins, 1969). It is assumed that each possible alternative has a certain threshold and is equally likely to be chosen if a (non-fixed) variable, inside the animal, exceeds all thresholds. Probably the information gathered by examinations during the weeks before the first egg-laying was used to adjust the value of the variable to such an extent that by the time the first egg had to be laid only one threshold would be exceeded.

Perhaps nest-examinations are of crucial importance in the selection of a nest. If so the hen's nest-site choice and perhaps the number of floor-eggs might be influenced by preventing these examinations to occur.

5.4. Conclusions

- * Glancing is regarded as a passive form of exploration, which is initially elicited by a change in the environment.
- * Nest inspections serve the acquisition of information, which may be used for the final selection of a nest.
- * Nest inspections in the laying period do not appear to have the same information gathering function as those in the weeks before laying; they are more likely to represent intention movements to enter the nests.
- * The final nest-choice seems to be established one day before the day of first oviposition.

CHAPTER 6

THE PERCENTAGE OF FLOOR-EGGS AS INFLUENCED BY EARLY EXPERIENCE WITH
DIFFERENT NESTS

6.1. Introduction

One of the goals of this thesis is to formulate measures that may reduce the occurrence of floor-eggs. Therefore in the present chapter it is investigated whether the percentage of floor-eggs can be effectively reduced by using the results obtained so far.

In the previous chapter it was concluded that hens gather information from different nests in the weeks before laying by inspecting them. This information was supposed to be used for the selection of a nest. Moreover, the final choice seemed to be established before the day of the first oviposition. This raises the question as to whether the choice to use either a nest-box or the floor for laying is affected by preventing the hens from inspecting the nests before they start laying. In other words, does experience with nest-boxes in the weeks before laying affect the hen's choice to use either the floor or a nest as a site for oviposition ?

Results presented in chapter 4 suggest that this is indeed the case. If hens were prevented from inspecting the roll-away nests in the weeks before laying by opening the nests at an age of 20 weeks (=late; tables 4.1 and 4.5: flocks 4 and 6) fewer floor-eggs were found as compared with opening these nests at an age of 16 weeks (=early ;tables 4.1 and 4.5: flocks 5 and 7). However, no differences were found between opening litter-nests late and early (tables 4.1 and 4.5: flocks 2 and 3). It may be concluded that early experience with roll-away or litter nests affects the hen's choice to use either a nest-box or to lay on the floor differently. However, since only a few flocks had been used, this can only be a preliminary conclusion. Moreover, in that study flocks were used of different strains (experimental line of the institute, Hisex and Shaver 288). Finally, in contrast to flocks 2, 3, 5, 6 and 7, flocks 1 and 4 were provided with a cock. Therefore it was decided to design an experiment in which the effect of early experience with different types of nests on the percentage of floor-eggs is studied.

At the start of the egg-laying period the percentage of floor-eggs is rather high. In the course of time it decreases and after about 5-6 weeks it stabilizes (chapter 4, figure 4.3). If this is a general pattern, the effectiveness of a treatment might be judged according to the percentage of floor-eggs laid in the 6th week of the egg-laying period. However, since a

poultry farmer is more interested in the total percentage of floor-eggs laid, not only the percentage of floor-eggs laid during the 6th egg-laying week, but also that found during the total 6-week egg-laying period will be used as a measure in judging the effectiveness of a treatment.

This chapter presents the results of two experiments. In the first one the effect of the properties of the nests (factor 1) and the moment the hens get access to the nests (factor 2) on the percentage of floor-eggs is studied. Moreover, the interrelationship between these two factors is examined and their effects are described over time. In the second one the effect of changing the nest-content at two different laying percentages on the percentage of floor-eggs is studied.

6.2. Experiment 1

6.2.1. Materials and methods

Twenty four flocks, each consisting of 18 cage-reared white laying hens (Shaver 288) were housed at an age of sixteen weeks in small floor-pens. The lay-out of the pen and management conditions have been described in chapter 3.

Experimental design

The experiment was designed according to a 2 x 2 factorial type i.e. the effects of the two variables (properties of the nests and the moment of nest opening) were investigated simultaneously (Cochran and Cox, 1957). Two types of nests were used: -1- nests provided with wood-shavings (=litter nests) and -2- nests provided with a wire basket (= roll-away nests). The hens got access to the nests at two different moments: -1- nests were opened on the day the hens were placed in the floor-pen (=early) and -2- nests were kept closed until the day the first eggs in a flock were laid; on that day the nests were opened (=late). Four treatments consisting of all combinations from these two factors were formed (table 6.1).

Each flock of hens was considered to be one experimental unit. Since differences may exist along the hen-house in several factors such as

lighting conditions, temperature, disturbance by humans and perhaps some unknown factors, the units were grouped according to a randomized block design. The four treatments were assigned randomly to the units in each block. Each treatment was represented by 6 flocks. Since the hen house only offered place for 3 blocks of 4 units the experiment had to be carried out in two stages (trial 1 and trial 2).

Table 6.1. Design of experiment 1

		Moment of opening nests	
Nest properties		Early (E)	Late (L)
Litter	(L)	LE (6)*	LL (6)
Roll-away	(R)	RE (6)	RL (6)

* : number of flocks

Observations

Floor-and nest-eggs were collected once a day at 15.00 p.m. For each flock the number of floor-and nest-eggs were registered daily during the first 6 egg-laying weeks. No behavioural observations were made.

Statistics

In order to test differences between the treatments a Mann-Whitney-U-test was applied (Siegel, 1956).

6.2.2. Results

Since the results of trial 1 and 2 did not show systematic differences, they were combined.

The flocks started laying at an age of 19-20 weeks. The percentage of floor-and nest-eggs was calculated over the subsequent six weeks of the

egg-laying period per pen. From these data the median percentage was computed per treatment. The results are presented in figure 6.1. A main effect was present of the properties of the nest: in pens provided with litter nests significantly fewer floor-eggs were found as compared with pens provided with roll-away nests ($n_1=n_2=12$; $U=20$; $p<0.01$). No significant differences were present between opening nests early and late.

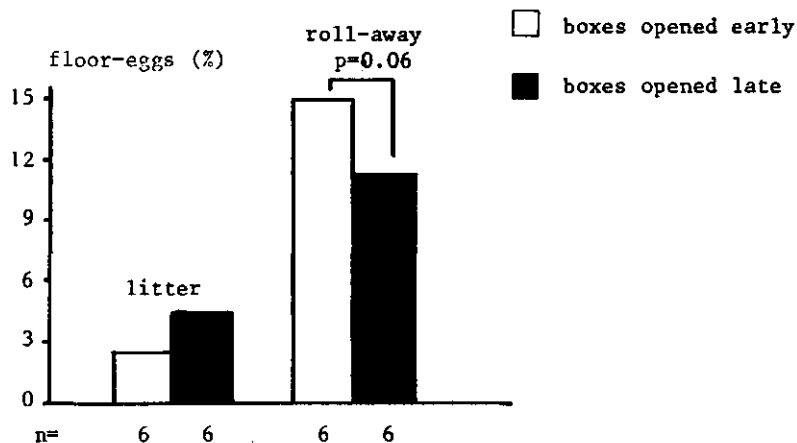


Figure 6.1. The median percentage of floor-eggs per treatment during the total 6-week egg-laying period. n= number of pens.

Furthermore, an interaction was detected between both factors. Opening roll-away nests early tended to result in more floor-eggs (15.0 %) than opening these nest-boxes late (11.5 %) ($n_1=n_2=6$; $U=8$; $p=0.06$). However, no significant differences were found between opening litter nests early and late (2.5 and 5.0 %, resp.; figure 6.1).

To describe the effects of the treatments over time the median percentage of floor-eggs was calculated per week. Figure 6.2. shows that in each of the four experimental groups most floor-eggs were laid at the start of the egg-laying period. In the course of time the percentage of floor-eggs decreased and stabilized during the sixth week of the egg-laying period.

In the 6th week a significant effect was present of the properties of the nests ($n_1=n_2=12$; $U=20$; $p<0.01$): in pens provided with litter nests fewer floor-eggs were found as compared with pens provided with roll-away nests.

No differences were present between opening litter-nests early or late (0.4 and 0.5 %, resp.). Opening roll-away nests early resulted in more floor-eggs during the 6th week of laying (8.1 %) than opening these nests late (5.4%), however, this difference was not significant.

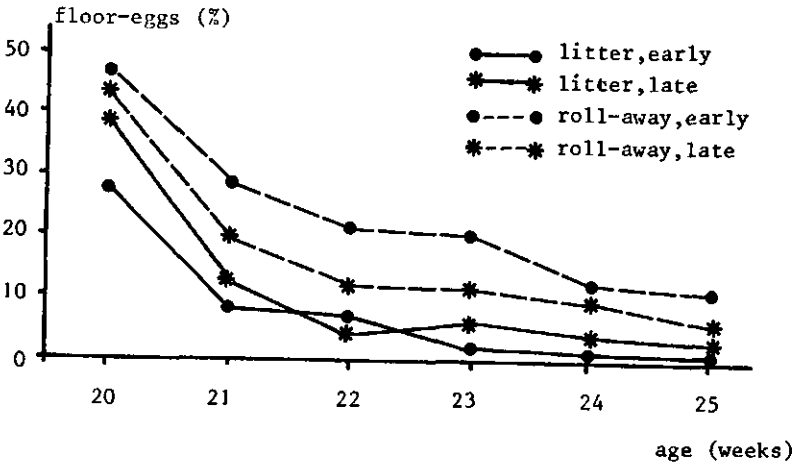


Figure 6.2. The median percentage of floor-eggs per treatment per week.

6.2.3. Discussion

The results revealed that more floor-eggs were laid in pens provided with roll-away nests than in pens provided with litter nests, indicating that characteristics inherent to the latter nest type are preferred to those of the roll-away nest. These results are in agreement with studies concerning nest-site choice in domestic fowl. If hens were offered a choice of different nests they clearly exhibited a preference for litter nests over roll-away nests (Kite, 1983; Huber et al., 1985; chapter 5).

If the type of nests offered is neglected, no significant effect was present of the moment the nests were opened. The results, therefore, do not support the opinion that hens should get access to the nests as early as possible in order to prevent them from floor-laying (Francis, 1970).

An interaction was present between the two factors under study. Opening roll-away nests late i.e. on the day the first eggs in the flock were laid, resulted in fewer floor-eggs than opening these boxes early i.e. immediately after placing the hens in the floor-pens. Such a difference was not found between opening litter nests early or late. Apparently the hen's site-choice is manipulable. Opening roll-away nests early enabled the hens to inspect the nests visually in the weeks before laying. As demonstrated in chapter 5 hens gather information from the nests by these early inspections. Perhaps a hen's willingness to use roll-away nests for laying is decreased by the information gathered in the weeks before laying from a roll-away nest, which may constitute a non-preferred stimulus. This effect may not have been present in pens provided with litter nests, since the presence of litter may constitute an attractive stimulus. It is concluded that the extent to which early experience with nests affects the incidence of floor-laying depends upon the type of nest-box used.

In order to reduce the occurrence of floor-eggs the use of litter nests is recommended. However, in contrast to roll-away nests, litter nests provided with wood-shavings need laborious manual egg-collection. Mechanising the egg-collection from litter nests is possible by using another litter type e.g. buckwheat husks. However, such nesting systems are more expensive as compared with roll-away nesting systems (pers. comm., Workamp, 1986). Here the hen's interests and those of the poultry farmer are conflicting.

Best results with roll-away nests were obtained if the nests were opened at the start of the egg-laying period. Nevertheless, this treatment still resulted in 11.5 % of floor-eggs if the total egg-laying period is considered. In the course of time the percentage of floor-eggs decreased and reached a stable level during the 6th week of laying. During this latter week still 5.4 % of the eggs were laid on the floor. This is a rather high level as compared with opening litter nests early and late (0.4 and 0.5%, resp.). Therefore it seemed worthwhile to examine whether the percentage of floor-eggs could be reduced to an acceptable level in pens equipped with roll-away nesting systems. Experiment 2 deals with this question.

6.3. Experiment 2

6.3.1. Introduction

The foregoing suggested that a hen's willingness to use roll-away nests was increased by preventing her to inspect these nests during the weeks before laying. In flocks all hens do not come into lay simultaneously. The day the first hen starts laying may be separated 3-4 weeks from the day the last hen starts laying. Therefore only a few hens were totally unacquainted with such nests by opening the nests on the day the first eggs were laid. If one could increase the number of hens that have had no experience with the roll-away nests until the day of first oviposition, this might reduce the number of floor-eggs even more as compared with opening roll-away nests on the day the first eggs in a flock are found. This effect can be achieved by opening the roll-away nests not until a number of hens will have started laying. However, since the nests are closed, most of these hens will be forced to use the floor for laying. Such a treatment is expected to stimulate floor-laying in stead of reducing it.

An alternative treatment might be to provide hens with litter nests until a laying percentage of for example 15-20 %. Subsequently the litter nests are converted into roll-away nests by replacing the litter with a wire basket (=treatment LT1). As demonstrated by the foregoing, litter nests are preferred over roll-away nests. So, if hens are initially provided with litter nests, they are expected to start using them. Since hens are very conservative in the use of a particular site (chapter 4), they are presumed to go on using the same nest site, even after the change in nest content. In that case we may expect the percentage of floor-eggs to be reduced even more by allowing more hens to start using the litter nests i.e. by postponing the moment of the nest-change (=treatment LT2) as compared to group LT1.

In this experiment the influence of converting litter nests into roll-away nests at about 15 and 35 % of lay on the percentage of floor-eggs is studied. Moreover, the effects of the treatments are described over time.

6.3.2. Materials and methods

Sixteen flocks (18 hens per flock) of cage-reared white laying hens (Shaver 288) were housed in small floor-pens at an age of 16 weeks. Housing and management conditions were the same as described in experiment 1.

Two treatments were formed: litter nests were changed into roll-away nests at approximately 15 (LT1) or 35% of lay (LT2). Each experimental group was represented by eight pens. In the first month of the laying period a number of hens from one pen belonging to experimental group LT1 died. This pen was excluded from further analysis and therefore group LT1 was represented by 7 pens.

For reasons mentioned before the experiment had to be carried out in two trials. In the hen-house blocks of two experimental units were distinguished. The two treatments were randomly allotted to the units within each block.

Observations

The same observations were made as described in experiment 1 (6.2.1.).

Statistics

In order to test differences in the percentage of floor-eggs between the two treatments a Mann-Whitney-U-test was applied (Siegel, 1956).

6.3.3. Results

Egg-laying in all flocks started at an age of 19-20 weeks. In group LT1 an average laying percentage was reached of 17.7 % (range 16.6-19.4%) about one week after the first eggs in the flocks had been laid. Subsequently litter nests were converted into roll-away nests. In group LT2 litter nests were changed into roll-away nests after two (four flocks) and three weeks (four flocks) of laying. By then an average laying percentage of 38.6 % (range 31.5-44.4%) was reached.

The total percentage of floor-eggs was calculated from the nest-change until the end of the experiment per pen. For group LT1 and LT2 this period consisted of five and four weeks, respectively. For each treatment the

median percentage of floor-eggs is presented in figure 6.3. Converting litter nests at about 17.7 % of lay resulted in more floor-eggs (17.5 %) than changing these nests at 38.6 % of lay (13.0 %; $n_1=7; n_2=8; U=14; p=0.06$)

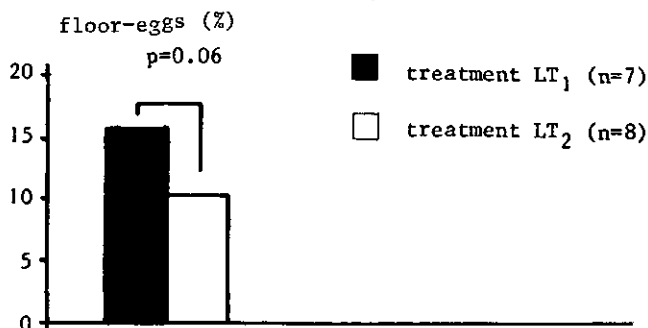


Figure 6.3. The median percentage of floor-eggs per treatment during the 5 (LT₁) or 4 (LT₂) weeks after the nest-box change. n= number of pens.

In order to study the effect of each treatment over time the median percentage of floor-eggs was calculated during the weeks preceding and following the nest-change. Figure 6.4 shows that in group LT₂ the highest percentage of floor-eggs is found at the start of the egg-laying period. In the course of time it decreased. In group LT₁ a median value of 21 % of

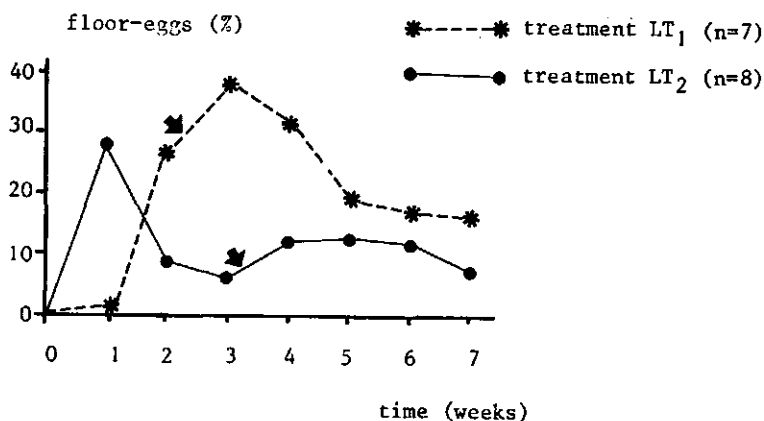


Figure 6.4. The median percentage of floor-eggs per treatment per week. The arrows refer to the moment of nest-box change. n=number of pens.

floor-eggs was found in the week preceding the nest-change. In group LT2 6.8 % of floor-eggs were found in the week preceding the nest-change.

In the first week immediately after the nest-change a significant increase was found in group LT1 (Sign-test, $n=7; x=0; p<0.05$). Similar results were found in group LT2, however, here the increase was not significant. In the course of time the floor-egg percentage decreased in both groups. In the last egg-laying week i.e. in the fourth (LT2) and fifth week (LT1) after the nest-change, fewer floor-eggs were found in group LT2 (7.7%) than in group LT1 (16.8%), however, this difference was not significant.

6.3.4. Discussion

The results of experiment 1 (roll-away nests opened late = group RL and early = group RE) are compared with those of experiment 2 (replacing the litter by a wire basket at approx. 17 and 38 % of lay = groups LT1 and LT2, resp.). Since the floor-egg percentage in the latter experiment did not follow the same pattern over time as compared with the first mentioned (see fig. 6.2 and 6.4), the period from the beginning until the end of the experiment is not comparable between both experiments. Thus the percentage of floor-eggs laid during that period is no useful measure to judge the effectiveness of a treatment. Therefore for this purpose the percentage of floor-eggs laid during the last week of the experiment was used. In group RL this week corresponds with the 6th egg-laying week. In groups LT1 and LT2 this week is represented by the 5th and 4th week after the start of the nest-change, respectively. By then all flocks from group LT1 and four flocks from group LT2 had been laying for 6 weeks, while the remaining four flocks from LT2 had been laying for 7 weeks. The results are summarized in table 6.1.

Replacing the litter with a wire basket at 17.7 % of lay resulted in more floor-eggs than opening roll-away nests at the start of the egg-laying period. So, this treatment was ineffective in reducing the incidence of floor-laying. It appeared indeed to have a negative effect as compared with opening roll-away nests late and even as compared with opening roll-away nests early. In the week immediately following the nest change the percentage of floor-eggs in group LT1 significantly increased. These results

suggest that once a hen has been able to inspect litter nests visually in the weeks before laying, she will be less likely to start using a roll-away box later on.

Changing litter nests into roll-away nests at 38.6 % of lay and opening roll-away nests late resulted in comparable percentages of floor-eggs. Thus the first mentioned treatment did not reduce the percentage of floor-eggs further as compared with opening roll-away nests late. However, as compared with opening roll-away boxes early, fewer floor-eggs were found, although the difference was not significant (table 6.1).

Table 6.1. Percentage of floor-eggs as influenced by opening roll-away nests early (RE) and late (RL) and by changing litter nests into roll-away nests at two different laying percentages (LT1 and LT2) presented during the last egg-laying week.

	Treatment			
	RL	LT2	RE	LT1
Floor-eggs (%)	5.4	7.7	8.1	16.8

As expected, replacing the wood-shavings with a wire basket at 38.6 % of lay (=group LT2) resulted in fewer floor-eggs ($p=0.06$) as compared with changing the nests at 17.7 % of lay (table 6.1). In the week immediately following the nest-change the floor-egg percentage in group LT2 only slightly increased. Postponing the moment of the nest-change allowed a larger number of hens to start using the litter nests as compared to the early change. Probably these hens were trained in the use of a nest-box and continued in using nests, even after the replacement of wood-shavings by a wire basket.

6.4. Conclusions

- * Litter nests are preferred over roll-away nests.
- * Whether a hen will start using the floor or a nest-box for laying depends upon the type of nests she has had experience with in the weeks before and during laying.

CHAPTER 7

EGG-LAYING RECORDS AND PRE-LAYING BEHAVIOUR OF FLOOR-AND NEST-LAYERS

7.1. Introduction

Previous results (chapter 4) revealed that, except for the first few eggs, hens kept under the same conditions showed individual differences in their nest-choice pattern. Some hens would use nests provided but others would always lay on the floor or on the wire. Similar results have been reported by Appleby et al. (1983a). They showed that in floor-pens with raised nests individual differences in site use were related to failure to perch. This factor could not account for individual differences in site use in our study, because the nests were placed at ground level. Furthermore, since floor-layers and nest-users were about equally represented among low, middle, and high ranking hens (see chapter 4), the difference in nest-use between individuals is unlikely to be due to competition for nests.

From the literature reviewed in chapter 2 it becomes clear that the physiological control of the reproduction in the hen, including the control of the nesting behaviour itself, is a rather complex process. Hence physiological irregularities may easily lead to abnormal nesting behaviour and thus to the occurrence of floor-eggs.

However, there are two other possibilities to consider. First, some hens may simply prefer to lay on the floor rather than using nest-boxes provided as has been pointed out before (chapter 2) and then floor-laying is regarded as normal. Second, it is suggested that floor-layers react differently to environmental stimuli than do their pen-mates that use nests.

In order to answer the question which factors may cause individual differences in site use, egg-production records (section 7.2) and pre-laying behaviour (section 7.3) of floor- and nest-layers are described and compared to each other.

7.2. Physiological factors

A physiological irregularity causing abnormalities in egg-laying is the occurrence of double ovulations within a short period. If two follicles are ruptured simultaneously and if both ova are engulfed by the infundibulum nearly always a double yolked egg is laid. However, if the ovulation of another ovum is separated by a smaller interval than the normal expected

25-26 hours from the previous one, two hard shelled eggs are laid within 24 hours (Gilbert and Wood-Gush, 1971). For some reason the first egg is held in the shell gland for several hours longer than normal and the second one is expelled prematurely. In broiler breeder hens this phenomenon occurred regularly in some individuals (Van Middelkoop, 1974). Hens with two shelled eggs in the gland were observed to nest at the normal time of laying; however, no egg was laid then. Only during the evening or the night the first egg of a pair was expelled. It remains unclarified whether the oviposition of the second egg is accompanied by normal nesting behaviour. Nevertheless, in this way many first eggs of a pair were not laid in a nest in broiler breeders kept on the floor. So, this type of floor-laying was associated with the laying of two eggs a day.

Another process, which might cause abnormalities in laying, is the production of hormones interfering with that of hormones responsible for the contraction of the uterine muscle leading to the oviposition of a hard shelled egg. Adrenaline, for example, is effective in delaying oviposition until the following day (Draper and Lake, 1967). Under these circumstances the egg is dropped somewhere in the pen long after the expected egg-laying time without being accompanied by nesting behaviour. If floor-laying is due to such types of irregularities, floor-layers are expected firstly to show a different lag-duration pattern and secondly to be less consistent in the use of a particular site in the pen as compared with nest-layers.

In this part of the chapter egg-laying records of floor-and nest-layers are described and compared to each other.

7.2.1. Materials and methods

To study differences in egg-laying patterns between individuals data were available of hens belonging to seven flocks. Five flocks had already been used in a previous study (chapter 4); the other two (flock M1 and B4) newly arrived and consisted of 15 white laying hens (Shaver 288) each. They were placed in floor-pens, containing one row of individual roll-away nests. Further housing conditions and management factors have already been described in chapter 3.

Observations

1) Daily egg-production per hen:

In order to find out whether the laying of two eggs a day occurred, the date and site of oviposition of floor-layers (n=12) and nest-layers (n=16) could simply be used. In 4 of the seven flocks such observations had been made by means of a video recorder. As mentioned in the introduction, delayed eggs could be laid during the evening or the night. Since the hens were only filmed during the light period, a number of ovipositions may have been missed. Moreover, in the remaining three flocks hens were fed gelatine capsules filled with a die in order to identify floor- and nest-layers (see also chapter 3). Because eggs were only collected once a day, a number of floor-eggs may have been lost in the litter or in the droppings pit. Thus the number of hens laying two eggs a day may be underestimated by using these two methods. Therefore another parameter representative for this phenomenon was used in addition viz. :

2) Egg-shell quality:

The shells of both eggs of a pair appear to show abnormalities as compared with a normal shelled egg as described by Simons (1971). The first egg of a pair nearly always shows an additional calcification band over the shell surface. The second one is characterised by abnormalities like a compressed-sided shell with incomplete shell deposition (Van Middelloop, 1974). Therefore the presence of abnormal shelled eggs provides evidence for the laying of two eggs a day.

3) Lag-duration

In order to study differences in the lag duration (=the duration of an interval between successive ovipositions minus 24 hours), data were available of 11 nest-users and 8 floor-layers from 5 different flocks. Three of the five flocks had been observed on alternating days, which made it impossible to determine the length of the lag between ovipositions per 24 hours. Therefore for each hen the duration of the lag between eggs laid on alternating days i.e. per 48 hours, was determined.

4) Consistency in site use:

For 11 floor-layers and 11 nest-layers the site of oviposition had been

recorded. In the case of floor-layers four possible sites were distinguished i.e. the left and right side of the litter and the left and right side of the wire. For nest-users the three adjacent nests on the right side of the pen were regarded as one nest and the remaining three on the left side as another.

Statistics

Differences between floor- and nest-users were tested by means of a Mann-Whitney-U-test (Siegel, 1956).

7.2.2. Results

7.2.2.1. Egg-production pattern

In order to compare and describe the egg-production pattern between floor- and nest-layers for each hen the total number of eggs laid (L) was divided by the total number of observation days (O). The results are presented in table 7.1. No differences were found in the egg-production pattern between floor- and nest-layers. Moreover, no abnormal egg shells were observed. Most hens from both groups produced an average of nearly one egg per day. The values smaller than 1 (table 7.1.) indicate a lower (hard-shelled) egg-production which may be due to e.g. normal pause days between clutches, internal laying or to shell-less eggs which are very difficult to detect, because they are nearly always lost in the litter or in the droppings pit.

Table 7.1. Egg-production records for floor-and nest-layers as expressed in the ratio (L/O) of number of eggs laid (L) and the number observation days (O).

Floorlayers	L/O	Nest-layers	L/O
A31	6/6 =1.00	B41	9/11 =0.82
A32	8/8 =1.00	B42	12/13=0.92
B44	8/9 =0.88	B43	11/12=0.92
B45	12/13=0.92	M12	10/10=1.00
B46	10/12=0.83	M13	9/9 =1.00
B47	6/6 =1.00	D11	7/7 =1.00
B48	6/6 =1.00	D12	7/7 =1.00
D13	6/6 =1.00	D14	5/5 =1.00
M14	10/10=1.00	A11	19/23=0.83
M15	7/7 =1.00	A12	10/13=0.77
M16	9/9 =1.00	M11	8/8 =1.00
A21	9/10=0.90	B21	14/17=0.82
		B22	19/22=0.86
		A33	10/10=1.00
		A34	11/11=1.00
		A35	8/8 =1.00

7.2.2.2. Lag duration-pattern

In the floor-and nest-laying group lag durations between eggs laid on alternating days were calculated. Figure 7.1. shows the frequency distribution of the number of intervals between ovipositions characterised by positive lag durations i.e. 0 to 1 hour, 1 to 2 hours and 2 to 3 hours and negative lag-durations i.e. 0 to -1 and -1 to -2 hours. No differences were found in the lag-duration pattern between both groups ($\chi^2 = 1.61$; $df=4$; N.S.). The lag duration most frequently reached a value of zero to one hour per 48 hours in both groups (figure 7.1).

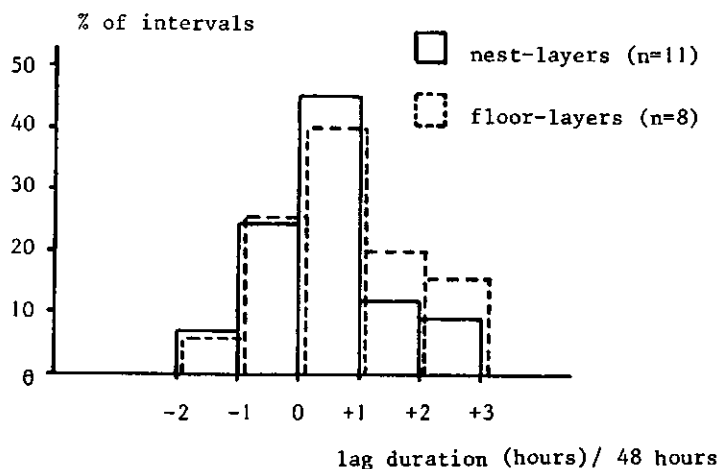


Figure 7.1. The frequency distribution of intervals between ovipositions characterised by different lag durations for floor- and nest-layers. For further explanation see text.

7.2.2.3. Consistency in site-use

Since each hen had not been observed on subsequent oviposition days a perseverance index (see chapter 4) could not be used to study consistency in site-use. Therefore only the frequency index ($=F(i)$) i.e. the number of eggs laid at the same site divided by the total number of eggs laid (chapter 4) was used.

No differences were found in consistency of nest-site use between floor- and nest-layers. Similar proportions of the nest- and floor-layers nearly always used the same site in the pen ($F(i) > 0.70$). Other hens more frequently changed nests ($F(i) < 0.70$). Two of the 11 nest-users in this study were observed to lay a floor-egg.

Table 7.2. Frequency - index for floor-and nest-layers indicating the consistency in site use in the pen. For further explanation see text.

Floor-layers	Frequency-index	Nest-layers	Frequency-index
A31	6/6 =1.00	B41	9/9 =1.00
A32	8/8 =1.00	B42	7/12 =0.56
D13	3/6 =0.50	B43	8/11 =0.73
B44	4/8 =0.50	M11	8/8 =1.00
B45	10/12=0.83	M12	5/10 =0.50
B46	6/10 =0.60	M13	6/9 =0.66
B47	6/6 =1.00	D11	7/7 =1.00
B48	6/6 =1.00	D12	4/7 =0.57
M14	6/10 =0.60	D14	4/5 =0.80
M15	4/7 =0.57	A11	14/19=0.74
M16	9/9 =1.00	A12	7/10 =0.70

7.2.3. Discussion

Nest-and floor-layers did not differ from each other with respect to egg-production records, egg-shell quality, lag-duration pattern and consistency in the site they use for laying. Apparently physiological irregularities did not occur in this strain of laying hens and therefore this phenomenon cannot account for the differences in site use between individual hens. The results support the statement that physiological irregularities are uncommon in laying strains (Jaap and Muir, 1968).

Two nest-users only occasionally appeared to lay an egg on the floor, which suggests that these ovipositions were not preceded by nesting behaviour. Probably we are dealing here with delayed ovipositions. As mentioned before, adrenaline is effective in delaying oviposition. Since a hen reacts to stressful conditions with a higher adrenaline production (Freeman, 1976) unexpected movements, restlessness or other types of alarming situa-

tions in the hen-house may have resulted in delayed ovipositions and thus to floor-eggs.

7.3. Pre-laying behaviour of floor-and nest-layers

Differences in site use between individuals were probably not due to irregularities in physiological processes as demonstrated by the foregoing. Another possibility that might explain such differences, is that individual hens react differently to environmental stimuli. In other words, the nesting tendency in floor-layers is normal but frustrated for some reason e.g. by properties of the nests or the lay-out of the pen. This may have produced a conflicting situation i.e. to nest or not to nest.

When unable to find a suitable nest brown leghorn hens respond with escape behaviour and stereotyped pacing (Duncan, 1970). In caged white laying hens excessive stereotyped back and forward pacing was observed, while these hens tended to sit for a considerable short time (Wood-Gush, 1969, 1972). This type of behaviour does not occur in nesting hens that are kept under semi-intensive conditions (see chapter 2) and therefore it may be regarded as abnormal. Since hens respond in a similar way to frustration in a feeding situation (Duncan and Wood-Gush, 1972a), it is suggested that the occurrence of stereotyped pacing, escape and the tendency to spend less time sitting is due to frustration in the nesting context.

Furthermore, in several species of bird (van Iersel and Bol, 1958; Rowell, 1961; McFarland, 1965) conflict or frustration sometimes leads to the performance of patterns of another behavioural system, which is not activated or, as has been hypothesized by van Iersel and Bol (1958), which has become disinhibited in the conflict. These so-called displacement activities have also been described in the domestic fowl. They are not sharply distinguished from the same activities appearing in the normal context except that they are performed more hurriedly (Kruijt, 1964). Displacement preening, for example, is characterised by a much shorter bout-length as compared with the same activity in a control situation (Duncan and Wood-Gush, 1972b). So, if floor-laying is caused by frustration floor-layers are expected to spend more time in pacing, escape movements and in displacement activities and less time in sitting quietly on the nest

as compared with nest-layers.

Finally, it is suggested that some hens may simply prefer to lay on the floor rather than using a nest-box provided. In that case floor-layers are expected to perform the same pre-laying behaviour as nest-layers without any signs of frustration and floor-laying is regarded as normal. Moreover, since hens concentrate on the preferred nesting-site in the hours before oviposition (unpublished data) such floor-layers are expected to pay little or no attention to the nest-boxes.

In the following the pre-laying behaviour of floor-and nest-layers is described and compared. To check in how far differences in behaviour are related to the egg-laying situation observations were also made during periods in which no eggs were laid, so-called control sessions. To find out whether displacement activities occurred, the bout-length of elements performed during pre-laying and control sessions are compared.

7.3.1. Materials and methods

In order to compare and describe the behaviour of floor-and nest-layers data were available of hens from flock M1 and B4 (see section 7.2.1.).

Observations

For identification purposes the hens were marked with a felt-pen on their backs or necks on the day of arrival. Observations were always made by means of a video-camera which was mounted above a pen.

During the first five weeks of the egg-laying period each flock was observed on alternating days from 8.00 am until 15.00 pm, except during week-ends. As a result for flock M1 and B4 twelve and thirteen daily records were obtained, respectively. Within each 7 hour sample session oviposition time and site were registered plus the hen's identity which enabled the identification of floor-and nest-layers.

In each flock a number of floor-and nest-layers was chosen according to the following criteria:

* Social rank index

Both groups should be represented by hens with comparable social rank indices. Therefore the rank-order was determined in both flocks. Since social rank before and after sexual development appeared to be strongly correlated (chapter 4), rank orders were only based on data (agonistic behaviour) scored for one hour each day in the weeks before laying. A more detailed description of the method has already been given in chapters 3 and 4.

* Consistency in site use

A hen had to be consistent in laying either on the floor or in a nest-box.

* The number of pre-laying sessions

At least 4 ovipositions preceded by pre-laying behaviour should be on tape.

As a result behavioural records were available of 3 floor- and 3 nest-users from flock B4 and of 2 floor- and 2 nest-users from flock M1. The

Table 7.3. The number of pre-laying (PS) and control sessions (CS) scored per hen.

Hen	nest-layers		Hen	floor-layers	
	PS	CS		PS	CS
04b	5	6	01b	6	6
07b	6	6	02b	4	6
10m	6	6	05m	6	6
14m	8	6	08b	6	6
17b	8	6	12m	7	6

number of pre-laying sessions varied per hen (table 7.3). The floor- and nest-laying group were both represented by 1 low, 2 middle and 2 high ranking hens.

During each half-hour sample session the frequency and duration of the

following behavioural elements, which have been defined before (chapter 3) were recorded via a two digit-code in the event recorder:

- * Pacing
- * Orientation away from the flock
- * Eating
- * Drinking
- * Preening
- * Sleeping/resting
- * Nest-box inspection
- * Nest-box entry

Floor-nest inspection and floor-nest entry could not be registered, because it was impossible to distinguish whether the hen was indeed inspecting or entering a floor-nest.

- * Sitting and rotating in a nest-box
- * Floor-nestsitting and rotating

Vocalisations like the pre-laying call were not registered, because in flocks of this size it was impossible to distinguish from tape which hen uttered the sound.

For each of these ten hens 6 half-hour control observations were taken either on non-laying days (brought about by failure to ovulate) or at least one hour after the egg was laid. However, within 15-75 minutes after oviposition the next ovulation occurs (Sturkie and Mueller, 1976), which is accompanied by a corticosterone peak (Beuving and Vonder, 1981). Hence, control observations may coincide with ovulation. Such controls and those taken on pause-days may not be comparable. To check this, behaviour scored during the two control types was compared to each other. No differences were found between control observations taken on pause-days and egg-laying days. Therefore these data were combined and referred to as control sessions.

Statistics

Egg-laying and control sessions of individual hens were analysed as follows. The total time spent in each of the elements scored was calculated per observation session i.e. per half hour. Moreover, the bout-length was calculated by dividing the total duration by the total frequency. Subse-

quently for each element the median total duration per observation session and the median bout-length was calculated for floor-and nest-layers. Differences between the five floor-and five nest-layers were tested by means of the Mann-Whitney-U-test. A Sign test was applied to detect differences between the egg-laying and control situation (Siegel, 1956).

7.3.2. Results

7.3.2.1. Pacing and orientation away from the flock

In floor-layers stereotyped back and forward pacing appeared to be one of the main activities (21.8 %) during the pre-laying session and they tended to spent more time in this behaviour than did nest-layers ($U=6$; $p=0.11$; figure 7.2). In both groups individual variability was rather large: some hens were never observed to pace, while others spent a considerable amount of time pacing.

Furthermore, floor-layers tended to spent more time in orientation away from the flock than did nest-layers ($U=5$; $p=0.07$; figure 7.2).

No differences were found with respect to the bout-length of these behaviours between both groups.

Neither pacing nor escape movements were performed during the control situation by both floor-and nest-layers.

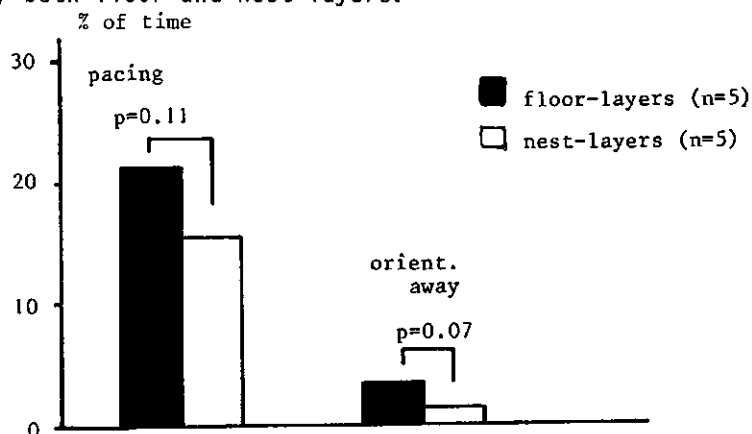


Figure 7.2. The percentage of time spent in pacing and in orientation away during pre-laying sessions. n=number of hens

7.3.2.2. Eating, drinking and preening

Floor-layers spent significantly more time in drinking ($U=1$; $p<0.01$; figure 7.3), while they tended to spend more time eating ($U=6$; $p=0.11$; figure 7.3). Drinking and eating occurred more frequently with the approach of oviposition.

No differences were found with respect to the mean bout-length of these behaviours between floor- and nest-layers.

During the control situation no differences were found in the median total duration and bout-length between floor- and nest-layers.

The median bout-length of eating and drinking was significantly longer during the control than during the laying situation in both nest- ($N=5$; $x=0$; $p=0.03$; table 7.4) and floor-layers ($N=5$; $x=0$; $p=0.03$; table 7.4).

Table 7.4. The median bout-length (seconds) of drinking and eating during pre-laying and control sessions.

	Drinking		Eating	
	Pre-laying	Control	Pre-laying	Control
Nest-layers	12	42	21	108
Floor-layers	17	45	35	148

No differences were found between floor- and nest-layers with respect to the median time spent preening during the egg-laying situation. Actually, only very little time was spent in this behaviour by both floor- (0 %) and nest-layers (0.01 %; figure 7.3).

During the control situation no differences were found between floor- and nest-layers with respect to the median total duration spent in preening and the median bout-length.

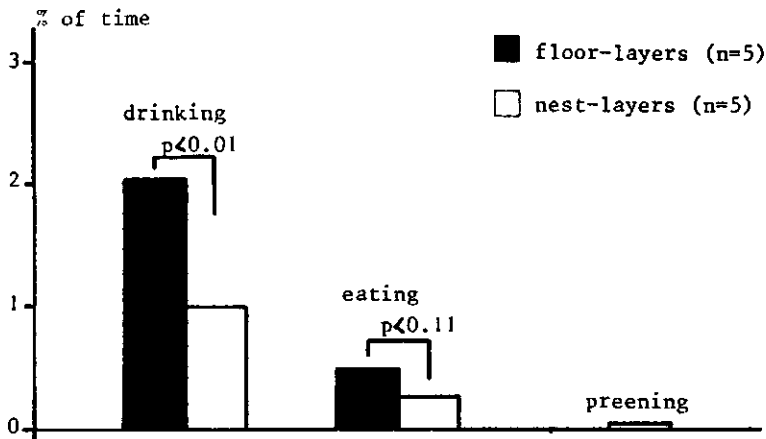


Figure 7.3. The percentage of time spent in drinking, eating and preening during pre-laying sessions. n= number of hens.

7.3.2.3. Sleeping/resting

Sleeping and resting occurred very infrequently during both the egg-laying and control sessions. Therefore these elements are given no further consideration.

7.3.2.4. Nesting behaviour

Nesting behaviour directed towards the nest-boxes did occur in floor-layers. As compared with nest-layers, they spent about the same time in inspecting and entering the nests (figure 7.4). No differences were found with respect to the median bout-length of these two behaviours.

Rotating and sitting in a nest-box, however, was never performed by floor-layers, while this was one of the main activities during laying in nest-layers (27.5%). Floor-layers only spent 7.3% of the time sitting on the floor. This behaviour was never performed by nest-layers.

Although the duration of nest-box sitting varied between individual nest-layers, there was a tendency to sit firmly on the nest for a considerable

time without leaving it until after oviposition. Individual differences were also present within floor-layers, however, here sitting only occurred with the approach of oviposition. The total time spent sitting was signifi-

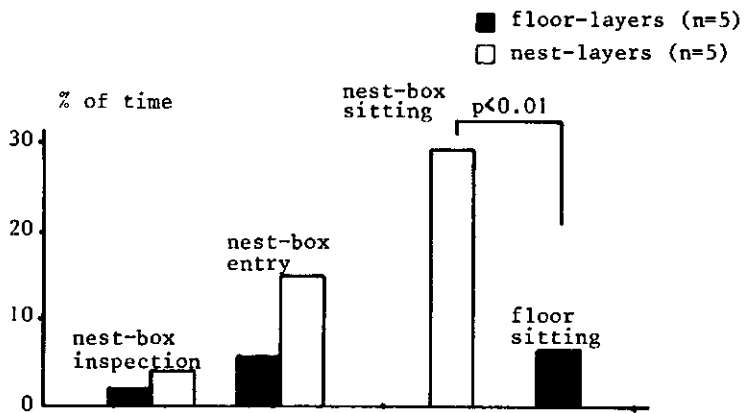


Figure 7.4. The percentage of time spent in nest-box inspections, nest-box entries, nest-box sitting and floor-sitting during pre-laying sessions. n=number of hens.

cantly higher in nest-layers than in floor-layers ($U=1$; $p<0.01$; figure 7.4). Since sitting in floor- and nest-layers occurred equally often (1.61 and 1.65 times / 0.5 hour, resp.), the bout-length of sitting in nest-layers was significantly longer than that in floor-layers ($U=0$; $p<0.01$; table 7.5).

Table 7.5. The median bout-length of floor- and nest-sitting in nest- and floor-layers.

	Bout-length (seconds)	
	floor-sitting	nest-box sitting
nest-layers	x	413
floor-layers	78.9	x

x : did not occur

During the control situation no differences were found between floor-and nest-layers. They both spent some time in inspecting the nest-boxes. Nest-box entries and nest-box or floor-sitting was never observed.

7.3.3. Discussion

Floor-layers spent more time in pacing and orientation away from the flock than did nest-layers, whereas sitting and rotating occurred for a significantly shorter time. Thus the first mentioned group was more restless than were nest-layers. In this respect pre-laying behaviour of floor-layers highly resembles that of caged hens (see section 2.5). Furthermore, floor-layers spent more time drinking and eating than did nest-layers. Although these are normal patterns, they were performed more hurriedly i.e. with a shorter bout-length as compared with the control situation. Therefore this type of behaviour may be regarded as a displacement activity. No differences were present between floor-and nest-layers in a control situation.

These results indicate that floor-layers performed more behaviour indicative of frustration due to the nesting situation than did nest-layers. Furthermore, floor-layers spent, like nest-layers, some time in nest-box inspections and nest-box entries during egg-laying sessions. Therefore the results do not support the view that floor-layers simply prefer the floor for laying.

Obviously the nesting tendency in these hens is frustrated by particular properties of the environment. In a previous study (chapter 6) it was concluded that roll-away nests were associated with more floor-eggs than litter nests. Since floor-pens in the present study were also equipped with roll-away nests, frustration may have been due to the properties of the nests. Several characteristics inherent to a litter nest may be important in eliciting nest-entry and sitting. These may include for example, the material the floor of the nest is covered with (Kite et al., 1980a; Huber et al., 1984; Breden et al., 1985) or the slope of the floor. Alternatively, it might be that the restricted environment and the inability to move away from the flock for laying may have caused frustration (Wood-Gush, 1972). This view is supported by the fact that floor-layers showed more orientation away from the flock than nest-layers. More research will be necessary to provide an answer to this question.

7.4. Conclusions

- * Physiological irregularities appeared to be uncommon in the laying strain under study. Therefore this factor probably does not account for the difference between individual hens to use either the floor or a nest-box for laying.
- * Floor-layers showed more behaviour indicative of frustration than did nest-layers. Therefore individual differences in nest site use may be caused by differences in response to environmental stimuli.

Chapter 8

General discussion

In the present study the development of nesting behaviour and nest-site selection in individual hens was described. Furthermore, a number of factors appeared to affect the hen's choice to use either the floor or a nest-box for laying. In this chapter these results are discussed in some detail. Moreover, recommendations in order to reduce the percentage of floor-eggs are formulated and their practical significance is discussed.

In the past, but also more recently, several other studies concerning nest-site selection and floor-laying in domestic hens have been carried out. A number of factors, other than those reported in the present study, appeared to affect the hen's nest-site choice. In order to reduce floor-laying as far as possible all factors that contribute to this problem must be taken into account. In this way the most adequate circumstances can be created to stimulate laying hens to use a nest-box. Therefore recommendations are not only based on results reported here, but also on those obtained in other studies.

8.1. Development of nesting behaviour and nest-site selection

The results revealed that hens do not enter nest-boxes nor show nest-building activities in the weeks before the first laying (chapter 4). During this period, however, they gather information from potential nesting sites by inspecting them visually. Probably this information is used for the selection of a suitable nest-site; this became overt only one day before the day of first oviposition (chapter 5). Moreover, preventing nest-inspections in the weeks before laying to occur, affected subsequent nest-site choice (chapter 6). From these results it may be concluded that nest-site selection in domestic fowl is, as expected, a process which starts several weeks before the hen comes into lay. Probably this process is under the control of oestrogens, which are produced by the developing ovaria (Wood-Gush and Gilbert, 1975). In this respect domestic fowl resemble species of nest-building birds; here the various stages of nest-building

are also synchronized with the development of the reproductive tract (Emlen, 1955).

Individual hens were consistent in using either the floor or a nest-box for laying (chapter 4). Similar results were reported by McGibbon (1976), Kite et al. (1980b) and Appleby et al. (1983a). Obviously the hen's choice to use a nest-box or the floor for laying is established at the start of the egg-laying period and is difficult to change. However, most hens were inconsistent in nest-box choice (Appleby and McRae, 1986; chapter 4), even if eggs were allowed to accumulate (Appleby and McRae, 1986) and not only between but also within clutches (chapter 4). In contrast, feral living hens were very consistent in using the same site, at least within clutches (McBride et al., 1969; Duncan et al., 1978). Consistency increased if adjacent nest-boxes were regarded as one nest-box. These results suggest, as mentioned before (chapter 4, discussion), that nest-boxes were probably placed too close to each other. Since nest-sites in feral fowl are all well separated from each other (McBride, 1970), hens may not have discriminated between adjacent nest-boxes.

An alternative explanation for inconsistency in nest-box choice within individuals was provided by Appleby and McRae (1986). In this study nest-boxes offered provided the hens with different dimensions of concealment. Boxes providing no concealment at all were rarely chosen, while those providing some dimension of concealment were mostly favoured. However, choices for concealment above a minimal level were equivocal. From this it was concluded that concealment is an important stimulus in nest-site selection and that artificial nest-boxes, which offer more concealment than natural sites, act as super-normal stimuli. Since choices between super-normal stimuli are supposed to be confusing (Appleby and McRae, 1986), this could explain the inconsistency in choice between nest-boxes used in these experiments. However, if hens are offered nest-boxes differing in nest-floor coverage, a rather consistent choice pattern is observed, not only within, but also between individuals (chapter 5). These results indicate that the nest-boxes used did not act as super-stimuli and in addition, that nest-floor-coverage is another important key-stimulus in the selection of a nesting site.

Throughout the whole study nest-boxes provided were used more often as a nesting site than the floor of the pen (chapters 4,5 and 6). Probably the

nest-boxes provided the hens with such a concealment, which made them more suitable nesting sites than the floor of the pen.

Generally, litter nest-boxes were preferred above roll-away boxes. However, if the litter boxes were absent, a number of hens would accept the alternative roll-away box, while other hens started using the floor. Obviously individual hens have different nesting requirements. In this respect penned domestic hens resemble feral living fowl. In the latter, nest-sites of individuals also varied widely (Duncan et al., 1978).

Preventing hens to inspect roll-away nests visually in the weeks before laying increased the hen's willingness to use these boxes later on. In contrast, experience with litter nests in the weeks before laying reduced the use of roll-away nests. Prior experience with the nesting alternatives was also reported to affect subsequent nest-choice in other strains of domestic fowl (Kite, 1983). Apparently a hen's nest-choice is affected by interfering with the process of nest-site selection in the weeks before laying. From these results it is concluded that, in contrast to for example a cavity-nesting Falcon species (the kestrel; Shutt and Bird, 1985), the domestic hen's nest-site selection is not completely derived innately through genotype; similar to another Falcon species (the peregrine falcon; Barclay and Cade, 1983), domestic hens appear to have more general nesting requirements, resulting in the acceptance of various types of nest-boxes. As mentioned before, feral living hens, like other ground nesting birds e.g. the Canada Goose (Collias, 1964), do not build nests in that they carry nesting material to the nest-site. Therefore they will have to rely upon the structures present in their natural environment. Probably these ground nesting birds evolved more general nesting requirements. Nevertheless, they will always choose the best option available.

8.2. Factors affecting floor-laying

Floor-laying was associated with a number of factors. Some hens only laid the first egg on the floor and started using nest-boxes for subsequent ovipositions (Appleby et al., 1983a; Breden et al., 1985; chapters 4 and 6). No clear explanation for this phenomenon is available. Oviposition is known to be accompanied by elevated plasma levels of corticosterone

(Beuving and Vonder, 1981). Moreover, first ovipositions appeared invariably to be preceded by restless behaviour such as pacing and trying to escape from the pen (chapter 4). Thus a hen may be thought of being under stress during the first egg-laying days (Wood-Gush, 1983). Restlessness may hinder her responding to the stimuli of the nest and thus the egg may be dropped on the floor. In the course of time in most hens restlessness disappeared probably because of habituation. This allowed sitting quietly on a nest, thus resulting in the laying of a nest-egg.

Floor-eggs caused in this way are difficult to control. However, other factors that appeared to contribute to the occurrence of floor-eggs are probably more suited to be controlled. These factors will be discussed in the next paragraphs.

8.2.1. Social factors

The effect of social dominance and the presence of a cock on the hen's nest-site choice was investigated. No relation was found between site use and social rank. Obviously competition for nest-boxes does not contribute to floor-laying. By contrast, a nest-box was frequently used simultaneously by more than one individual despite the fact that a number of boxes were unoccupied (chapter 4). Gregariousness in laying has also been reported by Kite et al. (1980b) and Appleby et al. (1984).

The results, however, suggested that the hen's choice to use either the floor or a nest-box for laying was affected by the presence of a cock. In a pen provided with roll-away nests and a cock fewer floor-eggs were found as compared with such a pen without a cock. Moreover, the cock was frequently observed enticing hens towards the boxes while cornering and he also entered nest-boxes (chapter 4). In this respect domestic fowl resemble feral living fowl (McBride et al., 1969). Therefore housing laying hens with cocks might prove to be an efficient manner in reducing floor-laying.

Under practical circumstances, however, flock size is much larger as compared to natural conditions (McBride et al., 1969). Flock size is known to affect mating behaviour of males. If hens and cocks were kept in large flocks (14 cocks and 247 hens and 15 cocks and 164 hens), dominant cocks frequently interrupted mating of sub-ordinates by threatening (Pamment et

al., 1983). Similarly, dominant cocks are expected to interrupt cornering of sub-ordinates. Therefore, in large flocks the positive effect of cornering, as mentioned above, will only be achieved partly. The best effect of the presence of a cock may be expected in very small flocks and if the natural ratio is followed (i.e. 1 cock per 6-8 hens ; McBride et al., 1969).

Flock-size also appeared to affect another social process i.e. social spacing (Hughes et al., 1974). In contrast to natural conditions (McBride et al., 1969), no stable groups were formed in flocks of four to 600 hundred White Laying hens. Some individuals were observed to move over only part of the total area. However, other hens moved over large areas. Since individual recognition in large flocks is unlikely, this may result in agonistic interactions between strange hens. Against this background we may explain why broiler breeders, that are kept in large flocks, removed pen-mates from the nest-boxes (Perry, 1977). Perhaps a resident bird may have chased away an intruder, and this may have facilitated the production of a floor-egg.

8.2.2. Nest-box management

Nest-box design

Litter nests were associated with fewer floor-eggs than were roll-away nests (chapter 6). Moreover, in a choice situation the majority of hens preferred litter nests provided with wood-shavings or buckwheat husks over roll-away nests provided with a wire basket or artificial grass (chapter 5). Comparable results were reported for White Laying hens (Huber et al., 1985; Breden et al., 1985) using a similar range of materials. White Leghorn hens and Bantams were also found to respond to the presence of nesting material in a nest: significantly more eggs were laid in nests provided with litter than in nests with a bare metal floor (Kite et al., 1980a). Apparently the presence of litter is an important key stimulus in eliciting nest-entry and sitting. Since nesting material is known to play an important role in protecting the eggs from the cold (Collias, 1964), this may explain the exhibited preference for litter-nests.

Opening roll-away nests provided with a wire basket on the day the first eggs in the flock appeared (=late), resulted in fewer floor-eggs than

opening such nests on the day the hens were placed in the pen (=early). Apparently, the willingness to use roll-away nests decreased if hens had been able to inspect such nests in the weeks before laying. Therefore, floor-laying is expected to reduce further, if the number of hens that have had no experience with roll-away nests before laying could be increased. Against this background, the positive effect of opening such roll-away nests late may not be present in large flocks. In contrast to small flocks, the interval between the days the first and last hens start laying is larger in large flocks kept in the same windowless hen-house (pers. comm.; Koolstra, 1986). Hence, more hens will be able to inspect the roll-away nests before they start laying, which is supposed to decrease the attractiveness of the boxes. However, the use of such roll-away nests in large flocks might be stimulated by bringing more hens into lay simultaneously at the start of the laying period. A crucial factor influencing reproductive performance is the lighting regime applied during the rearing and the start of the laying period (Morris, 1967). Under practical conditions hens are subjected to lighting regimes resulting in optimal reproductive performance. However, since many different schedules are known to affect reproductive performance (Morris, 1967), the existence of a lighting regime resulting in a more synchronous physiological development of flock-mates at the start of laying is not imaginary. Furthermore, more hens may be brought into lay simultaneously by composing uniform flocks. This can be achieved by selecting individuals according to body weight and comb-sizes. Adjusting the lighting scheme and composing uniform flocks may, in combination with opening roll-away nests on the day the first eggs appear in the flock, reduce floor-laying in large flocks. A similar effect is expected if such a treatment is applied to small flocks.

Providing nest-boxes with litter until a laying percentage of about 38.6 % (LT2) and replacing the litter with a wire basket, also reduced floor-laying, although its incidence was not reduced further as compared with opening roll-away nests late. However, fewer floor-eggs were laid as compared with replacing the litter at 17.7 % of lay (LT1). In the week after the change the floor-egg percentage in group LT2 increased only slightly. Postponing the nest-change, allowed a larger number of hens to start using the litter nests. Probably these hens were trained in the use of a nest-box and continued in doing so, even after the replacement of

litter by a wire basket. Postponing the moment of the nest-change until peak-production might reduce floor-laying even more.

Furthermore, roll-away nests provided with astroturf were preferred over those provided with a wire basket, a carpet floor or a wire mesh floor (Koolstra and Ehhardt, 1982; Breden et al., 1985).

If hens are kept in aviaries with nest-boxes in three or more tiers, a clear preference was observed for the nest-boxes located in the top-tier (Ehhardt, 1985; Breden et al., 1985). It is not very well understood why these originally ground-nesting hens, chose high located nests. Feral hens about to lay move away from the flock (Duncan et al., 1978). Perhaps the higher located nests provided these penned hens with some form of isolation.

Kite et al. (1980b) reported that hens prefer nests containing eggs to empty ones. Therefore the presence of eggs might stimulate hens to start using a nest-box, which was confirmed more recently: the use of roll-away nests provided with an artificial decoy egg was associated with fewer floor-eggs than the use of nests without such eggs (Breden et al., 1985).

Other studies concerning nest-site choice in domestic hens investigated the effect of light intensity in the nesting site. Brown Leghorn hens did not prefer dark nests, unless they had some experience with them (Wood-Gush and Murphy, 1970). White Leghorn hens laying their first eggs exhibited a preference for dark nests. However, if these hens had some laying experience in open pens, a greater preference was shown for light nests. In contrast, birds of a strain derived from Rhode Island Reds were more likely to lay in light nests (Appleby et al., 1983b). The majority of hens of three crossbreed laying strains (White Leghorn x Black Australorp; White Leghorn x New Hampshire and Black Australorp x New Hampshire) appeared to nest in unilluminated nests rather than in illuminated nests. This effect was more obvious in hens that had had nesting experience with nest-boxes than in hens that had been housed in cages (Kite, 1983). In dwarf White Leghorn pullets floor-laying was worse if nests were placed opposite a 25 W bulb than when they were placed underneath it (Dorminey, 1974).

These results demonstrate that different strains respond differently to nest-illumination. Moreover, nest-choice was affected by prior laying experience. Prior experience with the nesting environment in the weeks before laying affected subsequent nest-box use (see above). Therefore subsequent

choice for varying levels of illumination in nests may also be affected by prior experience with the nesting alternatives.

Other characteristics of nests such as entrance design (Kite et al., 1980a) did not affect the hen's choice of a nest-box. Therefore this factor is not expected to affect floor-laying. However, the material the boxes are made of appeared to influence their use; if offered metal nests, 55.1 % floor-eggs were found (Ehlhardt et al., 1984a). Hurnik et al. (1974a) showed that metal nests were associated with more floor-eggs than were wooden nests.

Nest-box number

Results on experiments in which nest/hen ratio has been varied have not been published. One study reported only a few floor-eggs (0.93 %) in a pen of 250 pullets provided with 40 nests (nest-ratio approximately 1: 6.25; Woods and Laurent, 1958). If 14 hens were kept in a pen with 2 litter nests no floor-eggs were found (unpublished data). A comparable ratio (8-9 hens per nest) was applied in larger flocks and here only 1.5 % eggs were laid on the floor (Ehlhardt, 1985). However, crowding in a nest frequently occurred, which may have resulted in cracked eggs (unpublished data; Ehlhardt, 1985).

Furthermore, not all nests offered are equally chosen. Hens kept in aviaries, for example, exhibited a preference for high located nests (Breden et al., 1985; Ehlhardt, 1985). Kite et al. (1980b) distinguished sociable and solitary nest-box layers. The first mentioned clearly preferred the presence of another hen to a vacant nest-box, while the solitary nesters generally avoided occupied nests. Shortage of nest-boxes may force some hens to start using the floor. Therefore it is recommended to choose a ratio lower than 1:8 or 1:7, not only to prevent floor-laying, but also to prevent crowding in nest-boxes. Under practical circumstances one nest for four (Anon., 1967) or five hens (Francis, 1970) has been recommended. Against the background of the foregoing these ratio's may be quite satisfactory.

8.2.3. Accessibility of the nests

Observations in broiler breeders suggested that accessibility of nests is an important factor in nest-use (Kite et al., 1980a). Hearn (1983) reported in broiler breeders that the incidence of floor-laying was reduced in those pens where the bottom tier of nest-boxes was at litter level. Since broiler breeders are heavy birds, it was suggested that the inaccessibility of the nests was primarily related to body weight. However, as demonstrated by Appleby et al. (1983a), floor-laying by individuals was more generally related to failure to perch. Hens reared with perches laid fewer floor-eggs than hens reared without perches. Since perching is important for access to raised nest-boxes, this factor has an indirect effect on nest-box use.

Housing hens several weeks before the start of the egg-laying period appeared to have a similar effect. Ehlhardt et al. (1984b) reared hens under three different conditions: in battery cages, in a litter-wire floor-pen and in a so-called Tiered-Wire-Floor-system (TWF-system). Moreover, the age of housing in the laying pen was varied: half of the hens were placed at an age of 16 weeks in the TWF-system, which was equipped with elevated nests and the other half at an age of 19 weeks. More floor-eggs were laid in the groups that had been reared in the battery-cage and in the wire floor-system as compared with those reared in the alternative system, at least if hens had been placed in the laying pen at an age of 19 weeks. However, this effect of rearing condition was not present in the group that had been placed in the laying pen at an age of 16 weeks. Obviously these hens were trained well enough in perching before the start of the egg-laying period, which enabled them to reach the raised nests and other elevated facilities provided in the floor-pen, as well.

8.2.4. Individual differences

Only a few nest-users occasionally appeared to lay a floor-egg, which may have been due to disturbances in the hen-house. However, some hens always used roll-away nests for laying, while other hens, kept under identical conditions, would lay on the floor, which allowed us to distinguish floor-

and nest-layers. This difference between individuals was not related to physiological factors. Since floor-layers showed more behaviour indicative of frustration, the difference between individuals may have been due to differences in responsiveness to environmental stimuli (chapter 7). Similar results were reported by Wood-Gush (1972), who compared the pre-laying behaviour of White and Brown laying hens housed in cages. The white strain showed more behaviour indicative of frustration than the brown strain, which spent more time sitting in the half hour preceding oviposition. Since the white and brown strain showed no differences in the strength of the nesting response under less intensive conditions, the difference between strains was supposed to be connected with the way they interact with sub-optimal stimuli. Furthermore, considerable variability in the sitting duration was present amongst the white strain hens suggesting that this trait has a genetical basis. If differences in nesting behaviour between floor- and nest-layers in the present study are heritable, it may be possible to select for and against hens that lay on the floor under conditions prevailing in our pens.

The existence of a genetical factor has been reported by McGibbon (1976). However, the results were affected by rearing circumstances. Increased floor-laying was only present in inbred lines that were reared in cages, whereas this effect was lacking in free range reared hens. Probably McGibbon selected for a trait that indirectly affected the use of a nest i.e. the ability to perch (see above).

Selection for a particular trait may result in an unforeseen selection against a desirable one. Furthermore, selection takes a lot of time. However, short term effects may be expected by changing the environment and therefore the latter approach may be more suitable. In that case further research will have to be carried out in order to find out what particular environmental factors frustrate the nesting tendency in floor-layers.

Several other factors than those discussed so far were reported to affect floor-laying or the hen's nest-site choice. Some of them concentrated on the design of the laying pen such as the location of the feed-troughs (Stappers, 1982) and the presence (Sainsbury, 1980a) or size and location of the droppings pit relative to the nests (Stappers, 1982). Furthermore, several unpublished data emphasized the importance of the type of material

used on the pen-floor or the micro-climate of the nest. However, experimental evidence supporting the findings is not always available, while most of these factors did not appear to have a systematic effect on floor-laying. Comparisons between studies are difficult to make, since these often differed from each other in many aspects.

In conclusion, a number of factors appeared to affect the hen's nest-site use. In designing alternative laying environments, it is important to take these factors into account in order to reduce floor-laying. As demonstrated in the present study an interaction was present between two factors: the properties of the nests and the moment the hens got access to them. Probably several other factors interact with each other and it may be worthwhile to elucidate their effects on the occurrence of floor-laying.

8.3. Recommendations and their practical significance

In this section recommendations in order to reduce floor-laying are formulated and their practical significance is discussed in relation to an alternative system that is being developed in the Netherlands, the so-called Tiered-Wire-Floor-system (Ehlhardt et al., 1984a,b; Ehlhardt, 1985).

In order to reduce floor-laying it is recommended:

- to use nests made of wood.

- to use litter nests provided with wood-shavings. However, in contrast to roll-away nests, litter nests provided with wood-shavings need laborious manual egg-collection. The mechanical harvesting of litter nests is possible by using a "belt" collectiontype (so-called tube-nests) provided with buckwheat husks as nesting material. The collection is achieved by moving litter and eggs together on a belt to an adjacent room. Here eggs and husks are separated and the litter is recycled. Since the use of such a nesting system is more expensive as compared with a roll-away nesting system (pers.comm.; Workamp, 1986), its introduction in the laying sector is not considered to be a competitive alternative to roll-away nesting systems.

-to open roll-away nests, which are not generally preferred by hens for laying, on the day the first eggs in the flock appear. Furthermore, this may prevent hens to get used to sleeping or resting in the nests during the weeks before laying. Nests may be cleaner and as a result the quality of the consumption eggs may be maintained.

If this treatment is applied to large flocks, it is recommended to compose uniform flocks, according to body weight and comb-sizes and, if possible, to choose a lighting regime that allows for a more synchronous physiological development of the pullets.

-to provide roll-away nests with astroturf and a decoy egg.

-to stimulate the use of roll-away nests by training some young hens with nest-boxes that are initially provided with litter, which is subsequently replaced by astroturf. Training all hens in the use of a nest may reduce floor-laying even more. This treatment implies that eggs will have to be collected manually during the first weeks of the egg-laying period. Moreover, a poultry farmer will have to spend some extra labour in converting litter nests into roll-away nests. Therefore the extra costs due to these factors will have to be weighed against the profits made by more nest-eggs later on.

-to provide the nests with a decent alighting rail; rails should be fixed close to the nest front.

-to use a nest/hen ratio of 1:4 or 1:5.

-to equip pens with nest-boxes provided in three or more blocks of two or three tiers, in stead of providing one block with many tiers. If possible, it might be considered to provide only one tier of high located nest-boxes.

Recently a nesting-system has been developed, which meets most of the requirements listed here (Anon., 1983; the Bressler nest). It is provided with a roll-away feature, which makes the nest compatible with belt collection systems. The special insert used in a single nest unit has been designed to be used as a litter training nest for young birds. The nest can

easily be converted into a roll-away nest. The nest-inserts have a removeable rubber or nylon pad with a decoy egg. An adjustable cover prevents the birds sleeping in the nests and a fixed perch is designed to make access easier. This nest-system is made of galvanised steel, however, it is recommended to construct such nests of wood.

-to take the variation between strains and the effect of previous housing conditions into account with respect to nest-illumination. Brown hens readily accept light nests, but White hens prefer darker nesting sites. Hens that have been reared and/or have had some laying experience under dark circumstances, will prefer to lay in a dark nest- box and vice versa, hens that have been reared and/or have been laying in light circumstances will prefer to use light nest-boxes.

-to rear hens on the floor with perches and to place them in the laying house at an age of approx. 17-18 weeks so that they can adapt to the new environment, or to place hens in the laying house at an age of 16 weeks.

-to avoid collecting eggs during the egg-laying peak in the morning to prevent disturbance to nesting birds.

-to keep hens in small flocks. Good results are obtained with a Tiered-Wire-Floor-system (TWF-system) where hens are kept in flocks of 270 individuals. If technically possible, it is recommended to place rows of these small systems in a hen-house, instead of designing one large TWF system.

-to place one cock on every 6-8 hens. However, this recommendation is only supposed to be affective if hens are kept in very small flocks (approx. 8 hens). However, since this way of housing is rather expensive, this recommendation is not supposed to be practically manageable.

SUMMARY

Since World War II livestock husbandry has been highly intensified. This trend was most obvious in the poultry industry. Laying hens used to be housed outdoors in free-range systems, but nowadays these systems have almost entirely been replaced by the battery-cage. In the early sixties scientists and the general public started to express much concern for the well-being of hens kept for egg-production in battery cages. In reaction to this concern for the well-being of farm animals, several research programs were started. One of them concentrated on the objective assessment of welfare. Moreover, investigations to improve existing systems and to develop alternative floor-systems were started (chapter 1). However, a problem common to all floor-systems is the reluctance of a various percentage of hens to use the laying nests provided. This has considerable economic implications, such as loss of eggs, dirty eggs and time consuming egg-collection. Acceptation of alternatives will be promoted if such a problem is solved. The general aim of the present study was to trace factors that cause floor-laying.

Chapter 2 reviews some literature on the physiology and the normal nesting behaviour of domestic hens. It is concluded that irregularities during, for example, the hormonal control of ovulation may easily lead to abnormalities in egg-production and nesting behaviour and thus to floor-eggs, as well. In chapter 7 these parameters were used in order to find out to what extent floor-laying is caused by physiological irregularities (see below).

Chapter 3 presents a description of the rearing and experimental housing conditions and of the hens used in this study. Furthermore, it provides a definition of the behavioural elements scored.

In chapter 4 the development of egg-laying behaviour and nest-site choice is described in seven flocks of hens housed in small floor-pens (2 x 2 square meter). Special interest is directed towards social dominance and the effect of the presence of a cock on the hen's nest-site choice.

In the weeks before the hens came into lay they frequently examined the nests, whereas nest-entries only occurred some days before or in the hours preceding the first oviposition. It was postulated that the early examinations serve the selection of a suitable nest-site.

In order to study perseverance in nest-box choice, two parameters were used: a perseverance index defined as the number of the same choices on successive oviposition days divided by the total number of choices and a frequency index, defined as the number of the same choices divided by the total number of choices. Hens were judged to persevere in their choice if both measures reached values larger than 0.7.

Only one of the 13 observed hens persevered in nest-box choice within clutches; she nearly always chose the same box on subsequent days, but started another egg-laying sequence in another nest-box. The other hens frequently changed nest-boxes. Consistency in nest-choice increased, if three boxes along one side of the pen were regarded as one nest; four of the 13 hens nearly always used the same side of the pen. Four other birds did choose the same side of the pen on successive oviposition days, but started another egg-laying sequence on the other side of the pen. One hen used nest-boxes on one side of the pen more frequently, although not on subsequent oviposition days. The remaining four hens did not show any consistency in their nest-choice behaviour. It was concluded that individual hens involved different factors in their nest-site choice.

Furthermore, individual hens were consistent in using either the floor or a nest-box as a nesting site. No relationship was found between social status and nest-box choice, nor between social status and using the floor or a nest-box for laying. Some evidence was provided that the presence of a cock could reduce the percentage of floor-eggs in a pen provided with roll-away boxes.

Chapter 5 presents the results of an experiment designed to investigate the effect of rearranging the sites of four different nest-boxes on the nest-examination duration in the weeks before and during the egg-laying period. Two types of examinations were distinguished: inspections and glances. Moreover, the development of inspections and glances in the weeks before laying is described and compared (experiment 1). Finally, in the first and in a second experiment the nest-examination pattern in the weeks before laying and its relationship with the final nest-choice is studied.

In the first experiment sixteen white laying hens were placed in 8 round floor-pens (1.5 m \emptyset); two hens per pen. Each pen was provided with four different nest-boxes; nest-floors were covered with astroturf, wood-shavings, buckwheat husks or a wire basket. In the weeks before laying the

hens were exposed to an exploration test in their home pen. During the first two weeks of the experiment the positions of the nests never changed. Subsequently the positions of the nests in four of the 8 pens were changed 3-4 times a week (=experimental group). In the other four pens nests were always in the same position (=control group). Exposing hens to an exploration test was continued in the egg-laying period.

No differences were present in the total time spent in inspections and glances in the period before the rearrangement of the nests between control and experimental hens. However, as a result of changing the positions of the nests regularly, experimental hens spent more time in nest-inspections than did control hens. Likewise, the inspection duration increased in the experimental group if days without a change were followed by days with a change and, vice versa, decreased if days with a change were followed by days without a change. From these results it was concluded that inspections during the weeks before laying serve the acquisition of information.

The total time spent in glancing at the nests remained unaffected by the treatment. Moreover, glances and inspections followed a different temporal pattern over time. In the course of time (in the weeks before laying) the glance duration decreased, whereas the time spent in inspections showed an increase. Apparently glances and inspections do not represent the same type of exploration. Glancing at the nests was regarded to be a passive form of exploration, which is initially elicited by a change in the environment. Nest-inspections were regarded as an active form of exploration during which information is gathered from the nests, which may be used for the final selection of a nesting-site.

Moving the nests to new places during the laying period did not result in an increase in the inspection duration. Obviously nest-inspections during this period do not serve the same function as those during the weeks before laying. Inspections in the hours before oviposition were supposed to represent intention movements to enter a nest-box. In the hours before oviposition glances were almost never performed.

To study the relation between nest-examinations in the weeks before laying and later nest-preference a correlation coefficient was computed between nest-preference in the weeks before and during laying. In none of the hens a significant coefficient was found. Apparently the final nest-choice could not be predicted by the amount of attention paid to the nest-

boxes during the period considered.

In the second experiment the nest-examination pattern and its relation to later nest-preference is studied in five hens that had been observed until the day of first oviposition. Experimental conditions were the same as described for experiment 1, however, nest-boxes were always in the same position. The results revealed that one day before the day of first oviposition all hens showed the tendency to spent most time in inspecting the nest they preferred for the oviposition of the first series of eggs. Apparently the final nest-choice was established one day before the day of first oviposition.

Chapter 6 presents the results of two experiments designed to reduce the percentage of floor-eggs. The effect of the properties of the nests (factor 1) and the moment the hens got access to the nests (factor 2) on the percentage of floor-eggs is investigated. Moreover, in experiment 1 the interrelationship between these two factors is examined. In both experiments the effect of the treatments are described over time. The effectiveness of a treatment was judged according to the percentage of floor-eggs laid during the whole 6-week egg-laying period and during the 6th week of the egg-laying period.

In the first experiment twenty-four flocks of white laying hens were housed at an age of 16 weeks in small floor-pens. Two types of nests were used (litter and roll-away nests); the nests were opened at two different moments (on the day the first egg appeared in a flock=late, or on the day the flocks were housed in the pens = early). A main effect was present of the properties of the nests: more floor-eggs were found in pens provided with roll-away nests than in pens provided with litter nests, indicating that litter was preferred over a wire basket. Furthermore, a significant interaction was present between the two factors under study; opening roll-away boxes late resulted in fewer floor-eggs than opening these boxes early, whereas no differences were found between opening litter nests early and late. It was concluded that the extent to which early experience with nests affects the incidence of floor-laying depends upon the type of nest-box used.

In order to reduce the percentage of floor-eggs even more as compared to opening roll-away nests late, the influence of converting litter nests into roll-away nests at about 15 and 35 % of lay on the percentage of

floor-eggs was studied (experiment 2). For this purpose sixteen flocks of white laying hens were housed in floor-pens at an age of 16 weeks. In 8 pens litter nests were converted into roll-away nests at an average laying percentage of 17.7 % (group LT1) and in the remaining 8 at an average laying percentage of 38.6 % (group LT2). More floor-eggs were found in group LT1 than in group LT2 , not only if the total period after the nest-change is considered, but also during the last egg-laying week.

A comparison of the results within and between both experiments showed that replacing the litter with a wire basket at 17.7 % of lay resulted in more floor-eggs during the 6th egg-laying week than opening roll-away nests at the start of the egg-laying period. Obviously the latter treatment did not reduce the incidence of floor-laying further. In contrast, it appeared to have a negative effect. In the week immediately following the nest-change the percentage of floor-eggs in group LT1 significantly increased. From this it was concluded that if hens have only been able to inspect nests visually in the weeks before laying, they are less likely to start using roll-away nests later on.

Changing litter nests into roll-away nests at about 38.6 % of lay resulted in a comparable percentage of floor-eggs as opening roll-away nests late, if the 6th egg-laying week is considered. Thus the first mentioned treatment did not reduce floor-laying further as compared with opening roll-away nests late.

Replacing the litter with a wire basket at 38.6 % of lay (LT2) resulted, as expected, in fewer floor-eggs during the 6th egg-laying week as compared with changing the nests at 17.7 % of lay (LT1). Postponing the moment of the nest-change allowed a larger number of hens to start using the litter nests. Probably these hens were trained in the use of a nest-box and continued in doing so, even after the replacement of wood-shavings with a wire basket.

As had become evident in chapter 4, some hens always used the floor for laying, while other hens, kept under the same circumstances always used a nest-box. Chapter 7 concentrates on the question which factors may cause individual differences in site use. Two possibilities that might explain such differences are considered. First, in order to detect whether floor-laying is caused by physiological irregularities, egg-laying records of

floor-and nest-layers are described and compared. The following parameters were used: daily egg-production per hen, egg-shell quality, lag duration and consistency in site use. No differences were found with respect to each of these measures between floor-and nest-layers. It was concluded that physiological irregularities are uncommon in this laying strain. Therefore this factor was not supposed to account for the differences in site use between individual hens.

Second, to find out whether floor-and nest-layers react differently to environmental stimuli or whether floor-layers simply prefer the floor for laying, the pre-laying behaviour of five floor-and five nest-layers is described and compared. The results indicated that floor-layers performed more behaviour indicative of frustration due to the nesting situation than the nest-layers. Furthermore, floor-layers spent like nest-layers some time in inspecting and entering nest-boxes during egg-laying sessions. Therefore the results did not support the view that floor-layers simply prefer the floor for laying. It is more likely that the nesting tendency in these hens is frustrated by particular properties of the (roll-away) nests or perhaps by the inability to move away from the flock.

In chapter 8 the development of nesting behaviour, the selection of a nest and factors that appeared to affect floor-laying are discussed in some detail. It was concluded that the selection of a nest is a process which starts in the weeks before laying. In order to reduce floor-laying it is recommended to take all factors, that affect the hen's nest-site choice, into account.

Furthermore recommendations to reduce the percentage of floor-eggs are derived from the results obtained in this and other studies concerning nest-site choice in domestic hens and their practical significance is discussed.

DE ONTWIKKELING VAN HET EILEGGEDRAG EN DE LEGNEST-KEUZE VAN WITTE LEGHENNEN

SAMENVATTING

Gedurende de laatste decennia heeft de veehouderij in Nederland en de andere Europese landen een sterke ontwikkeling doorgemaakt. Deze werd onder meer gekenmerkt door de betrokken dieren in grote aantallen per oppervlakte-eenheid te huisvesten in een monotone omgeving, terwijl de bewegingsvrijheid aanzienlijk beperkt werd.

Deze trend was het duidelijkst waarneembaar in de pluimvee houderij. Leghennen, bijvoorbeeld, werden tientallen jaren geleden nog gehuisvest in vrij kleine groepen in stallen voorzien van een uitloop. Vervolgens werd dit systeem vervangen door meestal vensterloze stallen zonder uitloop voorzien van een strooisel- of strooiselrooster vloer, terwijl het oppervlak per dier werd verkleind. Tegenwoordig zijn ook deze laatste systemen vrijwel geheel vervangen door het batterij-systeem. In het begin van de jaren zestig kwamen echter bezwaren naar voren tegen deze wijze van huisvesting voor leghennen, zowel vanuit maatschappelijke groeperingen als vanuit verschillende wetenschappelijke disciplines. Als gevolg hiervan werden onderzoekprogramma's gestart, die in hoofdstuk 1 in het kort beschreven worden. Een ervan richt zich op de vraag, hoe op objectieve wijze welzijn gemeten kan worden. Een ander onderzoek richt zich enerzijds op verbetering van bestaande huisvestingssystemen, terwijl anderzijds gezocht wordt naar alternatieve wijzen van grondhuisvesting voor leghennen. Echter, het huisvesten van hennen op de grond brengt enkele problemen met zich mee, zoals het voorkomen van buiten-nest- of grond-eieren, hetgeen een financiële strop voor de pluimveehouder inhoudt: eieren die niet in de daarvoor bedoelde legnesten gelegd worden, gaan verloren of worden bevuild met mest, terwijl het verzamelen van grond-eieren zeer tijdrovend is. Acceptatie van alternatieve grond-huisvestingssystemen zal worden bevorderd, als dergelijke problemen opgelost zijn. Het doel van dit onderzoek is factoren op te sporen, die het voorkomen van grond-eieren veroorzaken.

In hoofdstuk 2 wordt literatuur besproken met betrekking tot de fysiologie en het nestgedrag van de gedomesticeerde hen. Geconcludeerd werd, dat onregelmatigheden gedurende, bijvoorbeeld, de hormonale controle van de ovulatie kunnen leiden tot abnormale ei-productie en afwijkend eilegggedrag,

hetgeen weer tot het leggen van grond-eieren kan leiden. In hoofdstuk 7 worden die parameters (abnormale ei-productie en afwijkend eileggedrag) gebruikt om na te gaan in hoeverre het leggen van grond-eieren veroorzaakt wordt door afwijkingen in de fysiologie.

In hoofdstuk 3 wordt een beschrijving gegeven van de algemene opfok- en experimentele omstandigheden. Tevens worden hier de gescoorde gedragselementen gedefinieerd.

De ontwikkeling van het nestgedrag en de nest-keuze van individuele hennen worden beschreven in hoofdstuk 4. Tevens wordt de invloed bestudeerd van dominantie en de aanwezigheid van een haan op de legnestkeuze. In de weken voor de hennen aan de leg kwamen, werden de legnesten regelmatig bezocht; de hennen gingen er echter pas enkele dagen of slechts enkele uren voor de komst van het allereerste ei in. Verondersteld werd, dat deze vroege nest-bezoeken van belang zijn voor de uiteindelijke nestkeuze.

Om de consistentie in het legnestgebruik te kunnen bestuderen, werden twee parameters gehanteerd: een "perseverance-index", die werd gedefinieerd door het aantal gelijke legnest-keuzes op achtereenvolgende dagen te delen door het totale aantal keuzes en een "frequency-index", gedefinieerd als het totale aantal gelijke keuzes gedeeld door het totale aantal keuzes. Een hen werd consistent in haar keuze beoordeeld, als beide parameters een waarde bereikten van groter dan 0,7. Slechts een van de 13 hennen was consistent in haar legnestkeuze; zij gebruikte vrijwel altijd hetzelfde legnest op achtereenvolgende dagen, maar legde de volgende serie eieren in een ander legnest. De andere hennen wisselden regelmatig van legnest. Een consistent keuzepatroon werd verkregen, wanneer de drie legnesten aan een kant van het hok werden beschouwd als één legnest; vier van de 13 hennen legden bijna altijd aan de zelfde kant van het hok. Vier andere hennen gebruikten wel een nest aan dezelfde kant van het hok op achtereenvolgende eilegdagen, maar legden de volgende serie eieren aan de andere kant van het hok. Eén hen gebruikte frequent een nest aan één kant van het hok, echter niet op achtereenvolgende dagen, terwijl de overige vier hennen een random keuzepatroon vertoonden. Deze gegevens wijzen erop, dat de legnestkeuze van individuele hennen op verschillende wijze tot stand komt.

Hennen, die eenmaal gebruik maakten van een legnest, bleven dit altijd doen en omgekeerd, hennen die eenmaal op de grond legden, maakten nooit gebruik van een legnest, waardoor er "grond- en nestlegsters" onderscheiden

konden worden. Er bleek geen relatie te bestaan tussen dominantie en het legnestgebruik en ook niet tussen dominantie en het gebruik van een legnest of de grond. Echter, een andere sociale factor leek wel effect te hebben op de nestkeuze; er werden aanwijzingen verkregen, dat de aanwezigheid van een haan het aantal grond-eieren in een hok, voorzien van wegrolnesten, kon reduceren.

In hoofdstuk 5 wordt een experiment (experiment 1) beschreven, waarin het effect bestudeerd wordt van het onderling van plaats verwisselen van vier verschillende nesten op de totale duur van de nest-bezoeken in de periode voor en tijdens de leg. Twee typen bezoeken werden onderscheiden: de "glances", waarbij op een afstand in het nest getuurd werd en de "inspecties", waarbij de kop in het nest gestoken werd, hetgeen opgevolgd kon worden door het oppikken van nestelmateriaal. Tevens wordt de ontwikkeling van deze twee gedragselementen in de periode voor de leg beschreven en onderling vergeleken. Tenslotte wordt in dit en een tweede experiment de relatie bestudeerd tussen nest-voorkeur in de weken voor en tijdens de leg. In het eerste experiment werden 16 witte leghorn hennen (=WL) geplaatst in 8 ronde grondhokken; 2 hennen per hok. Ieder hok was voorzien van vier verschillende nesten; de bodems van de nesten waren bedekt met astroturf (=kunstgras), houtkrullen, boekweitdoppen of een gazen geplastificeerd groen korfje. Gedurende de eerste twee weken van het experiment bleven de nesten in alle hokken op hun plaats staan. Vervolgens werden de hennen in vier van de 8 hokken blootgesteld aan een exploratietest door de nesten van plaats te verwisselen (=experimentele groep). In de andere vier hokken bleven de nesten altijd op hun plaats staan (=controle groep). Dergelijke tests werden ook uitgevoerd tijdens de eilegperiode.

Contrôle en experimentele hennen besteedden even veel tijd aan het bezoeken der nesten in de periode, voordat er gewisseld werd. Echter, door de nesten van plaats te verwisselen, besteedden experimentele hennen meer tijd aan het inspecteren der nesten dan contrôle-hennen. Op grond hiervan werd geconcludeerd, dat tijdens het inspecteren der nesten in de weken voor de leg informatie opgedaan wordt omtrent de plaats en eigenschappen der nesten; deze informatie wordt vermoedelijk verwerkt en opgeslagen in het centrale zenuwstelsel.

Het verplaatsen der legnesten had geen effect op de glance-duur. Daarnaast vertoonde de glance-duur een andere ontwikkeling in de weken voor

de leg dan de inspectie-duur. Na verloop van tijd nam de tijd besteed aan glances af, terwijl de inspectie-duur toenam. Dit zou kunnen betekenen dat beide gedragselementen niet dezelfde functie vervullen. Misschien zou het glances naar de nesten beschouwd kunnen worden als een passieve vorm van exploratie, die alleen aan het begin van de test wordt vertoond. Het inspecteren der nesten zou als een actieve vorm van exploratie beschouwd kunnen worden, waarbij de hennen dagelijks informatie opdoen omtrent plaats en eigenschappen van de nesten. Deze informatie zou gebruikt kunnen worden voor de uiteindelijke nestkeuze.

Het verplaatsen der nesten in de legperiode had geen effect op de totale tijd besteed aan nestinspecties. Kennelijk heeft dit gedragselement nu niet meer een informatie verzamelende functie, maar kan het veeleer beschouwd worden als een intentiebeweging om het nest in te stappen. Glances werden vrijwel niet meer vertoond gedurende de legperiode.

Er werd geen relatie aangetoond tussen nest-voorkeur in de periode voor en tijdens de leg. Mogelijk werd de relatie niet ontdekt, omdat niet alle hennen tot het begin van de leg werden geobserveerd. Daarom werd in experiment 2 de relatie tussen nest-voorkeur voor en tijdens de leg opnieuw bekeken, maar nu werden vijf hennen geobserveerd tot en met de dag, waarop zij hun eerste ei legden. Er bestond een tendens om het nest, dat ook gebruikt werd voor de eerste serie eieren, een dag voor de komst van het eerste ei het meest te bezoeken. Dit zou kunnen inhouden, dat de legnestkeuze een dag voordat de hennen aan de leg komen al vast ligt.

In hoofdstuk 6 worden de resultaten van twee experimenten, ontworpen om het percentage grond-eieren te reduceren, beschreven. In het eerste experiment wordt het effect van de eigenschappen der nesten en het moment waarop de hennen toegang tot de nesten krijgen op het percentage grond-eieren bestudeerd. Tevens wordt het verloop van het percentage grond-eieren in de tijd beschreven. Om het effect van een behandeling te kunnen beoordelen, werd niet alleen gebruik gemaakt van het totale grond-eieren-percentage, gelegd gedurende de eerste 6 weken van de leg, maar ook van het grond-eieren-percentage, berekend over de zesde week van de legperiode.

In het eerste experiment werden 24 koppels 16 weken oude WL leghennen gehuisvest in kleine grondhokken. Twee typen nesten werden gebruikt (strooisel-en wegrolnesten); de nesten werden op twee verschillende tijdstippen geopend (op de dag van plaatsing in het hok (=vroeg) en op de dag,

waarop de eerste eieren in de koppels verschenen (=laat). Er werden meer grond-eieren aangetroffen in hokken voorzien van strooiselnesten dan in hokken voorzien van wegrolnesten. Het vroeg openen van wegrolnesten leverde meer grond-eieren op dan het laat openen. Een dergelijk effect werd niet aangetoond in hokken voorzien van strooiselnesten. Geconcludeerd werd, dat strooiselnesten de voorkeur hebben boven wegrolnesten en dat de mate, waarin ervaring met nesten in de weken voor de leg het aantal grond-eieren beïnvloedt, afhangt van het type nest.

Ten-einde het percentage grond-eieren nog verder te doen reduceren, werd in experiment 2 het strooisel bij twee verschillende legpercentages vervangen door een gazen korfje. Zestien koppels WL leghennen werden op een leeftijd van 16 weken gehuisvest in de grondhokken. In 8 koppels werd het strooisel vervangen door een gazen korfje bij een legpercentage van ongeveer 16 % (groep LT1) en in de andere 8 bij een legpercentage van ongeveer 35 % (groep LT2). Er werden meer grond-eieren gevonden in groep LT1 dan in groep LT2. De resultaten van dit experiment en experiment 1 werden onderling vergeleken. Het vervangen van het strooisel bij een legpercentage van ongeveer 16 % resulteerde in aanzienlijk meer grond-eieren dan het laat openen van de wegrolnesten. Blijkbaar had deze behandeling geen positief effect op het wegrolnest-gebruik, maar eerder een negatief effect. Dit zou kunnen betekenen, dat hennen, die de strooiselnesten hebben kunnen inspecteren in de weken voor de leg, maar er nog geen gebruik van hebben kunnen maken, minder geneigd zullen zijn later van wegrolnesten gebruik te gaan maken.

Het vervangen van het strooisel door een gazen korfje bij een legpercentage van ongeveer 38 % resulteerde in ongeveer hetzelfde percentage grond-eieren vergeleken met het laat openen van wegrolnesten. Door het moment van de nest-verandering uit te stellen, werden er meer hennen in staat gesteld gebruik te gaan maken van een strooiselnest. Misschien waren deze hennen getraind in het gebruik van een legnest en gingen hiermee door, zelfs nadat het strooisel vervangen was door het korfje.

Zoals vermeld, gebruikten sommige hennen altijd een legnest, terwijl andere hennen, die onder dezelfde omstandigheden werden gehouden, altijd op de grond legden. In hoofdstuk 7 wordt onderzocht welke factoren verantwoordelijk kunnen zijn voor deze individuele verschillen in de nest-keuze. Twee mogelijke verklaringen werden nader beschouwd. Ten eerste, om na te gaan of

verschillen in nest-keuze veroorzaakt worden door onregelmatigheden in de fysiologie, werden ei-produktie-, eileg-patroon- en nest-keuzegegevens van grond-en nestlegsters met elkaar vergeleken. Grond-en nestlegsters verschilden onderling niet met betrekking tot deze parameters. Kennelijk komen onregelmatigheden in de fysiologie niet voor. Daarom kan deze factor niet verondersteld worden verantwoordelijk te zijn voor de verschillen in nest-keuze tussen individuen.

Ten tweede, om na te gaan of grond-en nest-legsters anders reageren op stimuli van de omgeving of dat grond-legsters gewoon de voorkeur geven aan het leggen op de grond, werd het nestgedrag van vijf grond-en vijf nestlegsters onderling vergeleken. De resultaten wezen uit, dat grond-legsters meer gedrag vertonen dat wijst op frustratie, veroorzaakt door de situatie tijdens het eileggen. Tevens besteedden grond-legsters tijd aan het inspecteren der nesten terwijl zij er ook in gingen. Uit deze twee gegevens werd afgeleid, dat grond-legsters niet simpelweg een voorkeur hebben voor het gebruik van een grondnest. Waarschijnlijk zijn deze hennen gefrustreerd door de eigenschappen van de omgeving, bijvoorbeeld door de eigenschappen van de (wegrol)nesten of door het feit dat zij zich voor het eileggen niet kunnen afzonderen van het koppel.

In hoofdstuk 8 worden de ontwikkeling van het eileggedrag, de nest-keuze van individuele hennen en factoren die van invloed bleken te zijn op het voorkomen van grond-eieren besproken. Geconcludeerd werd, dat de keuze van een nestelplaats een proces is, dat al enkele weken voor de leg begint en dat de uiteindelijke nest-keuze vermoedelijk al een dag voor de komst van het eerste ei vastligt. Ten einde het voorkomen van grond-eieren in grond huisvestingssystemen te reduceren wordt aanbevolen alle factoren, die van invloed blijken te zijn op het legnestgebruik, te betrekken bij het ontwerpen van alternatieven.

Aanbevelingen werden geformuleerd tegen de achtergrond van het in Nederland in ontwikkeling zijnde alternatieve grondhuisvestingssysteem.

Aanbevolen werd:

-houten legnesten te gebruiken

-nesten te voorzien van strooisel b.v. houtkrullen. Echter, eieren gelegd in deze nesten moeten, in tegenstelling tot eieren gelegd in wegrolnesten,

met de hand verzameld worden. Automatische eiafvoer bij gebruik van strooiselnesten is mogelijk door het zogenaamde tunnel-nest te gebruiken, dat voorzien wordt van boekweitdoppen. Echter, daar het gebruik van boekweitdoppen als strooisel duurder is dan het gebruik van een wegnest, zal de introductie van dit nest weinig kans maken.

-wegnesten, voorzien van een gazen korfje, pas te openen op de dag dat de eerste eieren in de koppel verschijnen. Deze ingreep kan nog enkele positieve effecten met zich meebrengen. De kans wordt verkleind, dat de hennen er bij voorbaat al een gewoonte van gaan maken in de nesten te overnachten. De nesten zullen hierdoor minder bevuild worden met mest, waardoor de ei-kwaliteit gewaarborgd blijft.

Als deze behandeling wordt toegepast in koppels groter dan die gebruikt in deze studie, is het aan te bevelen het koppel zo synchroon mogelijk aan de leg te laten komen. Dit zou bereikt kunnen worden door (indien mogelijk) het lichtschema aan te passen en uniforme koppels samen te stellen door te letten op lichaamsgewicht en afmetingen der kopversierselen.

-wegnesten te voorzien van astroturf en een kunst-ei.

-het gebruik van wegnesten te stimuleren door een aantal jonge hennen te trainen in het legnestgebruik met behulp van strooiselnesten, die na verloop van tijd worden vervangen door wegnesten. Het percentage grond-eieren zou nog verder gereduceerd kunnen worden door alle hennen te trainen. Dit houdt echter wel in dat de eieren gedurende de eerste weken van de leg met de hand verzameld moeten worden. Daar komt bij, dat de pluimveehouder ook extra tijd zal moeten besteden aan het vervangen van het strooisel door een wegnest-bodem. Daarom zullen de hierdoor gemaakte extra kosten afgewogen moeten worden tegen de voordelen van minder grond-eieren verderop in de legperiode.

-een nest te gebruiken per vier of vijf hennen.

-om leghokken uit te rusten met nesten geplaatst in meer blokken van twee of drie rijen, in plaats van een groot blok met meer rijen nesten. Indien mogelijk, zou overwogen kunnen worden slechts een rij hooggeplaatste nesten

aan te brengen.

Onlangs werd een nest-systeem ontwikkeld, dat tegemoet komt aan de meeste aanbevelingen, die hierboven uiteengezet zijn (het zogenaamde Bresslernest). Dit systeem is voorzien van individuele nesten met een wegrolbodem, waardoor automatische eiafvoer mogelijk wordt gemaakt. In het nest is een speciale bodem aangebracht, die voorzien kan worden van strooisel opdat het nest gebruikt kan worden als "trainingsnest". Het kan gemakkelijk omgebouwd worden tot een wegrolnest. Een verplaatsbare plaat zorgt ervoor dat de nesten afgesloten kunnen worden. Tevens is het nest voorzien van een aanvliegstick. Dit type nest is gemaakt van metaal. Aanbevolen wordt het te construeren van hout.

-de variatie tussen lijnen en het effect van opfokcondities in overweging te nemen met betrekking tot de lichtintensiteit in de nesten. Bruine hennen maken wel snel gebruik van lichte nesten, WL hennen echter niet. Als hennen opgefokt zijn en/of leg ervaring hebben gehad onder vrij donkere omstandigheden, zullen zij de voorkeur geven aan donkere nesten en omgekeerd, als zij zijn opgefokt en/ of leg ervaring hebben gehad onder lichtere omstandigheden, zullen zij de voorkeur geven aan lichte nesten.

-om hennen op te fokken op de grond en hen te voorzien van hoger gelegen zitstokken, opdat zij hiervan gebruik leren maken en hen op een leeftijd van ongeveer 18 weken over te plaatsen naar het leghok, opdat zij zich kunnen aanpassen aan de omstandigheden in het leghok, of om hennen op een leeftijd van ongeveer 16 weken al in het leghok te plaatsen.

-het verzamelen van eieren te vermijden tijdens de eilegpiek in de ochtend.
-om hennen te huisvesten in kleine koppels. Goede resultaten werden verkregen in een alternatief Tiered-Wire-Floor systeem (= etage-systeem), waarin per afdeling 270 hennen gehuisvest werden. Als dit technisch mogelijk is, wordt aanbevolen rijen van dergelijke kleine systemen naast elkaar op te stellen, in plaats van een groot TWF systeem te ontwerpen.

-om een haan te plaatsen per 6-8 hennen. Echter, deze aanbeveling wordt enkel verondersteld optimaal effect te hebben, wanneer groepen worden samengesteld van niet meer dan 6-8 hennen. Aangezien deze wijze van huis-

vesting aanzienlijk meer kosten met zich zal meebrengen, lijkt deze aanbeveling niet praktisch haalbaar.

REFERENCES

- Altmann, J., 1974. Observational study of behaviour: sampling methods. *Behaviour* 49, p.225-265.
- Anon., 1967. Beperk de verliezen door grondeieren. *Hy-Line nieuws* nr.5.
- Anon., 1983. Governments turning against laying cages in Europe. *Feedstuffs* (55)2: p.11.
- Anon., 1983a. Nest System. *Poultry International*, September. p.92.
- Appleby, M.C. and McRae, H.E., 1986. The individual nest-box as a super-stimulus for domestic hens. *Appl. Anim. Behav. Sci.*, 15, p.169-176.
- Appleby, M.C., McRae, H.E. and Duncan, I.J.H., 1983a. Nesting and floor-laying by domestic hens: effects of individual variation in perching behaviour. *Behaviour Analysis Letters* 3, p. 345-352.
- Appleby, M.C., McRae, H.E. & Peitz, B.E., 1983b. The effect of light on the choice of nests by domestic hens. *Appl. Anim. Ethol.* 11, p.249-254.
- Appleby, M.C., McRae, H.E., Duncan, I.J.H. & Bisazza, A., 1984. Choice of social conditions by laying hens. *British Poultry Science* 25, p.111-117.
- Bahr, J.M. and Nalbandov, A.V., 1977. Reproduction in Poultry. In: Cole, H.H. and Cupps, P.T. (Eds): *Reproduction in domestic animals*. Academic Press. 3rd edition. New York, San Francisco, London. p.529-548.
- Bahr, J.M., Wang, S.-C., Huang, M.Y. and Calco, F.O., 1983. Steroid concentrations in isolated theca and granulosa layers of pre-ovulatory follicles during the ovulatory cycle of the domestic hen. *Biology of Reproduction* 29. p.326-334.
- Banks, E.M., Wood-Gush, D.G.M., Hughes, B.O. and Mankovich, N.J., 1979. Social rank and priority of access to resources in domestic fowl. *Behav. Process.* 4, p. 197-209.
- Barclay, J.H. and Cade, T.J., 1983. Restoration of the peregrine falcon in the eastern United States. In: Temple, S.A. (Ed): *Bird Conservation*. Madison, University of Wisconsin Press. p.3-40.
- Bareham, J.R., 1976. A comparison of the behaviour and production of laying hens in experimental and conventional battery cages. *Appl. Anim. Ethol.* 2, p. 291.
- Beilharz, R.G., 1982. Genetic adaptation in relation to animal welfare. *Int. J. for study of Anim. Problems* 3, p. 117-124.
- Beuving, G., 1983. Corticosteroids in welfare research of laying hens. In Smidt, D. (Ed.) : *Indicators relevant to animal welfare*. Proc. EEG Seminar Mariensee, Duitsland. p.47-53.
- Beuving, G. and Vonder, G.M.A., 1977. Daily rhythm of corticosterone in laying hens and the influence of egg-laying. *J. Reprod. Fert.* 51, p.169-173.
- Beuving, G. and Vonder, G.M.A., 1978. Effect of stressing factors on corticosterone levels in the plasma of laying hens. *General and comparative endocrinology* 35, p. 153-159.
- Beuving, G. and Vonder, G.M.A., 1981. The influence of ovulation and oviposition on corticosterone levels in the plasma of laying hens. *General and comparative endocrinology* 44, p. 382-388.
- Berlyne, D.E., 1960. *Conflict, arousal and curiosity*. London, McGraw-Hill.
- Birke, L.I.A., 1983. Some issues and problems in the study of animal exploration. In: Archer, J. and Birke, L.I.A. (Eds): *Exploration in animals and humans*. Workingham Van Nostrand Reinhold, p.1-21.
- Blokhuis, H.J. and Arkes, J.G., 1984. Some observations on the development of feather pecking in poultry. *Appl. Anim. Behav. Sci.*, 12, p.145-147.
- Boon, D., 1979. *Dierenwelzijn en recht*. Gouda Quint b.v., Arnhem. D. Brouwer en Zn.

- Boon, D., 1983. Beestwaardig bestaan gaat mensen aan. Arendina Kroese-stichting. Maastricht, The Netherlands.
- Brambell, R.F.W. (Chairman), 1965. Report of the technical committee to enquire into the welfare of animals kept under intensive livestock husbandry systems. Command Paper 2836, H.M.S.O., London.
- Brantas, G.C., 1981. Ergebnisse ethologischer Untersuchungen mit Legehennen in Get-away-käfige in Krefeld und in die Niederlande. Colloquium Legehennen, Celle.
- Breden, L., Rauch, H.W., Wegner, R.M., and Speck, J. 1985. Nest-site selection: environmental aspects. Second European Symposium on Poultry Welfare. p.146-154.
- C.B.S., 1985. Statistisch zakboek landbouwcijfers. Staatsuitgeverij, 's Gravenhage, p. 93-94.
- Cochran, W.G. and Cox, G.M., 1957. Experimental designs. Second Edition, John Wiley and Sons, Inc., New York. p.148-153.
- Code of Practice for the Welfare of the Domestic Fowl, 1983. Issued by the Australian Bureau of Animal Health.
- Collias, N.E., 1964. The evolution of nests and nest building in birds. Am. Zoologist 4, p.29-36.
- Collias, N.E. & Collias, E.C., 1967. A field study of the red jungle fowl in North Central India. Condor 69, p.360-386.
- Commissie Veehouderij - Welzijn Dieren. Rapport, 1975, N.R.L.O. Den Haag.
- C.E.C. report, 1984. Commission of the European Communities. Farm animal welfare programme. Evaluation report 1979-1983.
- Craig, J.V. and Adams, A.W., 1984. Behaviour and well-being of hens in alternative housing environments. World's Poultry Science Journal 40, 3, p. 221-240.
- Cronin, G.M. and Wiepkema, P.R., 1984. An analysis of stereotyped behaviour in tethered sows. Ann.Rech.Vet., 15. p.263-270.
- Cronin, G.M., 1985. The development and significance of abnormal stereotyped behaviours in tethered sows. Dissertation L.H.Wageningen.
- Davis, D.E., 1955. Breeding biology of birds. In: Wolfson, E.(Ed.): Recent Studies in Avian Biology. University of Illinois Press, Urbana, p.264-297.
- Dawkins, M.S., 1976. Towards an objective method of assessing welfare in domestic fowl. Appl. Anim. Ethol. 2 (3), p. 245-254.
- Dawkins, M.S., 1980. Animal suffering. Chapman and Hall. London.
- Dawkins, R., 1969. A threshold model of choice behaviour. Anim. Behav., 17 (1), p.120-133.
- Dorminey, R.W., 1974. Incidence of floor eggs as influenced by time of nest installation, artificial lightning and nest location. Poultry Science 53, p. 1886-1891.
- Draper, M.H. and Lake, P.E., 1967. Physiological reactions of the laying fowl to adverse environments with special reference to the defence reaction. In: Carter, T.C. (Ed): Environmental Control in Poultry Production. Oliver and Boyd. Edinburgh and London. p. 87-101.
- Dumke, R.T. & Pils, C.M., 1979. Renesting and dynamics of nest-site selection by Wisconsin U S A pheasants (Phasianus colchicus). J.Wildl.Managem., 43(3), p.705-716.
- Duncan, I.J.H., 1970. Frustration in the fowl. In: Freeman, B.M. and Gordon, R.F.(Eds): Aspects of poultry behaviour. British Poultry Science, Edinburgh. p.15-31.
- Duncan, I.J.H., 1978. An overall assessment of poultry welfare. First Danish seminar on poultry welfare in egg laying cages, p. 79-89.
- Duncan, I.J.H., 1981. Telemetry. In: L. Yding Sorensen (Ed): First European Symposium on Poultry Welfare , p. 15-23.

- Duncan, I.J.H. and Filshie, J.H., 1979. The use of telemetry devices to measure temperature and heart rate in domestic fowl. In: Almaner, C.J. and MacDonald, D.W. (Eds): A handbook on biotelemetry and radio tracking. London, Pergamon Press, Ltd. p.579-588.
- Duncan, I.J.H., Savory, C.J. & Wood-Gush, D.G.M., 1978. Observations on the reproductive behaviour of domestic fowl in the wild. *Appl. Anim. Ethol.*, 4(1), p.29-42.
- Duncan, I.J.H. and Wood-Gush, D.G.M., 1972b. An analysis of displacement preening in the domestic fowl. *Anim. Behav.* 20, p. 68-71.
- Duncan, I.J.H. and Wood-gush, D.G.M., 1972a. Thwarting of feeding behaviour in the domestic fowl. *Anim. Behav.* 20, p. 444-451.
- Ehlhardt, D.A., 1985. Development of an alternative housing system for laying hens: the Tiered-Wire-Floor system (TWF). C.O.V.P. Mededeling no. 433.
- Ehlhardt, D.A., Voermans, J.A.M., Frederiks, W., Laseur, E. and Koolstra, C.L.M. 1984a. Development of the Tiered-Wire-Floor (TWF) as an alternative housing system for laying hens. *Proc. and Abstracts. XVIIth World's Poultry Congress and Exhib. W.P.S.A. Helsinki, Finland.* p.437-438.
- Ehlhardt, D.A., Blokhuis, H.J., Pullen, D. and Koolstra, C.L.M., 1984b. Effect of rearing environment on subsequent adaptation of White Leghorn pullets to a Tiered Wire Floor Laying House. *Proc. and Abstracts. XVII th World's Poultry Congress and Exhib. W.P.S.A. Helsinki, Finland.* p.446-448.
- Elson, A., 1976. New ideas on laying cage design - the get-away cage. *Proc. 5th. W.P.S.A. European Poultry Conf. Malta 2*, p. 1030.
- Elson, A., 1981. Modified cages for layers. In: U.F.A.W. Alternatives to intensive husbandry systems. *Proc. Symp., Wye College, University of London. Ashford, Kent. 13th, 14th, 15th July 1981.* p.47-51.
- Emlen, J.T., 1955. The study of behaviour in birds. In: Wolfson, E. (Ed.) : *Recent Studies in Avian Biology.* University of Illinois Press, Urbana. p.111-117.
- Etches, R.J. and Schoch, J.P.A., 1984. Mathematical representation of the ovulatory cycle of domestic hens. *Br. Poultry Science* 25 (1), p. 65-76.
- Fölsch, D.W., 1981a. Das Verhalten von Legehennen in unterschiedlichen Haltungssystemen unter Berücksichtigung der Aufzuchtmethoden. In: Fölsch, D.W. & Vestergaard, K.: *The behaviour of fowl. The normal behaviour and the effect of different housing systems and rearing methods.* Birkhauser Verlag, Basel Boston Stuttgart. p.73-106.
- Fölsch, D.W. 1981b. Die Veranlagung zum Brutverhalten und zur Aufzucht bei Leghorn hybriden und Bankiva Hühnern. In: Fölsch, D.W. & Vestergaard, K.: *The behaviour of fowl. The normal behaviour and the effect of different housing systems and rearing methods.* Birkhauser Verlag, Basel Boston Stuttgart. p.133-141.
- Fölsch, D.W., Dolf, Chr., Ehrbar, H. and Bleuler, T., 1982. Ethologische Prüfung und Erhebung von Wirtschaftlichen Daten in der Volierenhaltung der Legehennen. Dritte Arbeitstagung der Internationalen Arbeitsgemeinschaft Gesunde Haltungstechnik und Stallbau. 2-3 Oktober, 1981. Gumpenstein.
- Francis, P.R., 1970. Solving the problem of floor-eggs. *Farming Zambia* 5 (2), p. 36-39.
- Fraps, R.M., 1965. Twenty-four hour periodicity in the mechanism of pituitary gonadotrophin release for follicular maturation and ovulation in the chicken. *Endocrinology* 77, p. 5-18.
- Freeman, B.M., 1976. Stress and the domestic fowl: a physiological reappraisal. *World's poultry science journal* 32, p. 249-256.
- Gilbert, A.B., 1971a. The ovary. In: Bell, D.J. and B.M. Freeman: *Physiology and biochemistry of the domestic fowl*, vol. 3. Academic press, London, New York, p. 1163-1202.

- Gilbert, A.B., 1971b. Control of ovulation. In: Bell, D.J. and Freeman, B.M. (Eds): Physiology and biochemistry of the domestic fowl. Vol. 3, p. 1225-1233.
- Gilbert, A.B. and Wells, J.W., 1984. Structure and function of the ovary. In: Cunningham, F.J., Lake, P.E. and Hewitt, D. (Eds): Reproductive Biology of Poultry. British Poultry Science Ltd. (Longman Group, Harlow). p.15-29.
- Gilbert, A.B. and Wood-Gush, P.G.M., 1965. The control of the nesting behaviour of the domestic hen III. The effect of cocaine in the post-ovulatory follicle. *Anim. Behaviour* 13, p. 284-285.
- Gilbert, A.B. and Wood-Gush, D.G.M., 1971. Ovulatory and ovipository cycles. In: Bell, D.J. and Freeman, B.M.: Physiology and biochemistry of the domestic fowl. Vol. 3, p. 1353-1378.
- Gilbert, A.B. and Wood-Gush, D.G.M., 1976. The effects of exogenous oestrogen and progesterone on laying and nesting behaviour in the hen. *Brit. poultry science* 17, p. 13-15.
- Green, H.H.E., 1982. Reproductive behaviour of female wild turkeys in northern lower Michigan. *J. Wildl. Manage.*, 46(4), p.1065-1071.
- Hanson, W.R., 1970. Pheasant nesting and concealment in hayfields (*Phasianus Colchicus*). *Auk*. 87(4), p.714-719.
- Harrison, R. 1964. Animal Machines. The new factory farming industry. Vincent Stuart Ltd., London.
- Hearn, P.J., 1983. The effect of nest-box design and management on floor-eggs in a flock of broiler breeders. Poultry section B, Quarterly Journal (special feature) no. 144, p. 39-43.
- Henderson, G., 1984. The perchery as an alternative to cages. *Poultry Intern.* april, p. 72.
- Hill, J.A., 1981a. Aviary system for layers. In: U.F.A.W.; Alternatives to intensive husbandry systems. Proc. Symp. held at Wye College. University of London, Ashford, Kent. 13th, 14th, 15th July 1981, p.40-45.
- Hill, J.A., 1981b. The aviary system. In: Yding Sorensen, L. (Ed): First European symposium on poultry welfare, p. 115-127.
- Hill, J.A., 1983a. Aviary system poses feather pecking and floor-egg problems. *Poultry International*, May, p. 109-112.
- Hill, J.A. 1983b. Indicators of stress in poultry. *World's Poultry Science Journal*, 39(1), p.24-32.
- Hubert, H.U., Folsch, D.W. and Stahli, U., 1984. Influence of various nesting materials on nest-site selection of the domestic hen. *British Poultry Science*, 26, p.367-373.
- Hughes, B.O. and Black, A.J. 1973. The preference of domestic hens for different types of battery cage floors. *British Poultry Science*, 14, p.615-619.
- Hughes, B.O. and Duncan, I.J.H., 1972. The influence of strain and environmental factors upon feather pecking and cannibalism in fowls. *British Poultry Science*, 13, p.525-527.
- Hughes, B.O., Wood-Gush, D.G.M. and Morley Jones, R., 1974. Spatial organization in flocks of domestic fowl. *Anim. Behav.*, 22, p.438-445.
- Hurnik, J.F., Reinhart, B.S. and Hurnik, G.I. 1973a. The effect of coloured nests on the frequency of floor-eggs. *Poult. Sci.* 52, p.389-391.
- Hurnik, J.F., Jerome, F.N., Reinhart, B.S. and Summers, J.D., 1973. Colour as a stimulus for the choice of the nesting site by laying hens. *Br. Poultry Sci.* 14, p. 1-14.
- Iersel, J.J.A. van, and Bol, A.C.A., 1958. Preening in two tern species. A study of displacement activities. *Behaviour* 13, p.1-88.
- Jaap, R.G. and Muir, F.V., 1968. Erratic oviposition and egg-defects in broiler type pullets. *Poult. Sci.*, 47, p.417-423.

- Johnson, A.L., 1984. Interactions of progesterone and luteinising hormone leading to ovulation in the domestic hen. In: Cunningham, F.J., Lake, P.E. and Hewitt, D. (Eds): Reproductive Biology of Poultry. British Poultry Science Ltd. (Longman Group, Harlow). p.133-144.
- Johnson, P.A. and Bahr, J.M., 1985. Relative luteinizing hormone-stimulable adenylyl cyclase of the preovulatory follicle: a predictor of ovulation in the hen. *Biology of Reproduction* 33, p. 445-450.
- Johnson, A.L., Johnson, P.A. and van Tienhoven, A., 1984. Ovulatory response, and plasma concentrations of luteinizing hormone and progesterone following administration of synthetic mammalian or chicken luteinizing hormone-releasing hormone relative to the first or second ovulation in the sequence of the domestic hen. *Biology of Reproduction* 31, p.646-655.
- Johnson, P.A. and Tienhoven, A. van, 1981. Role of the dopaminergic system in luteinizing hormone release and ovulation in the hen. *Poultry Science* 60, 11, p. 2551-2556.
- King, A.S. and McLelland, J., 1984. *Birds, their structure and function*. Second edition, Bailliere Tindall. London Philadelphia Toronto.
- Kite, V.G., 1983. Nest-site selection and nest preferences of the domestic hen. In: Fifth Australian and stock feed convention. Hilton International Adelaide, South Australia. p.208-214.
- Kite, V.G., Wodzicka Tomaszewska, M. and Cumming, R.B., 1980a. The problem of floor-eggs in relation to nesting behaviour and nest-design. In: South Pacific Poultry Science Convention, W.P.S.A., Auckland, New Zealand.
- Kite, V.G., Cumming, R.B. and Wodzicka-Tomaszewska, M., 1980b. Nesting behaviour of hens in relation to the problem of floor-eggs. In: Behaviour in relation to reproduction, management and welfare of farm animals. The University of New England. *Reviews in Rural Science* IV. p. 93-96.
- Konishi, M., 1963. The role of auditory feedback in the vocal behaviour of the domestic fowl. *Z. Tierpsychol.*, 20, p.349-367.
- Koolstra, C.L.M. and Ehlhardt, D.A., 1982. Nestkeuze van WL hennen. I.P.S. onderzoeksverslag no. 115.
- Kruijt, J.P., 1964. Ontogeny of social behaviour in Burmese Red Jungle Fowl (*Gallus Gallus Spadiceus* Bonnaterre). *Behaviour suppl.*, XII, p.119,162.
- Lack, D. 1968. *Ecological Adaptations for Breeding in Birds*. Methuen & Co., London.
- Lee, J.P., Craig, J.V. & Dayton, A.D., 1982. The social rank index as a measure of social status and its association with egg-production in white leghorn pullets. *Appl. Anim. Ethol.* 8, p.377-390.
- Masic, B. and Pavlovski, Z., 1984. Consumer and buyers attitudes to eggs produced in cages. *Proc. & Abstr. XVII th World's Poultry Congress and Exhib.* W.P.S.A. Helsinki, Finland W.P.S.A., p. 658-670.
- Mason, J. and Singer, P., 1981. *Dierenfabrieken*. Uitg. In den Toren, Baarn, 224 p.
- McBride, G., 1970. The social control of behaviour in fowls. In: Freedom, B.M. and Gordon, R.F. (Eds) : *Aspects of poultry behaviour*. British poultry science L.T.D., p. 3-13.
- McBride, G.P., James, J.W. and Shofner, R.N., 1963. Social forces determining spacing and head orientation in a flock of domestic hens. *Nature (London)* 197. p.1272-1273.
- McBride, G.P., Parer, J. & Foenander, F., 1969. The social organisation and behaviour of the feral domestic fowl. *Anim. Behav. Monogr.*, 2, p.127-181.
- McFarland, D.J., 1965. Hunger, thirst and displacement grooming in the Barbary Dove. *Anim. Behav.*, 13. p.293-300.
- McGibbon, W.H., 1976. Floor-laying - a heritable and environmentally influenced trait of the domestic fowl. *Poultry Science* 55, p. 765-771.

- Middelkoop, J.H.van, 1973. Physiological and genetical aspects of egg-production in white Plymouth Rock Pullets. Dissertatie L.H. Wageningen.
- Morris, R.G.M., 1981. Neural subsystems of exploration in rats. In: Archer, J. and Birke, L.I.A. (Eds): Exploration in animals and humans. Workingham Van Nostrand Reinhold, p.117-146.
- Morris, T.R. 1967. Light requirements of the fowl. In: Carter, T.C. (Ed): Environmental control in poultry production. Oliver & Boyd, Edinburgh and London. p.15-40.
- Muenchmeyer, H.J., 1984. Bodenhaltung - heute wirklich anders? Deutsche Geflügelwirtschaft und Schweineproduktion 36 (7), p. 207.
- O'Keefe, J. and Nadel, L., 1978. The hippocampus as a cognitive map. Oxford, Clarendon.
- Olton, D.S., 1982. Spatially organised behaviour of animals: behavioural and neurological studies. In: Potegal, M. (Ed): Spatial abilities, development and physiological foundations. New York, Academic Press, p.335-360.
- Pamment, P., Foenander, F. and McBride, G., 1983. Social and spatial organisation of the male behaviour in mated domestic fowl. Appl. Anim. Ethol. 9, p. 341-349.
- Perry, G.C., 1977. Social factors in intensive poultry husbandry. Appl. Anim. Ethol., 3(2), p. 202-203.
- Perry, G.C., 1983. Intensive animal production and animal welfare. World's Poultry Science Journal 39(2), p. 99-105.
- Persberichten Min. van L & V 1984., no.493.
- Putten, G. 1980. Objective observations on the behaviour of fattening pigs. Anim. Regul. Stud., 3. p.105-118.
- Putten, G. and Dammers, J. 1976. A comparative study of the well-being of piglets reared conventionally and in cages. Appl. Anim. Ethol., 2. p.339-356.
- Rauch, H.W. and Wegener, R.M., 1984. Legehennenhaltung im Volieren system. Ergebnisse aus sechs Versuchen. Vortragstagung Gesellschaft der Förderer und Freunde des Instituts für Kleintierzucht der Bundesforschungsanstalt für Landwirtschaft Braunschweig Volkenrode, 22. März.
- Riddle, O., 1908. The rate of growth of the egg-yolk in the chick, and the significance of white and yellow yolk in the ova of vertebrates. Science 27, p. 945.
- Roepke, W.J., 1984. De scharrelkip is een onhygienische ramp. U-blad, 13 april, p. 7.
- Rowell, C.H.F., 1961. Displacement preening in the chaffinch. Anim. Behav., 9. p.38-63.
- Ruiterkamp, W.A., 1985. Het gedrag van mestvarkens in relatie tot huisvesting. Dissertatie R.U. Utrecht.
- Rushen, J., 1983. The development of sexual relationships in the domestic chicken. Appl. Anim. Ethol. 11, p. 55-66.
- Sainsbury, D.B.W., 1980a. Poultry, health and management. Granada, London, Toronto, Sydney, New York.
- Sainsbury, D.B.W., 1980b. Poultry production and welfare. Anim. Reg. Studies 3 (1/2), p. 43-49.
- Scanes, C.G., 1984. Hypothalamic, pituitary, and gonadal hormones. In: Cunningham, F.J., Lake, P.E. and Hewitt, D. (Eds): Reproductive Biology of Poultry. British Poultry Science Ltd. (Longman Group, Harlow) p.1-14.
- Schenk, P.M., Meysser, F.M. and Limpens, H.G.M., 1984. Gakeln als Indikator für Frustration bei Legehennen. In: Aktuellen Arbeiten zur artgemässen Tierhaltung. 1983. K.T.B.L. Schrift, 299. Darmstadt, p.65-81.
- Scholz, H., 1984. Aktuelles zum Tierschutz. Deutsche Geflügelwirtschaft und Schweineproduktion 27, 837-838.

- Sherry, D.F., Krebs, J.R. & Cowie, R.J. 1981. Memory for the location of food in marsh tits. *Anim. Behav.*, 29, p.1260-1266.
- Shutt, L.J. and Bird, D.M., 1985. Influence of nesting experience on nest-type selection in captive kestrels. *Anim. Behav.* 33 (3), p. 1028-1030.
- Siegel, S., 1956. Non parametric statistics for the behavioural sciences. McGraw-Hill, New York.
- Simons, P.C.M. 1971. Ultrastructure of the hen egg shell and its physiological interpretation. *Dissertatie L.H. Wageningen.*
- Singer, P., 1975. Animal liberation. A new ethics for our treatment of animals. Avon Books, New York.
- Staatsblad 272, 1984. Wet van 25 juni 1984 houdende vaststelling van minimum eisen voor het houden van legkippen.
- Stappers, H., 1981. Effect van omgevingsfactoren op aantal grondeieren. *Pluimveehouderij* 15, p. 14-15.
- Studie Commissie Grondhuisvesting Leghennen, 1981. Technische en economische aspecten van grondhuisvesting leghennen.
- Sturkie, P.D. and Mueller, W.J., 1976. Reproduction in the female and egg-production. In: Sturkie, P.D. (Ed): *Avian Physiology*. Springer Verlag, New York, Heidelberg, Berlin. p.302-330.
- Sykes, A.H., 1955. The effect of adrenaline on oviduct mobility and egg production in the fowl. *Poultry Science* 34, p. 622-628.
- Tanaka, K., Goto, K., and Yoshioka, T. 1984. Changes in the plasma concentration of immunoreactive arginine vasotocin during oviposition in the domestic fowl. *British Poultry Science*, 25(4).p. 589-595.
- Tauson, R., 1984. Need for improvement in construction of cages. *Proc. 1st W.P.S.A. European Symposium on Poultry Welfare, Copenhagen*, p. 65-74.
- Toates, F.M., 1980. Animal behaviour - a system approach. John Wiley & sons, Chichester.
- Toates, F.M., 1983. Exploration as a motivational and learning system: A cognitive incentive view. In Archer, J. & Birke, L.I.A. (Eds): *Exploration in animals and humans*. Workingham, Van Nostrand Reinhold p.55-71.
- Tolman, E., 1948. Cognitive maps in rats and man. *Physiological Review* 55, p. 189-208.
- Unshelm, J.U., Andrae, U. and Smidt, D., 1982. Behavioural and physiological studies on rearing calves and veal calves. In: C.E.C. seminar IV. p.47-69.
- Walker, S. 1983. Animal thought. Routledge & Kegan Paul, London Boston, Melbourne and Henley, p.75-83.
- Watson, A., 1972. The behaviour of the ptarmigan. *Br. Birds* 57, p. 93-117.
- Watson, A. & Jenkins, D., 1964. Notes on the behaviour of the red grouse. *Br. Birds* 57, p. 137-165.
- Wegner, R.M., 1980. Evaluation of various maintenance conditions for laying hens. *Anim. Regulation Studies* 3, p. 73-82.
- Wegner, R.M., 1983. Erfahrungen mit Legehennen in Volieresystem in Celle. *D. Geflügelwirtschaft und Schweine Produktion* 35, p. 1204-1205.
- Wegner, R.M., Rauch, H.W. and Torges, H.G., 1981. Choice of production systems for egg-layers. In: L. Yding Sorensen (Ed): *First European Symposium on Poultry Welfare*, p. 141-149.
- Wennrich, G., 1978. Huhn. In: Sembraus, H.H., (Ed): *Nutztier Ethologie*. Verlag Paul Parey, Berlin, Hamburg, p. 249-271.
- Wiepkema, P.R., 1982. On the identity and significance of disturbed behaviour in vertebrates. In: Bessei, W. (Ed): *Disturbed behaviour in farm animals*. Hohenheimer Arbeiten, Heft 121. Eugen Ulmer Verlag, Stuttgart.
- Wiepkema, P.R., 1983. The usefulness of an inquiry on abnormal or disturbed behaviour. In: Wiepkema, P.R., Broom, P.M., Duncan, I.J.H. and van

- Putten, G.(Eds) : Abnormal behaviours in farm animals. C.E.C. report.
- Wiepkema,P.R.,1985. Abnormal behaviours in farm animals: ethological implications. *Neth.J.Zool.*, 35(1,2) p.279-299.
- Wilson, S.C. and Cunningham, F.J., 1980. Modification by metyrapone of the "open period" for the pre-ovulatory L.H.-release in the hen. *Brit. Poultry Science* 21, p. 351-361.
- Wilson,S.C. and Cunningham, 1984. Endocrine control of the ovulation cycle. In:Cunningham,F.J.,Lake,P.E.and Hewitt,D. (Eds):*Reproductive Biology of Poultry*.British Poultry Science Ltd. (Longman Group, Harlow).p.29-50.
- Wilt, J.G. de, 1985. Behaviour and welfare of veal calves in relation to husbandry systems.Dissertatie L.H.Wageningen.
- Wood, A.K. & Brotherson, J.D., 1981. Microenvironment and nest-site selection by ring-necked pheasants in Utah. *Great Basin Nat.* 41(4),p.457-460.
- Wood-Gush, D.G.M., 1954. Observations on the nesting habits of brown leghorn hens. *World Poultry Congress Edinburgh*, Dept. Agric. Scotland, p. 187-192.
- Wood-Gush, D.G.M., 1963. The control of the nesting behaviour of the domestic hen I. The role of the oviduct. *Anim. Behav.* 11, p. 293-299.
- Wood-Gush, D.G.M., 1971. The behaviour of the domestic fowl. London Heinemann.
- Wood-Gush, D.G.M., 1972. Strain differences in response to sub-optimal stimuli in the fowl. *Anim. Behav.* 20, p. 72-76.
- Wood-Gush, D.G.M., 1975.Nest construction by the domestic hen: some comparative and physiological considerations. In: Wright,P., Caryl,P.G. and Vowles, D.M. (Eds.): *Neural and endocrine aspects of behaviour in birds*. Amsterdam, Elsevier,p.35-49.
- Wood-Gush, D.G.M., 1983. Elements of ethology, Chapman and Hall, London, New York.
- Wood-Gush, D.G.M. and Duncan, I.J.H., 1976. Some behavioral observations on domestic fowl in the wild. *Appl. Anim. Ethol.* 2, p. 255-260.
- Wood-Gush, D.G.M. and Gentle, M.J., 1978. The hyperstriatum and nesting behaviour in the domestic hen. *Anim. Behav.* 26, p. 1157-1164.
- Wood-Gush,D.G.M. and Gilbert,A.B. 1964. The control of the nesting behaviour of the domestic hen. The role of the ovary. *Anim.Behav.*, 12.p. 72-76.
- Wood-Gush, D.G.M. and Gilbert, A.B.,1969a. Observations on the laying behaviour of hens in battery cages. *Brit. Poultry Science* 10, p. 29-36.
- Wood-Gush,D.G.M. and Gilbert, A.B.,1969b.Oestrogen and the pre-laying behaviour of the domestic hen. *Anim.Behav.*, 17.p.586-589.
- Wood-Gush, D.G.M. and Gilbert, A.B., 1970. The rate of egg loss through internal laying. *Brit. Poultry Science* 11, p. 161-163.
- Wood-Gush, D.G.M. and Gilbert, A.B., 1973. Some hormones involved in the nesting behaviour of hens. *Anim. Behav.* 21, p. 98-103.
- Wood-Gush, D.G.M., & Gilbert, A.B., 1975. The physiological basis of a behaviour pattern in the domestic hen. In: Peaker,M.(Ed.): *Avian Physiology*. The Zoological Society of London 35, p. 261-276.
- Wood-Gush, D.G.M. & Murphy, L.B.,1970. Some factors affecting the choice of nests by the domestic hen.*Br.Poult.Sci.*,11,p.415-417.
- Woods, R.E. and Laurent, C.K., 1958. A note of nest preference. *Poultry Science* 37, p. 1461.
- Zimmer,D.E., 1983. *Huehner, Tiere oder Eiweissmaschinen*. Rohwolt, Reinbek. Germany. 221p.

CURRICULUM VITAE

Beatrix Piepers werd geboren op 31 januari 1954 te Wisch. In 1972 werd gestart met de opleiding Biologie aan de R.U. te Utrecht. Begin 1978 werd de studie onderbroken. Na o.a. enkele maanden werkzaam te zijn geweest in het middelbaar Biologie onderwijs, werd de studie eind 1978 hervat en in april 1980 werd het doctoraal diploma Biologie met eerste graads onderwijs bevoegdheid behaald met als hoofdvak Ethologie (sociaal gedrag van primaten), als bijvak Natuurbeheer en met als nevenrichtingen Plantenfysiologie en Biohistorie.

Eind 1980 werd in het kader van een tijdelijke aanstelling als onderzoeks assistent aan de Faculteit voor Diergeneeskunde, Vakgroep Zootechniek van de R.U. te Utrecht voor het eerst kennis gemaakt met de ethologie van lanbouwhuisdieren. In november 1981 volgde een 3-jarige aanstelling aan de Vakgroep Veehouderij, Sectie Ethologie van de L.U. te Wageningen en het C.O.V.P. "het Spelderholt" te Beekbergen alwaar het onderzoek, dat uiteindelijk tot dit proefschrift geleid heeft, werd uitgevoerd.

Stellingen

I

Er bestaat bij leghennen geen relatie tussen sociale dominantie en nestkeuze.

(Dit proefschrift)

II

Acceptatie van een bepaald legnest door leghennen is afhankelijk van ervaring opgedaan met legnesten in de weken voor en tijdens de legperiode.

(Dit proefschrift)

III

Om desorientatie van leghennen, gehuisvest in grote stallen te voorkomen, b.v. bij het terugzoeken van een geprefereerd legnest, verdient het aanbeveling de stallen heterogeen in te richten.

IV

Individuele verschillen in fysiologische en ethologische stress reacties opgeroepen tijdens aversieve stimulus-situaties bij dieren zouden, zoals werd aangetoond bij mensen (Miller, 1980), terug te voeren kunnen zijn op individuele verschillen in de gevolgde "coping-strategie".

S.M. Miller, 1980. In: "Coping and Health". Plenum Press, New York.

V

Aangezien de kans groot is, dat proefdieren, die speciaal voor dierproefdoeleinden onder laboratoriumomstandigheden worden gefokt, abnormaal gedrag ontwikkelen, zullen de resultaten van biologische experimenten uitgevoerd met deze dieren met de nodige terughoudendheid moeten worden geïnterpreteerd.

VI

Door leghennen te huisvesten in alternatieve grondsystemen worden omstandigheden inherent aan huisvesting in batterij-kooien, die als welzijnsbeperkend worden verondersteld weggenomen. Desondanks verdient het aanbeveling de alternatieven niet alleen op technisch-economische parameters, maar

ook op het welzijn van de hennen te evalueren.

VII

Zelfmedicatie, zoals dat wordt mogelijk gemaakt door de verkoop van homeopathische middelen, kan de verantwoordelijkheid voor de eigen gezondheid verhogen. Dit positieve effect kan echter teniet worden gedaan, door het toepassen van zelfmedicatie als alternatief voor een bezoek aan een allopathisch of homeopathisch arts.

VIII

Probleemgestuurd hoger onderwijs leidt tot een doeltreffender integratie van de aangeboden leerstof dan de meer gangbare didactische methode (doceren).

H.G. Schmidt, 1982. In: "Probleemgestuurd onderwijs". SV0-reeks no.57. 's-Gravenhage.

IX

Als de af- en uitspoeling van fosfaten vanaf landbouwgronden blijft toenemen, zal defosfatering in rioolwaterzuiveringsinstallaties nauwelijks nog effect hebben op de kwaliteit van het oppervlaktewater.

X

Wat betreft de uitvoering van het beleid ten aanzien van deeltijd-arbeid geldt vaak: "...tussen droom en daad staan mensen in de weg en praktische bezwaren...".

Naar: W. Elsschot, 1910. In: "Het huwelijk".

XI

Gezien de recente ontwikkelingen rondom het gebruik van bloedzuigers in de plastische chirurgie, zou de naam van dit dier niet langer met een negatief denkbeeld geassocieerd moeten worden.

B.Rietveld-Piepers

The development of egg-laying behaviour and nest-site selection in a strain of white laying hens.

Wageningen, 4 februari 1987